NITROGEN AND ENERGY DEPLETION IN THE AMERICAN COCKROACH

THE IMPACT OF NITROGEN AND ENERGY RESERVE DEPLETION ON FEEDING AND DRINKING IN THE AMERICAN COCKROACH, *Periplaneta americana* (L.) (ORTHOPTERA:BLATTIDAE)

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ABSTRACT

Selective feeding in response to depletion of particular reserves was examined in the American cockroach, Periplaneta americana. Animals deprived of specific nutrients and subsequently provided with dietary choices, responded so as to restore their altered reserves. Since two foods of differing energy content were used, the fundamental hypothesis of optimality theory could be tested (i.e. do cockroaches behave so as to maximize energy intake?).

Adult male cockroaches were placed in a computer-monitored artificial habitat containing routes to shelter, water, protein and carbohydrate. Measures of behaviour were compared over treatments. Treatments included control cockroaches (no starvation), cockroaches fed agar (originally fed protein and sugar), protein-starved cockroaches (originally fed sugar only) and starved cockroaches (no food in the pre-treatment).

In all treatments, more time was spent feeding than drinking. In controls, feeding on carbohydrate took precedence over protein (for intake and duration). Protein-starved cockroaches showed increased intake (over controls) for protein, as expected, but also increased intake for both carbohydrate and water. Starved and agar-fed cockroaches displayed decreased carbohydrate and water

intake while protein consumption increased. The compensatory responses showed large initial peaks that gradually approached control behaviour.

The results indicate that feeding behaviour is strongly responsive to reserve state and reserves act as an integral part of a dynamic system which operates homeostatically. The fact that depletion of the protein reserve resulted in increased ingestion of both protein and carbohydrate strongly suggests that reserves are linked. Considerable variation in daily feeding was observed which may be related to overshoot/undershoot responses typical of homeostatic systems where time lags exist.

The results are strongly at variance with the predictions of optimal foraging theory. Cockroaches appear to feed to homeostatic set points, largely regulated by reserves. Reserves are largely ignored in optimal foraging theory. Furthermore, the animals regulate intake of nitrogen (protein) and/or energy, and do not simply maximize energy intake.

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INTRODUCTION

Feeding was examined as a function of a cockroach's state of reserves in conjunction with environmental food stimuli, an approach based on an examination of which proximal mechanisms seem most relevant to feeding regulation. During times of stress or deprivation, cockroaches mobilize stored nutrients from their haemolymph and fat body (Mullins and Cochran 1975b; Downer and Matthews 1976a; Downer 1981; King et al. 1986). These nutrients include uric acid (which can be used in amino acid synthesis), proteins, salts, lipids, glycogen and trehalose. Thus, by depriving the cockroach of a specific food (e.g. protein) and subsequently providing it with both foods (protein and carbohydrate), the elicited response will be a reflection of the altered reserves. This study's first objective was to examine selective feeding in response to selective reserve depletion. This has not been rigourously addressed in the insect literature.

The study of behaviour is complex. Specific behaviours, such as feeding and drinking, have been thoroughly studied in locusts and blowflies (Barton-Browne 1975; Bernays and Simpson 1982; Simpson 1982, 1983; Simpson and Ludlow 1986; Simpson et al. 1988). These insect behaviours have also been compared to vertebrate behaviours (Faber 1975; Simpson and Bernays 1983). Surprisingly, few

studies have attempted to link feeding and drinking together. The second objective was to present feeding and drinking as part of a dynamic system which responds to maintain homeostasis in male P. americana.

Optimal foraging theory has developed from an evolutionary perspective where researchers pursue the ultimate function(s) of an adaptation (such as foraging) (see Mayr 1963; Emlen 1966). They attempt to substantiate their hypotheses by specific tests. Thus, most optimization researchers propose some form of energy maximization and examine specific systems to see if the criteria are fulfilled. Even though optimal foraging hypotheses are frequently rejected, researchers simply introduce slight modifications, elaborations or constraints that were not included in the original experimental design to rescue optimal foraging theory itself. The current work is based on a model of homeostasis and regulatory feedback which is markedly at odds with one of maximized energy intake. It recognizes important criteria that are independent of energy (e.g. nitrogen and water).

There is another way of approaching foraging and feeding behaviour, and that involves abandoning "ad hoc" hypotheses and simply examining the mechanisms of the system empirically. This approach was pioneered by Holling (1963, 1966) and led to the extensive use of systems

analysis and modelling in ecology.

Both the proximal mechanism (Holling) and ultimate function (optimization) approaches generate strong research thrusts, but the relative effectiveness of the approaches can be appreciated when noting that several hundred scientists working on optimal foraging for about 20 years have now arrived at a perspective (see Pyke 1984) that Holling largely developed by himself in about 10 years. Since then there has been tremendous additional progress in proximal mechanism research which continues to be largely ignored by optimal foraging theorists. The current work tests the idea (arising from the proximal mechanism literature) that feeding is homeostatic and reserves are key regulatory elements.

Since this study deals with two different foods (protein and carbohydrate), the quantification of feeding changes in response to reserve alteration may test the fundamental tenet of optimality theory (i.e. do cockroaches maximize energy intake?). Using an empirical approach aimed at proximal mechanisms, this study attempts to generate useful insights into feeding through the following hypotheses. Based on the prediction that the state of reserves will determine the food preference, I predicted that animals depleted in nitrogen should initially prefer protein-based food over carbohydrate. To date, optimal foraging theory is based on a premise of energy

maximization. If valid, cockroaches should always prefer raw carbohydrate (nearly pure energy) over other food types and they should always maximize intake. Similarly, starved cockroaches should always prefer carbohydrate over protein.

Speculation concerning the physiological basis underlying the observed behaviours is included in a conceptual model. This physiological model compliments a behavioural model which is based directly on the results. Together, these models provide an empirically based theoretical framework for addressing feeding regulation in the American cockroach, Periplaneta americana.

LITERATURE REVIEW

The breadth of this study includes concepts from psychology, physiology and ecology. Consequently, even modest objectives can become overwhelmingly complex. To organize this complexity, the literature review is structured according to a "bottom-up" approach. The lowest level involves motivation which is the basis of feeding and drinking behaviour. These behaviours result in nutrient consumption and subsequent utilization. Over the last twenty years, research has examined consumption and utilization under the pretence of "optimal foraging theory". By considering the variables of each behaviour, the relevancy of optimization theory may be addressed. Finally, models which describe activity switches are introduced.

I. Models of Motivation

Behaviour serves as an interface between an animal's environment and physiology. Stimuli and constraints from the environment and physiology feed through a decision-making filter which consequently makes predictions difficult. For example, the same stimulus given to the same animal at different times often results in different responses (Manning 1979). Manning lists four physiological

factors which alter response to stimuli: (a) fatigue, (b) maturation, (c) learning and (d) motivation. There are others as well (e.g. circadian rhythmicity, cyclic physiological functions, etc.).

Many motivations are linked to some physiological deficit and such deficits are intimately linked to reserves. This study is primarily concerned with the impact of reserves on feeding and drinking motivations. This area is almost totally ignored by the currently popular proponents of optimal foraging theory. Motivation is based on a simple concept: the threshold of reponse to a specific stimuli is varied by motivation. Motivation therefore varies response possibilities of specific goal-oriented behaviour (Manning 1979).

Goal-oriented behaviour (i.e. feeding or drinking) can be divided into three phases: (1) searching (appetitive behaviour), (2) handling and consumption and (3) quiescence or switching to another activity (Manning 1979). Feeding and drinking motivations are related to fluctuations in physiological deficits (Hinde 1959). For example, dehydration leads to the lowering of the drinking threshold. Thus appetitive behaviour and responsiveness to water increase until water is found and imbibed. Subsequently, the threshold rises and responsiveness drops until water is depleted again. This process can be

extended to nutritional states as well.

Behavioural chain reactions can also be explained at the motivational level (Manning 1979). A behaviour can be divided into sub-behaviours, each with thresholds which rise and fall sequentially in conjunction with the intensity of the main behaviour (Baerends 1976). For example, feeding is comprised of search, handling and consummatory behaviour. A high feeding drive lowers all three thresholds. Once food is found, the search threshold rises, resulting in a switch to handling and subsequently consumption. When the intensity of the main behaviour is low the behavioural sequence is often truncated (Gardner 1964). For example, hungry jumping spiders display the following sequence: orientation to prey, pursuit, crouching and jumping. However, satiated spiders only orient to prey (Gardner 1964).

The array of responses to stimuli may be translated into mathematical equations. In modelling, such equations serve as a dynamic representation of the animal (Berryman 1981). Models based on motivation are of three main types: (1) hierarchial models in which all behaviours in an animal's repetoire are ranked (Davis et al. 1974a, b, 1977; Baerends 1976; McFarland 1977; Ludlow 1980, 1982; Rollo et al. 1983; Sibly and McCleery 1985), (2) Lorenz's (1950 as cited in Gould 1982) psycho-hydraulic model which adequately describes vacuum activity and the vigour of

response and (3) feedback models which have successfully predicted feeding and drinking behaviour (Deutsch 1960 cited in Manning 1979; Booth 1978; Toates 1978; Ludlow 1980, 1982). These models may be combined (e.g. hierarchies of feedback subroutines and behaviours that are interconnected).

The fact that these models are limited to specific animals or behaviours is a further testament to the complexity of behavioural modelling. For example, Lorenz's (1950) model represents most behaviours excluding feeding and drinking. The model predicts that once the motivational "reservoir" is empty, the behaviour cannot be elicited regardless of the stimulus strength. Consequently, the occurrence of quiescence is dependent on the performance of the behaviour (to drain the reservoir). Gould (1982) states that this model accounts for fluctuations in responsiveness but cannot be applied to internally controlled behaviours (see sham-feeding experiments in Manning 1979).

The most successful models describing feeding or drinking are based on feedback loops. Deutsch's (1960) model provides the clearest example of feedback flow. A receptor system detects a physiological imbalance and excites a central "link". The link activates the motor system (behaviour) which subsequently alters the internal

environment (ie. food in the gut). An analyzer component (stretch receptors) monitors the internal state and then inhibits the link so it is no longer receptive to stimuli from the receptors. Inhibitory decay will eventually start the cycle again.

Feedback can be positive or negative. In complex processes negative feedback frequently induces steady-state behaviour. In cases when negative feedback is delayed the behaviour is referred to as "oscillatory instability" (Toates and Archer 1978). Positive feedback results in exponential growth or decay. Logically, positive feedback will only occur when all the processes in a system are positive or there is an even number of negative processes.

Positive feedback plays an important role in behavioural persistence when there are conflicting motivations (McFarland 1971; Wiepkema 1971; Houston 1982; Houston and Sumida 1985). For example, when two behaviours have fairly even causal factor strengths, the current behaviour reinforces itself thereby promoting dominance (Toates and Archer 1978; Toates 1981). Houston and Sumida (1985) suggest that the maximum positive effect should be limited to the time immediately following a switch. This would eventually enable the model to switch to an alternate behaviour (by delayed negative feedback) (Slater 1978; Toates and Archer 1978; Toates 1981).

A less recognized mechanism underlying behavioural

regulation, and one virtually ignored by most optimal foraging studies, is the feedforward response. This mechanism operates by anticipating delays or deficits and responding before they occur (ie. when the transfer of material, energy or information through a loop takes too much time) (Berryman 1981). Feedforward mechanisms, because they can eliminate an anticipated disparity from a reference state, utilize learning and/or internal "clocks". Oatley and Toates (1969) showed that there is a rapid transition from feeding to drinking in rats which prevented the otherwise inevitable feeding-induced water deficit. Similarly, rats showed increased drinking when fed high protein diets, apparently to offset anticipated renal water loss (Fitzsimons and LeMagnen 1969).

The picture that emerges is that (1) storage deficits and excesses alter response thresholds, (2) behaviour is the product of conflicting motivations, (3) feedback models may adequately describe feeding and drinking behaviours, but (4) feedforward mechanisms may play an important role in regulation. Most optimization models have not considered points (1), (2) and (4) adequately, if at all.

II. Optimization

Understanding behaviour is facilitated by conceptual

models that act as frameworks for discussion. I synthesized the literature to provide general models for drinking and feeding that apply to most species (Figs. 1a-c). This study is primarily concerned with Figs. 1b and 1c (intra-patch movement and physiology), and will examine cockroaches within a relatively simple, general herbivore framework.

Cockroaches carry out their activities sequentially because various acts are mutually exclusive. Inefficiency at any step in the sequence may disrupt activity entirely (Oster and Wilson 1978). Williams (1966a as cited in Price 1975) defines fitness as "effective design for reproductive survival". In other words, since natural selection has moulded the cockroach design, the cockroach should display decision-making strategies geared to ensuring survival and reproductive success (i.e. increase the number of surviving progeny). Presumably, if cockroaches perform each activity in a sequence efficiently, fitness will be increased.

When the performance of an activity maximizes fitness, the activity is considered "optimal". Optimal foraging theory was originally developed to explain feeding and foraging dynamics from an energetic perspective (Emlen 1966; MacArthur and Pianka 1966; Schoener 1971; Pyke et al. 1977; Krebs 1978; Krebs et al. 1981; Pyke 1984) (Fig. 1b, c). Optimal foraging models may be tested if (a) the

assumptions implicit in the model are testable or (b) the model predicts behaviour that can be verified by observation (Vickery 1984). The difficulty in falsifying the implicit assumptions (Vickery 1984) has led to the testing of optimal diet models and their ability to predict actual food choice (Werner and Hall 1974; Emlen and Emlen 1975; Goss-Custard 1977; Krebs et al. 1977; Vickery 1984).

The assumptions associated with simple optimal diet models will be outlined as they are incorporated in some way in all optimization models (MacArthur and Pianka 1966; Schoener 1971; Pulliam 1974; Krebs et al. 1977; Vickery 1984). First, the diet is optimized according to one nutrient constraint, usually energy. Second, food items have a constant value for the appropriate nutrient and third, the food has a constant handling time. Fourth, food encounter rate is constant over the optimization period. Fifth, the forager has accurate and global knowledge of food values and encounter rates and sixth, the choice of an optimal diet (resulting from an optimal strategy) will maximize fitness. Since fitness is difficult to measure and to relate directly to a behavioural act, most researchers assume that maximizing a simpler currency such as net energy intake also maximizes fitness (Howell 1983).

The following predictions utilize the above assumptions: (1) the currency maximization hypothesis predicts that animals will always consume food with the

highest currency yield (C) per handling time (H) (Richards 1983) and the currency is usually some measure of energy (McCleery 1978; Pyke 1979; Townsend and Hughes 1981; Vickery 1984), (2) the constant preference hypothesis predicts that the food with the highest C/H ratio will be preferred even if it becomes rare compared to other foods (Vickery 1984) and (3) when encountered, a food type should either be eaten or completely ignored (the all-or-nothing hypothesis) (Pulliam 1974; Charnov 1976; Vickery 1984). The design of the present study favours the investigation of predictions 1 and 3. Thus cockroaches should always consume food with the highest energy content per unit handling time.

Evidence from rodents supports the currency maximization and constant preference hypotheses (Vickery 1984) but not the all-or-nothing hypothesis. Variance in caloric consumption rate within food types probably contributed to the failure of the latter hypothesis. The "all-or-nothing" failure may also be attributed to the varying nutrient requirements of rodents (Pulliam 1974, 1975; Slansky and Feeny 1977; Westoby 1978; Lucas 1983). Drawing from these studies, cockroaches should always maximize and prefer energy consumption.

In contrast to conventional optimal foraging theory, some researchers theorize that the choice of the currency

to be maximized is based on a key factor rationale: the most limiting nutrient (e.g. energy, lipid, protein) is maximized (Pulliam 1974,1975; McNair 1979; Rapport 1980; Orians 1982; Pyke 1984). In bees, nutrient maximization may occur through increased assimilation efficiency (physiological change) rather than foraging (Waddington and Holden 1979). In most cases though, currency maximization is achieved by (a) consuming food with the highest nutrient yield or (b) minimizing the handling time. This study will address the "key factor rationale" as an alternative to optimization theory: do cockroaches maximize intake of the most limiting resource and if so, how do they do this?

Optimal foraging theory poses another question "does an animal optimize gross or net nutrient intake?". Past research suggested that the load size (food) of animals maximizing net intake (i.e. which considers foraging costs) is greater than those maximizing gross intake (i.e. which does not account for costs), but this is not always so (Kacelnik and Houston 1984). Cockroaches should maximize net nutrient intake to maintain homeostasis.

Related to net intake, Schoener (1971) recognized that a forager may act to minimize the total foraging time necessary to obtain a fixed amount of food. It is apparent that time minimizers and energy maximizers are not exclusive as long as minimizing the feeding time results in energy maximization. They are exclusive when minimizing

time compromises energy returns (Hainsworth and Wolf 1983). The major advantage of minimizing feeding time (when there are no nutrient demands) is that it presents more time for other behaviours to be expressed (Hainsworth and Wolf 1983; Winterhalder 1983). If optimality theory is supported, then this study should categorize the cockroach as either an energy maximizer or a time minimizer. If the latter, then the cockroach may minimize handling time as well.

Energy plays a central role in the limitation of foraging by bees (Heinrich 1972). Maximum energy intake is achieved when the encounter rate with profitable flowers is high (violates assumptions 2 and 4 (see page 12), Fig. 1b). For bees in an unprofitable environment, it may be better to reduce foraging time (energy conservation strategy).

Maximizing energy intake on poor food may be accomplished by increasing the volume of food ingested (Bignell 1978; Sibly 1981). Bignell showed that cockroaches fed progressively carbohydrate-reduced diets compensated by increasing intake volume. Due to the limitations of crop capacity, total compensation wasn't achieved (Bignell 1978).

The time scale over which optimization is carried out must also be considered (Pyke et al. 1977). Animals with exclusive access to some resource can maximize their yield

over a large time period. Most others must learn their environment, a process which necessitates short-term inefficiency (Maynard-Smith 1978).

Learning involves sampling the patches within the environment (Fig. 1a). In a constant environment, the animal has nothing to gain by sampling once patch profitablities have been assessed (Lester 1984b). In a variable environment, animals should employ strategies based on experiences within a patch (Green 1984). But animals evolved in uncertain environments. Consequently, animals will act as they are designed, even in artificial (static) environments. Thus Lester (1984b) suggests that an animal should display decision rules that result in efficient behaviour.

Incorporating the principles of optimal diets (for foods A and B such that the profitability of A > B and thus C(A)/H(A) > C(B)/H(B), Richards 1983) (where C=consumption and H=handling cost), three main foraging strategies have been identified: (1) feed on type A only (specialist), (2) feed on type A and B as encountered (generalist) and (3) assuming that the forager can assess the food value required to make up its deficit (D), feed on type A if D is less than a given value, otherwise act as a generalist (expanding specialist, Heller 1980; Richards 1983). Cockroaches are considered generalists but this study will examine the "expanding specialist" possibility.

Models of optimal diets make no provision for the effects of hunger on foraging (Richards 1983). Thus cockroaches should respond equally to different foods (rhythms and reserves should have no effect). But feeding rate has been shown to be proportional to hunger (Ernsting 1977; McCleery 1977) and other aspects of predator foraging are affected by motivation as well (see Richards 1983; Ydenberg and Houston 1986). Optimality in the aforementioned cases may be realized by modifying basic components of foraging with respect to hunger (Holling 1963, 1966).

Hungry foragers effectively exploit food items when they correctly decide which food to eat and when to switch (Cowie and Krebs 1979) (Fig. 1b). Charnov's (1976) marginal value theorem (MVT) addresses the latter problem in terms of patch-switching (Fig. 1a). Briefly, the theory states that an optimal predator should leave a patch when it's capture rate falls below the average rate for that environment. Capture rate is presumed to be based on capture expectation and, if constant, an optimal forager should not leave the patch (Fitzpatrick 1981; McNamara and Houston 1985). Charnov's theory is not realistic. An animal does not possess omnipotent implicit knowledge of its environment. In order to determine foraging success, animals must sample their environment. Undoubtedly,

mistakes in patch or food selection will occur (Figs. 1a, b). Also, environmental changes will vary patch and food quality. Thus capture rates will be highly variable. Which rate will serve as the average? Do insects have the cognitive ability to compare capture rates? Such questions cast much doubt on the validity of Charnov's theory. Also, McNamara and Houston (1985) noted that foraging models must incorporate threshold (average rate) modification through learning. Important factors such as learning, rhythms and reserves are not considered in optimality models.

Applying Charnov's theory to food choice (Fig. 1b), it would be predicted that if a food item did not meet some "acceptability threshold", then a food switch would occur. Such comparisons require that all foods be sampled to assess their desirability (Vickery 1984) (Fig. 1b). This information (via learning) would then be used to modify the acceptance threshold (Townsend and Hughes 1981; Inoue 1983). Note the similarities between the patch and food choice models. In summary, sampling of patches or foods is necessary. Such sampling involves errors or inefficiencies which exclude optimal strategies. Rhythms, learning and reserves probably play an important role in patch or food choice.

McNair's (1982, 1983) giving-up time (GUT) strategy is an alternative to Charnov's MVT. McNair found that GUT

varies with patch quality: better patches were correlated with longer GUTs (Fig 1a). Depending on the habitat, optimal MVT or GUT result in greater energy intake compared to random foraging. Thus better patches result in greater intake and patch residence time (Harley 1981; McNair 1982; Sih 1982; McNair 1983; Lester 1984a). Moving down from the patch level, this study will examine the possibility that "better" foods will result in greater intake. If so, the choice procedure may be expanded to include habitats, patches and foods.

A model by Ydenberg and Houston (1986) incorporates the effects of hunger on patch residence time and travel time. Initially, when hunger is high, the model supports Charnov's (1976) marginal value theorem. But, as hunger is reduced, the model predicts a shorter patch residence time. Satiation also leads to a selective process which may follow one of two paths. First, the animal should behave as if food was abundant thereby choosing only profitable foods (Pulliam 1974; Charnov 1976). Second, the animal should expand it's diet to include lower value prey (Heller 1980; Richards 1983).

Following the consumption of acceptable food items, general foragers such as cockroaches decrease their searching periods and their speed of movement (Hassell and Southwood 1978). The latter strategy may increase the risk

of predation. Using backswimmers, Sih (1980) suggested that maximization of energy intake must be balanced with predator avoidance strategies.

There is an alternative empirical approach to studying animal behaviour. This was developed by Holling (1963) and is named the "experimental components approach". Basically, Holling's approach is one of proximate reductionism (i.e. where complex processes are broken down into key components). In contrast, optimization theory is based on the ultimate purpose of the process.

Component models are based on experimental data and test the realism of the chosen components of a system. Holling's (1963, 1966) procedure involves the following steps. First, the basic components of the system are identified and then expanded (basic components are those that are universally present in that system). Expansion is simply breaking down the basic components even further. Second, the subsidiary components are identified and expanded. Sub-components are not universal in a particular system. For example, in predator-prey systems the sub-component "hunger" may motivate a feeding response, yet some animals may show the response even if they are not hungry. Third, the effect of the sub-components on the basic components is observed. Finally, the results of step three are synthesized in a response equation which is then integrated into a model.

The experimental components approach is not based on any assumptions relating to ultimate function. In fact, its only assumption is that there are universal components underlying the process. Mathematical relationships are fitted to experimental data and these relationships are incorporated into a "streamlined" model. The functional ramifications of the model can then be explored.

Holling's (1963) empirical approach was used in this study. Attempts were made to isolate key variables comprising cockroach feeding and drinking behaviour. The effects of reserve depletion on these variables was then observed. The results were then developed into theoretical models. Optimal foraging theory's ultimate approach was useful for comparison only. The theory is based on too many unrealistic assumptions and an illogical research perspective (a top-down approach).

In the literature, optimal foraging theory's basic assumptions have been attacked on theoretical and practical grounds. For example, research has often shown that an optimal foraging strategy must be balanced with the risk of predation (Sih 1980; McNair 1982; Sih 1984; Sibly and McCleery 1985) and competition (Ydenberg and Houston 1986). These results violate assumption 6 (the choice of an optimal strategy will maximize fitness) because fitness may not be maximized. The failure of some models in predicting

foraging behaviour has been subscribed to the unrealistic nature of the assumption that the forager has accurate and global knowledge of it's environment (Comins and Hassell 1979; Waddington and Holden 1979; Orians 1982). Orians argues that a forager does not possess complete knowledge of it's environment and will therefore make errors regarding patch and food choice (refer to Figs. 1a and 1b). This usually results in suboptimal energy intake. Many models have reported suboptimal intakes for this reason (Green 1980; Harley 1981; Sih 1982; Lester 1984b; Munger 1984).

Lester (1984b) believes that optimality models are a short-cut to the discovery of rules which govern how animals integrate and respond to information. He believes these models are a guess of what the behaviour is to accomplish. Logically, the basis of behaviour must be understood first; only then may the ultimate goals of behaviour be proposed. For this reason, this study will integrate the results into a model which represents the physiological basis for the observed behaviour.

Heinrich (1983) believes that a greater understanding of foraging can be obtained by supplementing optimal foraging models (maximize fitness) with components of adaptive foraging (enhance fitness beyond some control level). Each foraging strategy has its own costs and payoffs and Heinrich suggests that the mechanisms which

enhance fitness deserve attention regardless of their optimality.

The perception that animals behave suboptimally often leads to the refutation of optimal foraging theory. Bookstaber and Langsam (1985) believe that animals facing uncertain environments tend to display rigid (or course) behaviours. Course behaviours are comprised of rules which do not adjust to environmental cues and ultimately lead to inflexible responses. These behaviours usually guard against losses to the animal. For example, ignoring other environmental cues, the cockroach escape system moves the animal in the opposite direction to gusts of wind. Bookstaber and Langsam (1985) note that this system would be suboptimal in any predation model (because of possible "false alarms") yet, it has proved adequate for a wide range of unanticipated predators.

The course behaviour theory would also work for animals with large storage reserves because they can afford to make small errors. Thus cockroaches may display set behaviour rules when faced with altered storage reserves (e.g. drinking rules may remain constant to guard against dehydration).

In terms of foraging, flexiblity in food sampling may be considered adaptive rather than optimal. Vickery (1984) suggests that it would be advantageous for animals in

uncertain environments to sample novel foods to assess their desirability as a future food source. Also, Geissler and Rollo (1987) showed that nutritionally deficient cockroaches sampled novel foods while still retaining familiar foods in their diet. Well nourished cockroaches avoided foods with novel tastes and odours. It is obvious that learning will play an important role in uncertain environments (Kamil 1983).

In summary, successful foraging models will undoubtedly incorporate components of optimal foraging theory (ultimate goals) in conjunction with adaptive mechanisms (proximate goals). Rather than producing omniscient maximizing foragers , natural selection tends to favour animals that can reliably meet minimal nutritional demands in the face of an uncertain environment (i.e. efficient foragers). Fitness may be thought of as the result of a tradeoff between the ability to (a) maintain physiological homeostasis and (b) allocate surplus nutrients to storage, growth and reproductive tissues.

III. Consumption and Utilization

The detection of food by cockroaches is a complex process incorporating olfactory receptors on the antennae (Sass 1978) with gustatory receptors on the maxillary/labial palps (Wieczorek 1978). Excellent reviews concerning the structure and function of antennal sensilla have been published (Norris and Chu 1974; Altner et al. 1977; Schaller 1978; Zacharuk 1980). The scope of this thesis does not include this area.

Sensory adaptation was first identified by Dethier (1964) in the blowfly Phormia. The sensory nerves connected to the proboscis sense organs show a drop in the rate of firing even though contact with a sugar solution remains constant. The concentration of the solution determines both the adaptation time and rate of firing (i.e. high concentrations show slow adaptation). For example, Dethier showed that hungry flies respond to more dilute solutions and feed longer on these solutions than satiated flies. Thus chemosensory stimulation may enhance subsequent feeding by diminishing sensory adaptation (Simpson and Bernays 1983; Shiraishi and Yano 1984).

A food type may be considered both a stimulant or a deterrent depending on the state of the insect. The stimulating effect of a nutrient generally correlates with its concentration and nutritional value. But if the body

is "saturated" with that particular nutrient then it may actually repel the insect. For example, Simpson and Bernays (1983) showed that water is a deterrent in well hydrated insects.

Adult P. americana show positive gustatory responses to many amino acids (Sugarman and Jakinovich 1986). Two conclusions can be drawn from this: (a) the particular amino acids are potentially limiting or (b) the amino acids (if novel) may have supported alternation behaviour. Alternation behaviour describes the tendency of cockroaches to choose the unfamiliar or changed alternative in a two-choice situation (Wilson and Fowler 1976). Naturally, the nutritional state of the animal must be considered when describing alternation behaviour.

Once located, food uptake is regulated (refer to Fig. 1c). Regulation is the subject of many reviews (Waldbauer 1968; Barton-Browne 1975; Bernays and Simpson 1982; Simpson 1983; Simpson and Bernays 1983). Important considerations of regulation include how much is consumed and at what rate. These factors vary during the course of a meal (McCleery 1977).

Energy balance is one factor which regulates food intake (Toates and Booth 1974). Feeding results in an energy gain which must be traded off against the cost associated with this behaviour (in terms of time, energy

and the exclusion of other behaviours) (Cook and Cockrell 1978; Sibly 1981). Regulation may also be based on a complex neural circuit as seen in slugs (Gelperin 1971; Senseman 1977) or amino acid dynamics (Rogers and Leung 1977).

The mechanics of food intake have a direct bearing on this regulation. Through injection of agar into the crop of grasshoppers, Bernays (1980) showed that crop stretch receptors regulate the release of hormones from the corpora cardiaca (Fig 1c). These hormones (a) increase the secretion of digestive enzymes (Simpson 1982) and (b) suppress feeding and consequent foraging behaviour by decreasing locomotor activity. Thus the crop has a finite capacity and once filled feeding stops. Consequently, the length of feeding will be determined by the amount of crop space remaining at the start of feeding (Cook and Cockrell 1978; Simpson 1983).

Often, food is present in both the mid and hindgut. Simpson (1983) showed that receptors in the ileum also influence crop filling. Thus feeding may be terminated through the dual effects of negative feedback from the crop and ileum. This is very important in this study. The long starvation period will undoubtedly drain specific reserves which cannot possibly be replenished in a day. Thus the effects of starvation will probably be carried over several days. This carry-over time is a compensation period

necessary to refuel the cockroach.

Crop space is dependent on the frequency of opening of the proventricular valve (which acts as a bottleneck and controls the rate of crop emptying) (Davey and Treherne 1963a, b, 1964; Wigglesworth 1974). The frequency of opening was found to be related to the crop glucose concentration, with dilute solutions causing rapid crop emptying (Treherne 1957). Davey and Treherne (1963b) postulated that osmotic pressure drives the alteration of the crop to midgut pressure gradient. This evidence supports the notion that the crop serves a protective function (to guard against osmotic stress): fluids with high osmotic pressure (detected by sense cells) are retained and passed slowly to the midgut (Wigglesworth 1974). Also, there is strong evidence suggesting that increased haemolymph osmotic pressure results in (a) a reduction in the rate of crop-emptying (Davey and Treherne 1963a, b, 1964; Gelperin 1971; Bignell 1981; Bernays and Simpson 1982; Simpson and Bernays 1983) and (b) a reduction in meal size and duration (Bignell 1981; Simpson 1983; Simpson and Bernays 1983) (see Fig. 1c).

Food quality also affects consumption and the rate of crop-emptying. Engelmann (1968) showed that the rate of crop-emptying increased on soft foods compared to solid foods. Also, hard foods reduce feeding behaviour or

necessitate increased time to ingest a given amount of food (Reingold and Gelperin 1980; Bernays and Simpson 1982). Slugs exhibit reduced feeding rate (Senseman 1978) or bite frequency (Reingold and Gelperin 1980) when feeding on hard foods.

The regulation of specific nutrients is often correlated to the insect's needs. Simpson and Abisgold (1985) showed that locusts regulate their intake of protein but not carbohydrate. This suggests that protein was limiting (likely during growth) (Waldbauer et al. 1984). When not growing, cockroaches regulate carbohydrates to meet energy demands (Gordon 1968; Bignell 1978). Thus, control cockroaches should eat more carbohydrate than protein (i.e. energy demands are greater than growth demands).

Such regulation is exemplified in female blowflies. These insects display a variable control system: normally female blowflies eat sugar for survival, but gravid females may consume protein (for the eggs) even if the blowfly is bloated with sugar (see Belzer 1970; Bernays and Simpson 1982).

An insect may respond to poor food quality by either changing food (Mattson 1980) or continuing to feed, thereby increasing catabolism, excretion, food volume intake (Bignell 1978; Sibly 1981; Slansky and Scriber 1985) and incurred feeding costs. For example, Simpson and Ludlow

(1986) believe that recent excretion may stimulate feeding. Thus, insects feeding on low quality diets must balance the costs of increased consumption with those of not altering consumption. The latter strategy has been shown to have a negative impact on adult homeostasis (Taylor 1980a, b; Slansky 1982) probably supplemented by the fact that compensation can never be completely realized (see Simpson and Abisgold 1985). Thus cockroaches presented with a choice between protein and agar pellets should display greater protein consumption as a direct response to poor food quality (agar).

Sugars are universal phagostimulants as well as an energy source. With free access to sugar, cockroaches stabilized their intake rates at a level which offset daily requirements (Gordon 1968). Short-term food deprivation resulted in greater intake in the first few days following food reinstatement. The effect eventually stabilized suggesting that reserves are monitored (Gordon 1968). In contrast, feeding deterrents (ie. salts and excess protein) play an important part in determining both the initial choice and the amount of food eaten (see Haydak 1953; Bernays and Simpson 1982).

Summarizing, the following are key factors affecting consumption: (a) phagostimulants and deterrents, (b) food consistency, (c) limited crop size, (d) osmotic pressure of

crop contents and (e) osmotic pressure of haemolymph.

Following the consumption and breakdown of food, assimilated nutrients are transported by haemolymph to active or storage tissues (Wigglesworth 1974; Downer and Matthews 1976a, b) (Fig. 1c). Eventually, the nutrients (containing C, N, P, S and salts) are used for growth, reproduction and energy production.

Haemolymph moves freely within the cockroach body cavity (Fox 1981). Because it transports particulate matter and bathes all tissues, haemolymph is well buffered (Wigglesworth 1974). Hydrated adult males possess 130-200 uL of haemolymph (Wall 1970; Heit et al. 1973). These authors suggest that haemolymph acts as a water reservoir which tissues can draw upon in times of deprivation. Interestingly, water-deprived cockroaches showed strong haemolymph osmolarity regulation without the excretion of solutes (Edney 1968; Wall 1970). Instead of excretion, sodium and potassium were sequestered by fat body (Hyatt and Marshall 1977).

Heit et al. (1973) suggested that the haemolymph Na/K ratio influences drinking rate. They used NaCl to increase the osmolality of the water and found that increased osmolality leads to greater imbibition rates. Related to this, the haemolymph Na concentration increased while K remained unchanged. In adult male cockroaches, the haemolymph ratio of Na/K was measured as 132/9 but these

values depend largely on diet and hydration (Weidler and Sieck 1977).

Diet affects the haemolymph state by contributing nutrients or requiring the fat body to supply proteins and fats (Wigglesworth 1974; Downer and Matthews 1976a). Most proteins are enzymes and many are conjugated with lipids and carbohydrates. Protein is important during starvation as rapid haemolymph protein utilization has been measured in some insects (Wigglesworth 1974).

Early work by Mullins and Cochran (1974, 1975a, b) showed that diets high in nitrogen (N) resulted in whole-body increases in uric acid (UA), potassium (K) and sodium (Na). Low protein diets resulted in the mobilization of these compounds (Cochran 1985). These results suggest that UA functions as an ion sink for the haemolymph by forming urate salts in the fat body (see Fig. 1c).

Even though most nitrogen is stored as uric acid, diets high in nitrogen result in increased ammonia excretion compared to regular diets. Small amounts of ammonia may serve as a gut buffer or a nitrogen source for gut bacteroids. The major benefit in storing uric acid is water conservation. Ammonia is highly toxic and must be excreted with water. Thus storing uric acid in the fat body (or excreting small amounts of it) saves water (Mullins and Cochran 1974).

Storing UA is not a cost-free strategy. Mullins and Cochran (1975a, b) discovered that carbohydrate (C) reserves are utilized for the synthesis and storage of uric acid. Thus, diets high in protein cause a depletion of stored carbon. Therefore, the best strategy must integrate the excretion of excess N (see Haydak 1953). Yet cockroaches may store uric acid to lethal limits suggesting that this mechanism may not be overridden. A review of N dynamics (including the factors contributing to the nitrogen equation) has been compiled by Cochran (1985).

The close link between haemolymph and fat body is realized when considering sugar dynamics. Based on the decline of fat body glycogen and the corresponding increase in haemolymph trehalose, Matthews and Downer (1974) suggested that the fat body stores trehalose precursors. Spring et al. (1977), through injection of labelled glucose, showed that haemolymph trehalose is synthesized initially followed by a switch to fat body glycogen. Glucose absorption is facilitated by the rapid conversion to trehalose as this creates a steep glucose gradient (Wigglesworth 1974). Trehalose is a disaccharide that readily breaks down into glucose subunits for energy use (Matthews et al. 1976; Downer 1981). Trehalose is then replenished by mobilization of fat body glycogen (Downer and Matthews 1976b; Downer and Parker 1979).

Ion fluxes between the fat body and haemolymph are

related to fat body hydration (Spring et al. 1986). Potassium showed variable results (but of less magnitude than Na), suggesting that the former is less important in maintaining haemolymph osmotic and ionic balance. Both of these ions rise and fall (in fat body concentration) in response to hydration, especially Na (Hyatt and Marshall 1977, 1985). In water-stressed cockroaches, Na is sequestered by fat body urate cells (Hyatt and Marshall 1980). Rehydration causes restoration of haemolymph volume suggesting that ions are released from the fat body. Spring et al. (1986) believe that the Na release is under hormonal control and identified the terminal abdominal ganglion as the source of these hormones.

The ramifications of a 10 minute flight on the haemolymph composition of cockroaches was studied by King et al. (1986). Complete restoration takes at least 24 hours. During the first 2 minutes of flight, haemolymph K and trehalose concentrations increase. Between 1-6 hours after flight, the haemolymph volume increased 30%, osmolarity decreased 25% and trehalose increased 35%. As osmolarity increased towards normal (after the 6th hour), all haemolymph ion concentrations stayed constant except for Na. King et al. (1986) believe that the early release of K stimulates the release of hormones which act to increase haemolymph volume. The post-flight increase in

trehalose was probably used to resynthesize muscle glycogen which was shown to drop by 75% after a 10 minute flight.

Fat body not only stores fats, glycogen, protein and uric acid, but also functions in intermediary metabolism (Fig. 1c). Fat body contains mitochondria and a variety of enzymes capable of liberating and converting, among others, amino acids, sugars and fatty acids (Wigglesworth 1974). Also, proteins and uric acid can be synthesized. Bacteroids in the fat body are believed to contribute to uric acid metabolism (Donnellan and Kilby 1967; Cochran 1975; Cochran 1985).

Starvation has a great effect on the fat body constituents. The main components have been ranked according to ug/mg fresh weight fat body of adult male P. americana (Cochran et al. 1979): lipids 112, uric acid 41, protein 29 and carbohydrates 17 (Fig. 1c). The following components (and their energy provision) were utilized by starving cockroaches: lipids 66%, carbohydrates 22% and protein 12% (Cervenkora 1960).

Models based on energy have been applied to the starvation process (Sibly and McCleery 1983, 1985). These models assume that death by starvation occurs when the energy reserves or an essential nutrient are exhausted. Energy reserves act to lower the risk of starvation in gulls but excessive reserves reduce fitness (Sibly and McCleery 1985). These models are based on two major

assumptions: (a) there is a constant energy drain from the reserves when not feeding and (b) when feeding, each food type results in a constant energy-replenishment rate (Sibly and McCleery 1983). The models and field studies identified a critical energy reserve value below which the animal dies of starvation.

Starvation eventually results in a reduced metabolic rate (partially through the reduction of foraging behaviour, Fig. 1a, b) as this strategy decreases energy and nutrient demands (Barton-Browne 1975; Calow 1977; Jones 1977; Bernays and Simpson 1982).

Drinking is closely linked to feeding. As food sits in the crop, water following a pressure gradient moves from the haemolymph to the gut. The resulting increase in haemolymph osmotic pressure necessitates drinking (Bernays and Simpson 1982). Specific metabolites or nutrients from feeding may affect drinking to a larger degree.

Uric acid metabolism has also been directly linked to drinking. Uric acid is a end product of protein catabolism and is stored in fat body urate cells (Downer 1981). Cockroaches fed high protein diets were shown to deposit large amounts of fat body uric acid (Mullins and Cochran 1975a). If active protein breakdown occurs, then often the rate of uric acid formation exceeds its diffusion rate out of the cell (and hence crystallization occurs)

(Wigglesworth 1974). Wharton and Lola (1970) had previously discovered that uric acid deposition changes the haemolymph Na/K ratio. This occurs because potassium is correlated with uric acid concentration (Mullins and Cochran 1974, 1975a, b; Tucker 1977a, b), and these readily combine to form urate salts. Urate salt storage also liberates hydrogen ions which are buffered predominantly by bicarbonate. This reaction results in the production of metabolic water.

Water balance and lipids have also been linked. Lipids alleviate desiccation problems in many ways (see Downer and Matthews 1976a). Most important is the fact that fat oxidation yields twice the metabolic water as carbohydrate oxidation. Thus the storage of greater amounts of fat (relative to carbohydrate) provides a potentially useful source of non-imbibed water (Downer and Matthews 1976a). The large lipid content of the cockroach fat body (Cochran et al. 1979) partially explains to its higher caloric content per weight compared to carbohydrate (Downer and Matthews 1976a).

In summary, the energy balance at the moment affects the metabolic state of the fat body. During energy expenditure, the fat body mobilizes the reserves. Nitrogen storage and mobilization have not been adequately addressed in the literature. Also, its interaction with other reserves has not been investigated. A feeding animal is in

a state of positive energy balance and therefore accumulates reserves. Hence, the fat body is a dynamic tissue responding to prevailing physiological conditions (Downer 1981). One aim of this study was to investigate cockroach feeding after fat body alteration. The results should show that reserves are not independent and that they must be considered together when studying feeding and drinking behaviour.

IV. Activity-switch Models

McFarland (1969) pioneered research concerning mechanisms underlying activity transitions. Roper and Crossland (1982) supplemented McFarland's suggested mechanisms with three of their own (see Roper and Crossland for a summary of all six mechanisms). They suggest that competition and/or satiation are responsible for the eat/drink and drink/eat transitions in rats. Houston (1982) categorizes these two mechanisms as "dependent-2" meaning that the intensity level of activity 2 controls the time of switching (i.e. increasing the intensity of activity 2 results in an earlier switch from activity 1 to 2).

The belief that the activity with the highest intensity (or causal factor strength-CFS) will be performed

is common to many models concerned with activity transitions (Houston 1982). Contributors to the CFS for feeding include: (a) the food deficit in the gut, (b) the availability of food (sensory stimuli) and (c) the osmotic state of the blood (Fig. 1c). The CFS for an activity declines gradually as the activity is performed due to negative feedback from internal physiology (Toates 1980; Roper and Crossland 1982) and adaptation of the sense organs (Senseman 1978).

The fact that animals can usually only perform one behaviour at a time (McFarland 1977) has been taken a step further by Ludlow (1982). Ludlow's model incorporates a switch mechanism which prevents two activities from occurring at the same time by employing reciprocal inhibition. In finches, such competition was investigated by Slater (1978). He found that some behaviour patterns do not follow each other randomly (i.e. some order is present) and that feeding is often cyclic. These results indicate that competing activities are probably linked and comprised of an underlying negative feedback mechanism. This contrasts with Ludlow's (1980, 1982) model of the switch mechanism: if the causal (direct) factors for the inhibited activity reach a threshold value, then the activity will be elicited- eventually inhibiting it's competing activity completely. Thus a positive feedback cycle promotes the

activity switch.

Animals must also consider the cost (often in terms of energy) of switching from one activity to another. In natural settings, components of cost may include work (energy), time and risk of predation (McFarland 1976 cited in Larkin and McFarland 1978). The energy used when feeding is offset by a reduction in the food deficit, but the transitional cost (i.e. energy used while searching) when compounded with the cost of the next behaviour, often necessitates longer durations for the latter behaviour (Larkin and McFarland 1978). Recent data using mice have indicated that the energy cost associated with each behavioural bout is very low compared to the daily energy intake suggesting that energy costs may not be a constraining factor (Meyer and Guillot 1986).

Simpson and Bernays (1983) believe that the concepts of "drive" or "motivation" cannot be practically applied to the study of feeding behaviour due to their abstract nature. Models formulated by Lester (1984a, b), however, not only build on research concerning initial-choice behaviour but also show that motivational and causal factor levels are experimentally definable and may be quantitatively characterized.

Feeding and drinking are influenced by internal and external stimuli (Lester 1984a; Geissler and Rollo 1987). The feed/drink decision has been studied in the past (Sibly

1975; Larkin and McFarland 1978) and the research showed that the behaviour with the larger deficit times incentive product will occur first. "Deficit" is defined as the amount of food required to restore nutrient balance. "Incentive" is a measure of food availability which affects the rate of deficit change.

Interruption experiments provide a useful tool for investigating dominance (Sibly and McFarland 1976) and causal factors (McFarland 1969, 1974; Houston 1982; Roper and Crossland 1982). For example, by plotting dominance points in 2-dimensional deficit space (see Lester 1984a) a dominance boundry can be identified. Under conditions of constant food and water, Sibly and McCleery (1976) found that the slope of this boundry was invariant suggesting that the slope depends on availability.

Lester's (1984a) feed/drink model is primarily based on "relative payoff" models (Harley 1981; Lester 1984b). The basic premise is that behaviour is a product of a recent payoff (food reward) and an expected payoff (feeding rate). The model treats causal factor and motivational levels separately thus eliminating the need for the previously described switching mechanisms (competition, inhibition etc.) and interruption experiments.

The model flow begins by calculating motivation. Motivation is the product of deficit times expectation (the

latter is learned from availability in previous trials and is constant within a trial). Lester (1984a) realized that motivation changes within a trial and thus added an "excitation term". This term is the summation (over n time frames) of [the product of deficit times amount obtained (over time frame in question) times a recency factor]. The recency factor works in the following manner: food eaten in the distant past has less effect on present excitation.

The Lester model predicts a motivation curve similar to those observed for birds (see Lester 1984a). The curve begins at a level equal to its food deficit but as the bird eats the curve rapidly increases to a maximum and then gradually declines. Concurrently, the deficit curve steadily declines. The initial rise in motivation is the result of the excitation term previously outlined. The decision-making process can now employ the motivations calculated for each behaviour by converting them into probabilities of occurrence (relative to the other behaviours).

The term expectation (when calculating motivation) is based on the calculation of a "switching slope" (i.e. on one side of this line the animal feeds, on the other it drinks). As long as food and water expectations do not equal their availability, the slope may be defined as the sum of expectation and availability for resource one (i.e.

food) divided by the same for resource two (i.e. water).

Finally, causal factor levels may be defined by withdrawing the common factor "deficit" out of the motivation equation and noting that during feeding, food intake matches availability: causal factor level equals deficit times the sum of expectation and availability. Thus causal factor levels decrease as the deficit is reduced (as long as expectation and availability are constant) and therefore behave differently from motivational levels.

In summary, the rationale for using deficit models (Sibly and McFarland 1976; Lester 1984a, b) is that deficits in various physiological parameters are measurable and thus the models are probably realistic. Such models suggest that animals efficiently regulate an assumed "ideal internal state". Deviation from this ideal state incurs costs (usually described as a function of deficits) and in order to minimize this cost the behaviour is elicited until the "boundry line" is reached. From this point on the animal adopts a stable strategy of time allocation to each behaviour. This causes both deficits to move along the boundry towards the origin until both have zero deficit.

Feedback and deficit models successfully describe feeding and drinking behaviour, and Lorenz's (1950) "psycho-hydraulic" model can explain most others. This

supports Gould's (1982) postulation that evolution may have resulted in only two major strategies for regulating animal behaviour: one relying on feedback loops and the other employing the principles of Lorenz's (1950) "psycho-hydraulic" model.

When weighing the merits of maximization and homeostatic models, it should be noted that systems regulated homeostatically to set points are widespread in nature and include growth, reproduction and feeding.

The central hypotheses of optimal foraging theory are: animals forage to maximize their net intake of energy and/or (depending on the situation) animals attempt to minimize their time devoted to foraging. Maximization is not easily applied to homeostatic systems so that the whole assumption of optimality may not apply- or it may have to be reformulated to consider the degree of deviations from the evolutionary-determined set points.

The current work, being based on an experimental components framework (see Holling 1963, 1966), tests the idea that homeostasis may be geared towards set points (associated with major metabolic reserves). Experiments and hypotheses were derived to endanger this idea and these are expounded in the methods.

MATERIALS AND METHODS

I. Animals

Healthy adult males of P. americana were obtained from colonies fed ground Purina Dog Chow (protein), granular sucrose (carbohydrate) and water ad libitum. Colonies were maintained at 24 °C and with a 8L:16D photoperiod. All experimental animals were subsequently kept individually in plastic containers (20x10x8 cm deep) with 1 cm of moistened sand on the floor and a darkened retreat. Water was supplied ad libitum in a 4 cm diameter petri dish. The water was accessible via an 8 mm hole in the lid which prevented evaporation and drowning. The plastic containers were kept in an environmental chamber maintained at 23-25 °C with a photoperiod of light:dark 16:8 (h), 1600:0 lux for at least 2 weeks to entrain the cockroach's circadian activity rhythm (Sutherland 1981). During the photophase, cockroaches remained in their retreat and commenced activity near the onset of the scotophase (see Harker 1955, 1956 and 1958). Various experiments provided specific dietary regimes in pre and post-treatment formats and these will be detailed as appropriate.

This study divided a day into a photophase and scotophase. Since the photophase was devoid of activity, all data were collected from the scotophase (8 h). All

experiments were comprised of two parts. The first involved examining patterns of activity (drinking, eating, homing) over a minimum 12-day and maximum 34-day period. Long observation periods were required to detect reserve dynamics (as indicated by behavioural changes). As with many studies involving such long-term behavioural patterns, detail was necessary (see Faber 1975) at the expense of large numbers of repetitions. In addition, essential features of individual patterns may be lost when the behaviour of large numbers of animals is averaged together. For example, a possible bimodality in individual behaviour may be obscured when a population pattern is examined because each individual might have slightly different timing. Because we are ultimately interested in predicting activity of individuals, low numbers of cockroaches were used to minimize any pattern distortion that would result from the averaging process and because the monitoring apparatus could not handle more than two cockroaches at once. (Ideally, the patterns of individual cockroaches should be compared, but this was not feasible due to time constraints). Control and protein-starved treatments used 4 males each while completely starved and agar treatments used 2 males each (see page 50). Some of the effects of individual variation were reduced by selecting males of similar size and weight.

The second part investigated daily means for comparison between treatments and behaviours. Thus large quantities of data were collected: control, 64 days (512 h of scotophase); protein-starved, 96 days (768 h); starved, 24 days (192 h); agar-fed, 28 days (224 h). Thus, although low numbers of animals were used, the study considers 212 days (1696 h) of observation.

II. Food and Water

Agar-based food pellets were prepared to provide standardized diets: 62.5 mL of boiled distilled water was added to a mixture of 1.5 g of agar (Difco Bacto-Agar), 62.5 g of finely ground dog food pellets (Ralston Purina Inc.: protein 21%, moisture 12%, fat 8%, fibre 4.5%, salt and vitamins) and 10 drops of a 10% solution of Tegosept fungicide. The carbohydrate and agar pellets were made similarly with the following changes: carbohydrate pellets were comprised of 32 g sucrose and 3 g agar dissolved in 125 mL distilled water; agar pellets were 3 g agar dissolved in 125 mL distilled water. The mixture was set in a refrigerator for at least 24 h. An aluminum tube (1 cm in diameter) was forced into the mixture, the resulting core was extruded and 1 cm long pellets were sliced off. These pellets were larger than an individual cockroach could consume in 24 hours.

Consumption was estimated by oven-drying 10 sample pellets (taken from the food source) to estimate their water content. This hydration value was used to estimate the initial dry weight of the pellets presented to the cockroaches. Prior to the onset of the next scotophase, the partially eaten pellets were replaced with fresh ones and subsequently oven-dried at 60 °C. Daily consumption (dry weight) was calculated by subtracting the dry weight of the eaten pellet from its original dry weight (estimated from the wet weight).

At the time of food pellet replacement, water intake was calculated by taking the difference between the original water level in a graduated drinking tube (measured the day before) and the final water level. An identical tube (not accessible to the cockroach) measured evaporation within the environmental chamber. This value was subtracted from the measured intake to correct for possible evaporation. These parameters were added to the data file and analyzed with the temporal parameters.

III. Experimental Habitat

The experimental habitat consisted of a transparent plexiglass box (13 cm cubed) with 4 transparent plexiglass tubes (12 cm long, 7 cm in diameter) leading to the

following resources: a protein pellet, a carbohydrate pellet, a tube supplying water and a darkened retreat (Fig. 2). The resource stations were continuously monitored by infrared light-emitting diodes (LEDs) with complimentary phototransistors (FPT 120s). To prevent non-feeding or non-drinking activities from triggering a response, the resource was separated from the cockroach by a baffle with a hole that allowed the head of the insect to reach the food or water while preventing the legs from triggering the LED. The habitat was wired to a Commodore "PET" microcomputer and a parallel interface adaptor (PIA) (see Fig. 2). This setup enabled behaviour to be continuously monitored over extended periods. The habitat was located and monitored inside the same environmental chamber as the treatment containers, under the same conditions.

IV. Experiments

Regressions between water intake and relative humidity were performed in all treatments because relative humidity fluctuated between 24 and 66% in the chambers. This was the only environmental variable which was not kept constant.

Cockroaches were allowed 5 days in the plexiglass habitat to reduce possible novelty effects. During this period the habitat contained only the food(s) and water

which constituted the pre-treatment the cockroach had experienced.

Cockroaches were weighed before each experiment so that intake of food and water could be calculated per unit body weight. The control and protein-starved animals were each monitored for a month to identify the compensation period. This was found to be approximately 9 days. Thus the starved and agar-fed animals were run for 12 days minimum (to guard against variation in the compensation period).

Treatments were as follows:

All cockroaches were reared to adulthood on a diet of carbohydrate, protein and water. "Controls" were maintained on this diet for all aspects of the experiment including the 5-day adjustment period and subsequent monitoring in the artificial habitat.

"Protein-starved" cockroaches were offered only sucrose and water for 7 months. Only 5 out of 12 cockroaches survived this lengthy starvation period. Carbohydrate pellets and water were present in the artificial habitat during the 5-day entrainment period. Protein pellets were added once data collection began. It was assumed that such a severe treatment would force the cockroach into a state of negative nitrogen balance while maintaining energy in abundance. Assuming that each reserve

acts independently: Hypothesis 1- animals depleted in nitrogen should initially prefer protein.

"Starved" cockroaches had access to only water for 20 days. Protein and carbohydrate pellets were introduced after the water-only adjustment period of 5 days. The intent of starving the cockroaches was to concurrently deplete the carbohydrate and protein reserves, thus effectively ensuring an overall negative nutrient balance. Hypothesis 2- cockroaches depleted in carbohydrate and protein should initially prefer carbohydrate. This was based on the predictions of optimal foraging theory which sets the greatest priority on energy, and because energy is probably required to power various features of nitrogen and protein metabolism.

"Agar-fed" cockroaches were entrained as in the controls. After the adjustment period, pure agar pellets (undigestable by animals) replaced the carbohydrate pellets for the rest of the experiment. This should provide insight concerning the importance of nutrient detection and responses to a depleting carbohydrate reserve. Hypothesis 3-cockroaches offered a choice between protein and agar pellets should prefer protein.

V. Measures of Behaviour

Cockroaches may be considered input-output devices

linked to the environment by a "behavioural control program". Behaviour acts to maintain physiological homeostasis as well as obtaining necessary resources for maintenance and spermatophore production. This approach gives a holistic view of animals as opposed to traditional studies which usually concentrate on either inputs (foraging) or outputs (reproduction) but not their linkage. Therefore, the study of behaviour provides an indirect account of physiological demands constrained by the environment.

The following variable means were recorded or calculated for each treatment and behaviour:

BLOCK- a single behaviour (e.g. drinking, homing, feeding on a particular food). When a different behaviour is elicited a new block starts, and the former ends. A block may include considerable amounts of "dead" time when nothing happens.

1. Block no. is the number of blocks during the scotophase.
2. Block dur. (BLKD) is the daily length (s) of blocks.

BOUT- a single record at food or water within a block (i.e. triggering of photocell). Once contact is over, the bout is complete.

3. Bout no. (BTS) is the daily number of bouts.
4. Activity dur. (DUR) is the daily length (s) of bouts. Since bouts are a measure of sustained contact with

food or water, this parameter accurately defines the daily length of a behaviour. The computer was accurate to 1/60 th of a second.

5. Non-Activity Time (NAT) is the difference (s) between block duration and activity duration. It estimates the relative length of rests between bouts or the intensity of the activity.
6. Consumption/Intake (INTK) is the daily amount of food or water consumed per unit body weight of the cockroach (mg or uL/gm).
7. Bout length (ADUR) is the activity duration divided by the number of bouts.
8. Bout size (AINT) is the intake divided by the number of bouts.
9. Rate (RATE) is the daily intake divided by the activity duration.
10. Elicitation percentage (EP) is the activity duration divided by the block duration multiplied by 100.

The computer stored the time and location of each triggered LED on a "raw data" disk file. The raw data files were subsequently analyzed by a program which separated each behaviour block (a continuous sequence of one behaviour) and calculated the number of bouts, bout duration, average bout length and block duration. This was done for each cockroach for every day. The next stage

involved the daily totalling of each variable according to behaviour. The resulting information was transferred and analyzed on a CYBER mainframe. Each variable for each behaviour was lumped according to treatment and analysed by regression, ANOVA procedures and Duncan's multiple range test.

The above analysis does not provide insight into the temporal patterning of events. Consequently, cockroach rhythms within the 8 h scotophase were also examined.

RESULTS

The computer monitored experimental habitat enabled large quantities of data to be collected, stored and analyzed. Three primary behavioural variables were identified from which most others were calculated: bout number (BTS), activity duration (DUR) and block duration (BLKD). All experiments utilized the same variables and units to allow comparison. Most results are interpreted relative to controls.

Variables 2-9 (see Methods) were subjected to correlation/regression analysis. Block number showed minor changes between treatments and was not considered in the ANOVA and Duncan analyses. Variables 2 and 5 were not used because they were highly correlated with variable 4 (Tables 6-9). Variables 7 and 8 were also not considered for ANOVA because it was assumed that variables based on direct observations (Variables 3 and 4) would provide a better indication of activity length and intake.

Tables 1-3 represent variables averaged over all cockroaches and days for a given treatment. Note the differences in the y-axis scales when comparing Figs. 3-15.

When comparing means for each behaviour, the percent values represent a decrease or increase over controls. For example, a 100% increase represents a doubling over the control value while a 50% decrease represents half the

control value.

A. Water Intake

i. Patterns in Drinking Behaviour

Control Drinking Behaviour

Regression analyses indicated that drinking bout number and duration were correlated for controls (Table 6). This relationship is supported by the results in Figs. 3 and 4. The 18-day patterns were nearly identical and cyclic with peaks occurring on days 2, 5, 7, 11 and 16. Both patterns showed steady drops between days 12 and 14, followed by the largest peak at day 16. Interestingly, the intake pattern matched these patterns only after day 7 (Fig. 5), but the regressions between these variables and intake were not significant.

Protein-Starved Drinking Behaviour

The 34-day patterns concerning bout number and drinking duration were again closely matched. The large peaks on day 2, 12 and 22 coincided for each variable (Figs. 6 and 7). This suggested that a cycle with a 10-day period existed, except that the expected peak on day 32 did not occur. The intake pattern, as in the controls, did not coincide with either bout number or drinking duration (Fig.

8). This is supported by Table 7 which showed no correlation between these variable pairs. The intake pattern seems to be comprised of three phases: days 1-9 fluctuating around a mean intake of approximately 75 uL, days 10-30 around 130 uL and days 31-34 around 275 uL. The increase in drinking from an average of 75 to 275 uL (Fig. 8) represents a major increase in water demand compared to controls (Fig. 5).

Relative humidity was correlated to water intake for protein-starved cockroaches (Fig. 9). This was a negative linear relationship given by the following equation:

$$INTK = 329.8687 - 3.8347 * (RH)$$

where INTK = water intake (uL/day)
RH = relative humidity (%)
$p<0.05$, $r = 0.5877$, d.f.= 32

Thus, as the relative humidity increased, the intake of water decreased. This is clearly evident when comparing Figs. 8 and 9. Therefore, interpretation of the imbibition results will require the inclusion of this environmental factor.

Starved Drinking Behaviour

Starved cockroaches showed similar patterns to controls for bout number and drinking duration with peaks occurring on days 4-5, 7 and 12 (Figs. 10 and 11). The ranges of bout number (7-34) and drinking duration (6-48) and their means (see Table 1) were lower than controls.

The intake pattern (Fig. 12) showed many fluctuations. Peaks occurred on days 2, 5, 7 and 12 (the latter three corresponded to the peaks of bout number and drinking duration). Even though these variables were not correlated to intake (Table 8), their reduction resulted in decreased intake compared to controls (see Table 1).

Agar-Fed Drinking Behaviour

The agar experiment showed the same relationship between bout number and drinking duration as the starved treatment (Figs. 13, 14 and Table 9) with peaks occurring on days 2, 5, 8 and 11. Relative humidity was not correlated to any of the water variables. Both variable means were lower than controls (Table 1) and it appeared that this lowering resulted from the reduction of peak number and duration. The intake pattern gradually declined until day 8 when a large peak (203 uL) occurred (Fig. 15). After this peak, the pattern gradually increased. The day 8 peak coincided with peaks in bout number and drinking duration as well.

Summarizing, it appears that the patterns for bout number and drinking duration are very similar, not only within each treatment but across treatments as well. This suggests an invariant drinking strategy. Across treatments, all patterns had similar peak periods: on days

2, 4-5, 6-8, 11-12 for all treatments, including day 16 for controls and protein-starved and days 18, 22, 24-26, 29 and 32 for protein-starved only.

ii. Comparison of Means and Regressions for Drinking

In terms of drinking duration, control cockroaches were not tenacious as only 12% of time within drinking blocks were actually spent drinking. The 48 s spent drinking per day encompassed 27 bouts and resulted in 108 uL intake of water per gram cockroach (see Table 1).

The protein-starved cockroaches were protein deprived for seven months. The treatment affected drinking variables as increases were observed for non-drinking time (22%), bout size (26%) and drinking rate (20%) compared to controls. An 18% increase in block duration concurrent with a 16% drop in drinking duration resulted in a drop in elicitation percentage (EP) from 12 to 9% (refer to methods section for definition of EP). All other variables were slightly reduced (Table 1).

All drinking variables also decreased in starved cockroaches (Table 1). Notable reductions included rate (41%), intake (50%), bout size (50%), block duration (51%), drinking duration (51%) and non-drinking time (51%) compared to controls. The fundamental difference between the completely starved and protein-starved cockroaches was

a large carbohydrate reserve in the latter. The presence of this reserve appears to have altered water intake.

The agar experiment resulted in predominantly decreased behavioural variables compared to controls. The most notable decreases occurred in drinking duration (59%) and bout length (39%). Only bout size (20%) and drinking rate (74%) increased. Since agar is comprised of undigestible bulk, the carbohydrate reserve should have become depleted over the course of the experiment. The effect was similar to the starved cockroaches: a reduction in most drinking variables. Daily intake and rate were both greater than the starved treatment indicating that the greater agar bulk necessitated extra water (Table 1).

To determine whether statistically significant differences existed between treatments, an analysis of variance (ANOVA) was carried out (see Table 4). Only daily intake was significantly different among the treatments.

Duncan's multiple range test determined which treatments differed significantly at the 5% level of probability. Table 5 indicates that, as well as the intake difference between controls and starved cockroaches, drinking in the protein-starved cockroaches varied significantly from the starved and agar-fed cockroaches.

It is equally important to supplement investigations involving variable differences between treatments with the

relationships among variables within each treatment. These results (Table 6-9) aid in identifying possible rules which govern a specific behaviour and the consequences of physiological alterations caused by each treatment.

Table 6 showed positive linear relationships between bout number, drinking duration, non-drinking time and block duration. Thus the variables which comprise the block variable were all positively related. Concerning individual bouts, increased drinking resulted from increased amounts per bout while average bout length remained relatively constant (Table 6).

The variables comprising drinking behaviour appeared to be fixed in their relationship to each other as the same pairs were correlated in every treatment (see Tables 7-9). Note particularly the highly significant relationship (in all treatments) between non-drinking time and block duration and, to a lesser degree, intake rate and bout size.

Summarizing, intake may be envisioned as an operation at one of two levels: short-term or long-term. For example, the extra water required by the protein-starved cockroaches may have been obtained by increasing variables within the scotophase (e.g. bout size and rate = short-term). In contrast, the starved and agar treatments decreased drinking by reducing the daily or long-term variables (e.g. drinking duration and intake).

B. Carbohydrate Consumption

i. Patterns in Carbohydrate Consumption

Control Feeding Behaviour on Carbohydrate

Figures 3 to 5 support the relationships (as outlined in Table 6) between bout number, feeding duration and intake. The patterns were similar and cyclic with peaks occurring on days 1, 4-5, 7-8, 10, 12-13 and 16-17. Number of bouts and feeding duration could be divided into three phases. Days 1-4 contained the largest peaks followed by a lower, level period on days 5-11 which then escalated into the final phase containing large peaks (days 12-17). After an initial large peak on day 1, intake fluctuated around a mean of 17 mg/day.

Protein-Starved Feeding Behaviour on Carbohydrate

In terms of bout number and feeding duration, protein-starved cockroaches immediately reduced the duration and frequency of visits to the carbohydrate station compared to controls (compare Figs. 6 and 7 to Figs. 3 and 4). These variables and intake (Figs. 6-8) displayed similar patterns thus indicating their correlation to each other (Table 7). Peaks occurred on days 1-2, 4-5, 6, 8-9, 11, 14, 16-17, 19, 21-22, 25, 27, 29 and 32-33 (approximately every 2 or 3 days).

The initial days following re-instatement of protein would be expected to show the compensatory effects concerning carbohydrate most dramatically. [Note that because bout number is highly correlated to feeding duration it will not be interpreted (see Tables 6-9)]. Figures 7 and 8 show distinct changes in feeding patterns over time. The transition identifies the compensation point and marks the end of the compensation period (CP). The values before and after this point were averaged resulting in two phases which can be compared to controls.

The compensation period was 7 days for the carbohydrate feeding duration. During this time duration was only 40 s on average compared to 236 s for controls. After this period, duration doubled but remained lower than controls. Although duration of carbohydrate feeding was reduced as was expected, intake was surprisingly opposite: during the 8-day compensation period, intake was 29 mg/gm of carbohydrate compared to 21 mg/gm for controls. Later, intake rose even further to 43 mg/gm while the controls dropped to 12 mg/gm. These results support the enormous increase in consumption rate compared to controls (Table 2), especially during the compensation period (716% increase). These results were very surprising as it was expected that energy demands had been fulfilled or surpassed during the long entrainment period on a pure sugar diet.

During the compensation period, water intake decreased compared to controls resulting in a lower intake rate (from 2.32 uL/s to 1.65 uL/s). This result is also unexpected as increased sugar consumption usually necessitates increased drinking.

Starved Feeding Behaviour on Carbohydrate

As in the former two treatments, starved cockroaches displayed similar patterns and correlations for all three variables (compare Figs. 10-12 and Table 8). The patterns of bout number and feeding duration fluctuated at a significantly higher level than controls (compare to Figs. 3 and 4 and see Table 5). The intake pattern was not only similar in shape to controls, but also fluctuated at a similar mean (17 mg/day). Peaks occurred on days 1, 3-4, 6, 8 and 10.

Starved cockroaches increased carbohydrate feeding duration both before and after the 4-day compensation period (Figs. 11 and 12). During the compensation period duration was 655 s on average compared to 337 s for controls. This dropped to 331 s while the controls dropped to 31 s. Despite the trends in durations, initial intake was the same as controls (22 mg/gm) during the 4-day CP, after which intake dropped to 14 mg/gm compared to 12 mg/gm for controls. This resulted in an overall drop in

consumption rate (Table 2) which comprised a 49% drop in feeding rate during the CP. So even though their behaviour indicated strong compensation, actual consumption did not show it. This does not support Hypothesis 2.

Water imbibition and duration were lower compared to controls during the CP but the lower duration resulted in an increase in drinking rate (1.59 uL/s to 2.33 uL/s).

Feeding Behaviour on Agar

Table 9 and Figs. 13-15 also show the correlation between bout number, feeding duration and intake. The patterns of bout number and feeding duration fluctuated at a slightly higher mean than controls, but this was not significant (Table 5). Peaks occurred on days 2, 4, 5-6, 8, 11 and 13-14 for each variable. Intake displayed an interesting pattern: days 1-9 contained fluctuations ranging from 2-6 mg/day and days 10-14 contained peaks ranging from 19-58 mg/day.

Agar-fed cockroaches showed similar duration compared to controls (205 s and 202 s respectively) during the 9-day CP (Figs. 14 and 15). This coincided with a lower intake of agar (4 mg/gm) compared to 20 mg/gm of carbohydrate for controls. After the CP, duration was 368 s (compared to 140 s for controls) and intake jumped to 36 mg/gm of agar (compared to 14 mg/gm of carbohydrate for controls). These two phases resulted in a lower overall rate compared to

controls (Table 2), especially during the CP (80% drop). The compensation results indirectly support Hypothesis 3 as agar consumption dropped compared to controls.

The drinking results were lower than controls during the CP. As in the starved results, the decrease in duration resulted in an increase in rate (from 2.32 uL/s to 9.63 uL/s).

ii. Comparisons of Means and Regressions for Carbohydrate Feeding

Controls displayed an elicitation percentage of 41%. The 184 s feeding per day included 36 bouts which resulted in 17 mg of carbohydrate intake (Table 2).

Protein-starved cockroaches were characterized by large increases in carbohydrate bout size (334%) and feeding rate (1825%). These increases resulted in an increased daily consumption of 93% over controls (Table 2). All variables comprising the carbohydrate blocks (block number, block duration, bout number, feeding duration and non-feeding time; hereafter referred to as block variables) showed marked reductions (30, 62, 59, 56 and 66% respectively). In terms of actual feeding time, this treatment was the most efficient with an elicitation percentage of 48%.

Compared to controls, the variables of the starved cockroaches were opposite to those of the protein-starved. Substantial decreases in bout size (73%) and feeding rate (62%) resulted in a slight reduction in daily carbohydrate consumption (2%) (see Table 2). Interestingly, all the block variables increased (48, 442, 137, 138 and 656% respectively). Obviously, consumption efficiency was low (with respect to the increased block variables). The differences may be attributed to the depleted carbohydrate reserve. Only 18% of the block time was actually spent feeding in starved cockroaches, even though this duration was longer than controls.

Cockroaches fed agar as a substitute for carbohydrate ate it despite its indigestibility (Table 2). Surprisingly, the increases in block number (25%), block duration (357%), bout number and feeding duration (both 42%) resulted in 9% less intake compared to controls. Reduced bout length (36%), bout size (58%) and feeding rate (31%) contributed to the reduced intake. Another contributing factor may be feeding tenacity as only 13% of the block time was spent feeding.

ANOVA showed that bout number, feeding duration and intake differed significantly between treatments (Table 4). Duncan's multiple range test identified differences in bout number between protein-starved and each of the remaining

treatments. Also, differences existed between starved/controls and starved/agar (Table 5). The same pairs of treatments differed for feeding duration which indicates that these variables may be correlated. Table 5 shows that significant intake differences existed between the protein-starved and each of the remaining treatments.

Table 6 outlines the significant positive linear relationships between all possible variables for the controls. Bout number, feeding duration, intake and non-feeding time were all correlated to block duration. At the level of individual bouts, bout size (carbohydrate intake per bout) was correlated to bout length and consumption rate was correlated with bout size. Thus changes in carbohydrate feeding largely appear dependant on varying intake rates as opposed to changes in duration.

Even though all the block variables were correlated in protein-starved cockroaches, non-feeding time was not correlated to feeding duration or intake (Table 7). Thus within a block less time was "wasted" which was reflected in increased elicitation percentage (see Table 2). Also, there was no longer a correlation between bout size and bout length.

The starved cockroaches displayed the most interesting changes in variable relationships (Table 8). Only five out of a possible twelve correlations remain. For this treatment, bout number, feeding duration and intake were

important variables as they were correlated to each other. Bout size was positively correlated to bout length but neither of these variables could aid in predicting consumption rate.

Table 9 shows that agar-fed cockroaches differed from controls with respect to the following eliminated correlations: intake with block duration and non-feeding time and bout size with bout length.

All treatments concerning carbohydrate behaviour reinforced the correlation between block duration and non-feeding time (compare r values for this pair in Tables 6-9).

In summary, protein-starved cockroaches acquired carbohydrate by eating more per bout and this was reflected by an increased consumption rate. The starved and agar treatments showed reduced feeding as a result of reduced bout size and feeding rate. The carbohydrate feeding variables are not fixed relative to one another since the feeding correlations varied among treatments. In other words, the treatments changed the structure of carbohydrate feeding.

Summarizing, carbohydrate feeding was characterized by close relationships between bout number, feeding duration and intake. These variables displayed patterns with similar peak periods (every 2-3 days), even over the

different treatments. In terms of compensation period, the increase in carbohydrate intake and rate was surprising for the protein-starved treatment and indicates that reserves are not independent. The intake for the starved treatment (same as controls) was unexpected and the lower carbohydrate feeding rate compared to controls appears to violate the energy currency assumption of optimal foraging theory. The lower intake and rate of agar consumption during the compensation period for the agar-fed treatment initially supports Hypothesis 3 (cockroaches offered a choice between protein and agar should prefer protein).

C. Protein Consumption

i. Patterns in Protein Consumption

Control Feeding Behaviour on Protein

The correlations between bout number, feeding duration and consumption (Table 6) are supported by the patterns displayed by these variables (Figs. 3-5). Peaks occurred on days 3, 6, 10, 14 and 16.

Protein-Starved Feeding Behaviour on Protein

The protein-starved patterns for all three variables may be separated into two phases: an initial phase which gradually slopes downward during days 1-23, and a later phase from days 24-34 (see Figs. 6-8). The peaks for the

three variables coincided on days 3, 5-6, 8, 12, 14-15, 18, 21, 24-25, 28, 30 and 32-34. The patterns for bout number, feeding duration and consumption (for both phases) differed from controls, but the overall means were not significantly different (Table 5).

The 8-day compensation period showed a feeding duration of 192 s on average compared to 173 s for controls. During this time, protein intake was much higher (22 mg/gm compared to only 14 mg/gm for controls) indicating strong feedback from depleted reserves. After the compensation period, duration fell to 40 s which was one-third of the controls. This paralleled a drop in consumption (to 5 mg/gm) compared to 10 mg/gm for controls. These changes resulted in a 10% drop in overall rate (Table 3) even though the rate increased (42%) during the compensation period.

Starved Feeding Behaviour on Protein

The three variable patterns for the starved treatment were similar with peaks occurring on days 1, 3, 5, 7, 9 and 11-12 (Figs. 10-12). These relationships are supported by correlation analyses (Table 8). The peaks declined in size over the 12-day experimentation period but overall they were larger than the control patterns. This resulted in significant differences from controls for all three

variables (Table 5). Note the occurrence of enormous peaks on days 1 and 3 for the three variables.

Starved cockroaches displayed a ten-fold increase in duration compared to controls (1220 s compared to 116 s) while protein consumption was three-fold higher than controls (48 mg/gm compared to 16 mg/gm) during the 3-day compensation period. Later, duration dropped to 170 s while the controls increased to this level but intake dropped in both treatments (16 mg/gm compared to 10 mg/gm for controls). The large initial duration was clearly the major factor contributing to the decreased consumption rate overall (Table 3) and during the compensation period (72% drop).

Agar-Fed Feeding Behaviour on Protein

The agar-fed cockroaches displayed large fluctuations in bout number and feeding duration over the 14-day period (Figs. 13-15). The peaks of these two variables occurred on days 1-3, 5, 8-9, 11 and 13. The similarity between the patterns of bout number and feeding duration supports their correlation (Table 9). Intake was not correlated to either of these variables even though several peaks overlapped. The large ranges for bout number and feeding duration were not significantly different from controls. Surprisingly, the intake range was significantly different from controls (Table 5).

Protein consumption was three times higher on average than controls (42 mg/gm versus 14 mg/gm). During this 5-day compensation period, duration was also higher than controls (249 s versus 136 s). Subsequently, duration and consumption dropped (to 181 s and 30 mg/gm) but these averages were still higher than controls (160 s and 10 mg/gm). The difference in early protein intake was large enough to increase the protein consumption rate overall (Table 3) and during the compensation period (64% higher).

Protein feeding behaviour was characterized by varying inter-peak periods for each treatment. Therefore, the patterns were not as predictable as they were for carbohydrate consumption and water intake. The peaks may represent overshoot/undershoot compensatory responses.

ii. Comparison of Means and Regressions for Protein Feeding

Control cockroaches spent 38% of the block duration feeding on protein. Only 13 mg was consumed over an average of 23 bouts within the 142 s feeding period (Table 3).

Protein-starved cockroaches unexpectedly showed only small increases for two variables: bout number (10%) and consumption (6%). All other variables decreased, the largest of which was bout length (58%) (Table 3). These

results do not support Hypothesis 1 (animals depleted in nitrogen should initially prefer protein). But Tables 1-3 only show the overall differences between treatments and behaviours (because they are averaged over the entire study period). Therefore, these tables will undoubtedly mask expected (and unexpected) results within this study period. This draws attention to the importance of the compensatory response analysis presented previously. The utilization of patterns is vital in behavioural studies. Subsequent pattern analysis will ensure that important short-term responses, like those displayed in the compensation periods, will not be missed.

Starved cockroaches showed increases in all block variables: block number (72%), block duration (170%), bout number (213%), feeding duration (205%), non-feeding time (149%) and consumption (82%) (Table 3). Parameters involving individual bouts decreased: bout length (28%), bout size (42%) and feeding rate (54%). Thus, consumption increased because bout number and feeding duration increased (daily variables).

Table 3 indicates that agar-fed cockroaches displayed large increases in several variables compared to controls: block duration (525%), non-feeding time (824%), consumption (174%), bout size (155%) and feeding rate (188%). Agar-feeding also increased the block number (58%), bout number and feeding duration (85 and 45% respectively). Only bout

length was reduced (19%).

Bout number, feeding duration and intake all differed significantly between treatments in terms of protein consumption (see ANOVA, Table 4).

In terms of bout number and feeding duration, starved cockroaches were significantly different from control, protein-starved and agar-fed cockroaches (Table 5). Again, this indicates that a close relationship exists between bout number and feeding duration. In terms of intake, every possible pair of treatments were significantly different except controls and protein-starved.

Regression analyses concerning protein consumption for controls yielded eleven significant equations between variables (Table 6). Similar to the carbohydrate behaviour, all the protein block variables were correlated. Consumption rate was again correlated to bout size as opposed to length.

It appears that the difference between the control and protein-starved treatments is primarily based on the elimination of three previously significant correlations (block duration versus intake, bout number versus non-feeding time and consumption versus non-feeding time) and the addition of a correlation between bout length and bout size (Table 7).

Starved cockroaches showed the same variable

correlations as controls (Table 8). Therefore, any quantitative differences in variables for this treatment were probably derived from time budget and efficiency changes as opposed to tactics involving the change of variable importance (as determined by correlations).

Differences from controls in the agar treatment were based on only three correlations (Table 9). Therefore, these variables must be the most important in determining the quantitative differences observed.

Block duration and non-feeding time were again highly correlated throughout the various treatments (Tables 6-9).

In summary, protein-starved and completely starved cockroaches increased protein consumption by increasing bout number. Agar-fed cockroaches increased bout size and feeding rate in order to acquire more protein. Tables 1-3 show that Hypotheses 1 and 2 may be violated. The agar-fed treatment supports Hypothesis 3. As in the carbohydrate section, the treatments had a varied impact on feeding.

Summarizing the compensation period results for both carbohydrate and protein, Hypothesis 1 (animals depleted in nitrogen should initially prefer protein) is supported as protein consumption was increased by increasing duration and rate of feeding. Surprisingly, carbohydrate consumption in the protein-starved treatment increased as well (by increasing intake rate). In terms of optimality (starved treatment), Hypothesis 2 (cockroaches depleted in

carbohydrate and protein should initially prefer carbohydrate) is rejected because carbohydrate consumption and intake rate did not increase compared to controls. The enormous increase in protein feeding duration and intake was unexpected. Hypothesis 3 (cockroaches offered a choice between protein and agar should prefer protein) is supported because protein consumption and feeding rate increased in the agar treatment.

D. Behavioural Trade-offs

The controls in Table 10 show that most feeding variables were greater than their corresponding drinking variables by a ratio of at least 2:1 (Feeding:Drinking). Some dominated the corresponding drinking variable: activity duration 7:1 and bout length 12:1. The drinking variables which were greater than their corresponding feeding variables included intake 1:4, bout size 1:3 and intake rate 1:7. These variables should always be greater for drinking because of the ease of water uptake compared to food which must be masticated and digested.

If the combined feeding variables for controls are separated into their carbohydrate and protein components, it is apparent that more time was invested in carbohydrate consumption than protein (Table 10). Only bout size and consumption rate were larger for protein.

The difference between total feeding and drinking variables was marginally reduced in protein-starved cockroaches (Table 10). Feeding dominated in block number (F:D) 2:1, activity duration 4:1 and bout length 7:1. Drinking dominated intake 1:3, bout size 1:2 and intake rate 1:2. All remaining variables were slightly larger for the feeding behaviour. Thus protein starvation necessitated a slight drinking increase.

Protein starvation reversed the carbohydrate dominance

shown in controls. In fact, the first five variables in Table 10 show a larger protein component. Thus a greater time investment increased the protein variables at the expense of carbohydrate.

Starved cockroaches displayed feeding domination over drinking for all variables but three. The feeding preferences ranged from (F:D) 4:1 to 36:1 depending on the variable. It is obvious that the replenishment of both reserves was vital. The three variables dominated by drinking were again intake, bout size and intake rate.

The starved cockroaches were assumed to be depleted in their carbohydrate and protein reserves. They invested time at each feeding station depending on the variable. For example, carbohydrate behaviour comprised a greater component than protein for bout number, block duration, non-feeding time and bout length. The opposite was true for consumption, bout size and consumption rate (similar to controls). The remaining variables were even.

The investment into drinking compared to total feeding was small for agar-fed cockroaches. Only intake, bout size and drinking rate were larger (ranging from slight to (F:D) 1:5). Feeding dominated drinking by a minimum of 4:1 to a maximum of 23:1 depending on the variable.

Cockroaches presented a choice between protein and agar pellets consumed much more protein even though more

time was invested at the agar station. Block number, block duration, bout length and non-feeding time were all greater for protein and only bout number and feeding duration were greater for agar. The protein component of bout size and consumption rate was much larger than the agar component and this resulted in greater protein consumption.

In terms of behavioural trade-offs, Figs. 3-15 may provide insight into the long-term time budgets for each behaviour. These figures show that all three behaviours fluctuated in a cyclic pattern. Peaks occurred every few days depending on the behaviour and the treatment. The controls showed some interesting trends when all three behaviour patterns were examined for each variable. Figures 3-5 show that a single behaviour peak (carbohydrate or protein feeding or drinking) may be found on 77% of the days which contained at least one peak (averaged over all three variables). Furthermore, if there were two peaks in one day, they were usually both food peaks. This suggests that drinking behaviour is strongly separated in time from feeding, usually dominating a particular day when feeding is suppressed.

The same trend persisted for protein-starved cockroaches (Figs. 6-8). A single peak (one behaviour) occurred on 73% of the days containing at least one peak (averaged over all three variables). The remaining days had more than one peak and these peaks followed a pairing

trend different from controls: water and carbohydrate peaked on the same day most often followed by carbohydrate/protein and water/protein.

Starved cockroaches displayed single-peak days on 66% of all days with peaks (averaged over three variables) (Figs. 10-12). The pairing trend of the multi-peak days was as follows (starting with greatest frequency): carbohydrate/protein, water/protein and water/carbohydrate. Note that this is different from the protein-starved treatment.

Finally, the agar-fed cockroaches in Figs. 13-15 displayed single behaviour peaks in just over half (57%) of the days with at least one peak (averaged over three variables). Days with two or more peaks usually involved the following pairs (starting with the most frequent pair): water/carbohydrate, carbohydrate/protein and water/protein.

E. Summary

After examining each behaviour over the treatments, it appears that the drinking variables are relatively fixed. In terms of time spent on each behaviour, feeding was always greater than drinking. In control cockroaches, more time was spent feeding on carbohydrate than protein. Each treatment will now be summarized with all behavioural

changes relative to controls.

In the protein-starved treatment, carbohydrate consumption increased significantly (Table 2, Figs. 6-8). This increase appeared to necessitate increased drinking (Tables 1 and 10). Protein consumption also increased (Table 3) but this was most evident during the compensation period (Table 10, Figs. 6-8). Hypothesis 1 (animals depleted in nitrogen should initially prefer protein) is accepted.

Starved cockroaches showed less carbohydrate consumption overall and during the compensation period (Table 2, Figs. 10-12). Subsequently, a significant drop in overall drinking occurred (Tables 1 and 10). Surprisingly, overall protein consumption increased significantly (Table 3). Hypothesis 2 (cockroaches depleted in carbohydrate and protein should initially prefer carbohydrate) is rejected.

Cockroaches fed agar as a substitute for carbohydrate displayed decreased consumption overall and during the compensation period. This was accompanied by a decrease in drinking (Tables 1 and 10). Protein consumption increased significantly overall (Table 3) and increased during the compensation period (Table 10 and Figs. 13-15). Hypothesis 3 (cockroaches offered a choice between protein and agar pellets should prefer protein) is accepted.

DISCUSSION

The discussion is divided into six sections. The first section deals with models and optimality and how they may conform to the results described in this thesis. The next four sections deal with the treatments (controls, protein-starved, starved and agar-fed). These sections will link the results to the literature through an examination of the appropriate hypotheses and models. Finally, the summary section will compare the major findings of this study to the objectives outlined in the introduction.

I. Models and Optimality

This study provided cockroaches with a stable, relatively unconstraining environment such that behavioural selection would arise simply from interacting, competing drives (Ludlow 1976; Slater 1978; Toates and Archer 1978; Toates 1980; Lester 1984a, b). Understanding a dynamic system entails observation of an animal's behaviour as it responds to various inputs (water, energy, other nutrients) altered by the investigator (Berryman 1981). Deduction of the system's design follows. The physiological state of the cockroach may be deduced through observation of the responses to these inputs. Isolated adults were assumed to

use carbohydrate and protein for maintenance as growth was not applicable. Also, the process of resource acquisition was assumed to incur additional nutrient and energy loss. Summarizing, physiological changes produce drives which affect behaviour. Behaviour aids in the achievement of homeostasis which ultimately reduces surpluses, deficits and associated drives.

The behavioural model (Fig. 16a) outlines the decision flow based on the state of reserves. Each nutrient has an assumed preset homeostatic level and any deviations from this level will affect the central excitability value (CEV) for that nutrient. For example, the largest nutrient deficit will have the largest CEV. Other nutrients will be bypassed until the nutrient with the highest CEV is found. If not found, the food with the next highest CEV will become the goal. Once food is found the model leads into Fig. 16b. Note that in Fig. 16a, if a food search is unsuccessful yet water is found, water may be imbibed.

The physiological model (Fig. 16b) represents established components and their links. This model was built on a foundation of flow-through models presented by Bernays and Simpson (1982). It has been modified and updated according to the scope of this study and the results (see literature review and results section).

The major assumptions linked to the behavioural model

include: (a) circadian rhythmicity dominated all behaviours regardless of the cockroach's physiological state and (b) memory and learning resulted in negligible behavioural changes. The static structure of the habitat ensured that the latter would have been a small component.

Both models are based on the concept of central excitablity which is modified according to the cockroach's state and reinforced by positive feedback (Simpson and Bernays 1983). The level at the start of feeding influences ingestion rate and the amount of negative feedback tolerated before feeding stops (Fig. 16b).

Central excitability can be inferred from the duration, rate and frequency of activity. For example, a hungry animal will eat longer and ingest more nutrients (Barton-Browne 1975; Bernays and Simpson 1982; Simpson and Bernays 1983). Thus elicitation percentage (or tenacity) provided useful comparisons of efficient time use within a block.

Block duration includes both the time related to consummatory acts as well as quiescence between and following this behaviour (Manning 1979). Other activities occurring within a block (i.e. grooming) are considered subdominant (Rowell 1961) and were ignored in this study. The elicitation percentages (motivations) calculated for controls were 12% for drinking, 41% for carbohydrate consumption and 38% for protein consumption. Both feeding

values were at least 3 times greater than drinking indicating that tenacity is greater towards food than water.

Central excitability is also influenced by external stimuli (phagostimulant and deterrent concentration, as seen in blowflies), blood composition and hormones (both in locusts) (Bernays and Simpson 1982; Simpson and Bernays 1983; Lester 1984a) (see Fig. 16b). Of these, deterrents play a large part in determining both the initial choice and the amounts of food eaten (Bernays and Simpson 1982; Simpson and Bernays 1983). Thus, the greater food motivations for controls (compared to water) may be a reflection of greater phagostimulation, physiological factors or the fact that greater quantities of water may be consumed per unit time than food (thus drinking time within the block is reduced, hence the smaller elicitation percentage).

Once feeding begins, phagostimulation must remain favourable (Dethier 1964; Shiraishi and Yano 1984). The "continue feed" component (Fig. 16b) represents ingestion rate (efficiency) which is comprised of a time and volume component. The volume of food ingested starts the physiology section which ultimately feeds back to an excitability comparator. The comparator decides whether or not to terminate the present behaviour. If it does,

termination marks the end of a bout for that behaviour. If central excitability remains high for that particular behaviour, negative feedback would eventually decay resulting in the resumption of the activity and the start of another bout.

Once the "stop feed" component (Fig. 16b) has been reached, the reserves are updated (Fig. 16a). The deficit values for each reserve component (e.g. fat body carbohydrate and protein, blood water supply) are calculated and translated into updated CEVs for the decide component. The decide component will start the cockroach feeding or drinking (Fig. 16a). Ingestion starts the physiological model again.

The scope of this thesis does not include the modelling of behaviour switches which occur when central excitability falls below that of a competing behaviour. Such switching models are described by Ludlow (1980, 1982), Lester (1984a, b) and Houston and Sumida (1985). In the future, the reanalysis of the results (within the scotophase) would contribute data to such models.

Interpreting the results in terms of dominance is simple in experiments which keep nutrient availabilities constant (such as the control study). Under these conditions, Sibly and McCleery (1976) found that the dominant behaviour had a higher deficit than the others. Also, because cockroaches learn resource availability in

predictable environments, they respond close to the optimal switching times predicted for feeding and drinking (Lester 1984a). This study demonstrated that control cockroaches responded more to food (41% elicitation percentage (EP) for carbohydrate, 38% EP for protein) than water (12% EP). Thus feeding was dominant to drinking.

The goal of the physiological model (Fig. 16b) is the efficient regulation of internal state on a daily basis. This is an adaptive or homeostatic goal as opposed to optimality models which also assume that an ideal state exists but incorporate maximization principles (Sibly and McFarland 1976). In other words, optimization models reduce deficits by maximizing intake rates and this leads to enhanced fitness (ultimate goal).

Optimality theory revolves around two separate views: the maximization of some resource intake per unit time or the minimization of time to obtain a fixed amount of nutrient (Pyke et al. 1977; Krebs et al. 1981; Pyke 1984). These views are exclusive only when time minimization compromises energy returns (Hainsworth and Wolf 1983). Since it is unlikely that optimization is exclusive to a particular behaviour, it is probable that an animal's entire behavioural repetoire is optimized by natural selection. Overall optimization implies that any one behaviour must occur suboptimally due to tradeoffs with

other behaviours. Other factors contributing to suboptimal behaviour include environmental or physiological constraints or risk avoidance.

Optimal foraging theory has been expanded to include limiting nutrients as well as energy (Pulliam 1974, 1975; Slansky and Feeney 1977; Rapport 1980; Lucas 1983). Thus, in terms of the model, the optimal response to deprivation would involve maximizing the ingestion rate of the limiting nutrient. This response can take the form of increased intake and/or decreased duration. A simple adaptive response would involve increasing the ingestion rate or intake above a control level.

Since optimality is difficult to measure, it is often inferred from intake rates. The intake rates over the compensation period for each treatment were compared and the greatest were found to be 0.73 mg/s for carbohydrate and 0.17 mg/s for protein. Optimality theory predicts that intake rates must remain constant at these levels. The remaining discussion argues that optimal intake rates are not realized or necessary. Rather, cockroaches maintain homeostasis through adaptive responses (e.g. intake rates above controls; not necessarily maximal).

II. Controls

According to duration, the controls showed the

following hierarchy: carbohydrate consumption > protein consumption > water intake (Tables 1-3). This hierarchy may be altered by intense, competing motivations as seen in marine gastropods (Davis et al. 1974a, b, 1977). Presumably the arrangement of the hierarchy is related to opportunities and costs associated with the resource in natural environments.

The control hierarchy, in terms of average intake per day, was carbohydrate (17 mg/gm) taking precedence over protein (13 mg/gm) (Tables 2 and 3). These values are slightly larger than those reported by Faber (1975). In other treatments, intakes of 33 and 34 mg/gm for carbohydrate and protein respectively were observed (Tables 2 and 3). These lower intakes for controls challenge the primary assumption of optimal foraging theory, especially since the observed maxima may still not reflect the true capability. Rollo (1984) showed that P. americana could eat four times more food than normal following starvation. This evidence suggests that cockroaches do not maximize their daily food intake.

Ingestion rate is comprised of a duration and quantity component. Optimality predicts that animals either maximize quantity or minimize time. Therefore, if feeding duration increased and the animal was maximizing feeding, then the rate would also have to be greater than normal.

Concurrent increases in consumption and duration were evident (note correlations in Table 6), but the patterns for duration and consumption within controls (Figs. 4 and 5) do not match (all peaks and troughs should match for a possible optimal response). Also, the overall intake rates observed for control carbohydrate and protein were much less than observed maxima (control carbohydrate 0.16 mg/gm/s, maximum 3.08 mg/gm/s; control protein 0.84 mg/gm/s, maximum 2.42 mg/gm/s) (Tables 2 and 3). This strongly suggests that an optimal strategy is not operating.

Maximization of size or rates of meals or drinks have frequently been reported (Slansky and Feeney 1977; Pyke 1984; Simpson and Abisgold 1985), but examination of ingestion rates across treatments shows many instances of sub-maximal performance (see Tables 1-3). This result supports Rollo's (1986) contention that cockroaches normally operate submaximally and consequently are not optimal in the classical sense.

Optimal foraging theory usually assumes that food is valued only for energy yield (e.g. energy content). Thus a food lower in energy will be ignored once a higher-yielding food is encountered. If this is true, sugar should be the ideal substrate since it has very high and rapid energy yield with low feeding or digestive costs. Table 3 shows that protein was still consumed in the presence of

carbohydrate which agrees with knowledge gained from nutritional studies indicating that these foods are complimentary (Rapport 1980; Pyke 1984). This illustrates that optimization cannot be carried out exclusively with an energy criterion (Haydak 1953; Pulliam 1974; Charnov 1976; Hassell and Southwood 1978; McNair 1979; Orians 1982; Vickery 1984).

Furthermore, the results illustrate the existence of trade-offs possibly due to handling constraints (e.g. food type, hardness etc.) (Pulliam 1974, 1975; Rapport 1980; Pyke 1984) and that the value of the currencies of protein and energy vary depending on reserve state. Optimality theory rests on an assumption of constant value. Thus central excitability differs for protein and carbohydrate resulting in varied flow through times for Figures 16a and 16b.

Protein was consumed faster than carbohydrate (supports Vickery 1984). Thus Richard's (1983) prediction that food with the lowest handling time will be preferred may be a reflection of optimality and not necessarily desirability.

Even though this study has shown that optimization strategies are not operating (maximization of intake rate, consuming the highest energy-yielding food only, constant currency value), control cockroaches still preferred

carbohydrate over protein (see Table 10). This supports research which showed that rodents desired foods which provided the greatest energy (Vickery 1984). (Note that this does not exclude other foods nor does it imply optimization). This preference is likely supported by positive gustatory responses to sucrose (see phagostimulation in Fig. 16b) (Wieczorek 1978; Jakinovich et al. 1981) and the fact that cockroaches stably maintain their energy reserves (Gordon 1968). This result was expected as control cockroaches use energy to run all processes including protein metabolism.

Energy plays a central role in many feeding models (Treherne 1957; Gordon 1968; Gelperin 1971; Toates and Booth 1974). Toates and Booth (1974) postulated that food intake is mediated by energy balance involving feeding rate, gut energy content, energy absorption rate from the gut and energy flow to the fat body (Fig. 16b). This study indicates that the greater carbohydrate consumption for controls was attributable to increased duration (probably to replete the energy reserve) (Table 10). Therefore, feeding models must integrate temporal variables with intake variables.

Although protein had a larger bout size than carbohydrate, the bout number and feeding duration for protein were actually less (Table 10). This was achieved by a greater protein consumption rate (higher

chemostimulation?). These data do not support an energy maximization hypothesis. Rather, they suggest that separate control strategies may exist for each food. In other words, spending more time eating does not necessarily maximize intake rate.

Food type is a major consideration in determining investment into feeding behaviour. The consistency of the protein pellets was harder and necessitated greater handling than the sugar pellets (activity duration and intake, Table 10). Hard foods generally reduce feeding duration and the amount ingested (Bernays and Simpson 1982). In addition, soft foods exit the crop faster than solid ones (Engelmann 1968; Barton-Browne 1975) thereby decreasing the length of post-ingestinal inhibitory feedback (Davey and Treherne 1963a, b) (Fig. 16b). This ultimately results in greater absorption (Treherne 1957). The expected reduction in the rate of crop-emptying suggests a slower rate of nutrient absorption. Therefore, in the model, glucose is rapidly absorbed so carbohydrate pellets would exit the crop faster and reduce the inhibiting feedback period.

Clearly the different rates of crop-emptying necessitate the implementation of a process which governs the ordering of events. An adaptive response might ensure that carbohydrate feeding occurs early in the scotophase and compensation period to rapidly replace energy reserves. Otherwise, the time required to digest protein may prohibit carbohydrate consumption and undoubtedly this would create an energy deficit. Adaptive regulation must promote equilibrium consumption for both foods. The existence of such a process is manifested in Figs. 3-5. For each

control variable, carbohydrate was initially larger than protein. Once energy demands were fulfilled, certain protein variables became larger than carbohydrate.

The larger consumption rate for protein (compared to carbohydrate) is opposite to findings concerning slugs. Slug feeding rate (Senseman 1978) and bite frequency (Reingold and Gelperin 1980) are lowered when feeding on hard foods. This contrast indicates that either the mechanisms underlying feeding are different for gastropods and insects, or the preference for protein overrode the increased hardness of the pellets.

Control cockroaches were reared on high protein dog chow so large protein reserves may have resulted in lower daily protein consumption compared to carbohydrate (Table 10). Haydak (1953) showed that enforced high protein diets may lead to an excess of stored urates in the cockroach fat body, ultimately reducing longevity. Harper (1967) demonstrated that cockroaches preferred a diet containing 25% protein over one containing 50% protein. Therefore, high protein may be likened to a feeding deterrent (when reserves are full). These results indicate that cockroaches cannot physiologically control reserve size on a fixed diet, but behavioural mechanisms may regulate reserves when choices are available.

The aforementioned contrasts between carbohydrate and

protein feeding behaviours, supplemented with differences in (a) variable correlations (Table 6) and (b) long-term patterns (Figs. 3-5) further suggest that these behaviours are regulated differently.

For example, the patterns for feeding duration, number and consumption differed. For the carbohydrate behaviour, all three variables were correlated (Table 6), yet only the duration and number patterns were similar and tri-phasic (Figs. 3-5). For protein behaviour, all three variables were correlated and shared similar patterns with 3-4 day peak periods (Table 6 and Figs 3-5). These slightly different patterns may (a) act to reduce competition for a daily dominant motivation, (b) be the result of digestive processes with different periods or (c) be dominated by low frequency rhythms (2.5 days or longer) (van der Driessche 1975). It is difficult to determine which of these mechanisms, or combination thereof, are operating in this study.

The large variability in day-to-day feeding was surprising (Figs. 3-5) as adult males do not grow and presumably have low reproductive costs (sex was prevented through isolation). Such variability has been noted previously (Rollo and Gunderman 1984). Simpson and Bernays (1983) suggest that ingestion rate may produce this variability. Also, variation may be the result of over-shoot and under-shoot oscillations due to attempts to

maintain homeostasis. Thus different foods are associated with specific consumption rates, crop-emptying rates, digestive rates, absorption rates, storage and excretion rates (see Fig. 16b). These interactive effects (including water dynamics) and their staggered rhythms ensure that the daily physiological demands are variable.

Foraging and eating are required by males for tissue maintenance, spermatophore production and behavioural costs. Control cockroaches spent more time eating than drinking (Table 10). Similar results were found by Meyer and Guillot (1986) using mice. Besides being easy, drinking was lower likely because of the cockroach's ability to (a) regulate its haemolymph osmolality and (b) conserve and reabsorb water efficiently (Wall 1970; Tucker 1977a, b; Simpson 1982; Hyatt and Marshall 1985; King et al. 1986; Spring et al. 1986). The control of drinking has been studied (Barton-Browne 1964, 1975; Oatley 1967; Heit et al. 1973) but few address the obvious link of drinking to feeding (McFarland and Wright 1969).

Table 10 shows that water was easier to acquire than food. Obviously water does not impose limitations on intake to the extent of food (no mastication required, less negative feedback from gut, easier absorption into haemolymph etc., see Fig. 16b). Thus, with less constraints than food, drinking duration provides a good

indication of drinking drive (Oatley and Dickinson 1970).

Both feeding and drinking cause major homeostatic disturbances. The fat body plays a major role in maintaining haemolymph homeostasis by mobilizing and taking up salts and sugars (Barton-Browne 1968; Bernays and Chapman 1974; Downer 1981; Fox 1981; Mullins 1981; Cochran 1985; Spring et al. 1986) (see Fig. 16b). Even though carbohydrate pellets were processed faster, protein probably had a major impact at the physiological level because of its many constituents (see Fig.1a, b).

Spring et al. (1977, 1986) showed that the level of haemolymph glucose is controlled through conversions to trehalose (short-term) and fat body glycogen (long-term). Controls were assumed to have large glycogen stores because of the available sucrose (which is catabolized to yield blood glucose). These high sugar levels probably contributed to an increase in blood osmotic pressure thereby necessitating drinking (Pond 1981). Table 1 shows that the controls drank an average of 108 uL water per gram cockroach per day. Cockroaches with access to only protein drank 70 uL/gm/day (Gunderman and Rollo, unpublished). Therefore, the ingestion of carbohydrate necessitated drinking.

Feeding increases haemolymph osmotic pressure because water moves from surrounding tissues to the gut (Gelperin 1966; Bernays and Chapman 1974). Starved cockroaches drank

only 48 uL/gm/day compared to 70 uL/gm/day for those eating a protein diet (Gunderman and Rollo, unpublished). These values compare favourably with past results: starved P. americana drank 21 uL/male/day (Heit et al. 1973) while protein-fed cockroaches drank 104 uL/male/day (Mullins 1974). Thus, feeding enhances drinking behaviour (Reynierse et al. 1972). Interestingly, starved male cockroaches have been shown to increase their hydration (Wharton et al. 1965), possibly due to the mobilization of urates (Rollo 1984).

These studies stress the importance of water in maintaining homeostasis. Therefore, many authors insist that feeding and drinking must be studied in tandem (Fitzsimons and LeMagnen 1969; Oatley and Toates 1969; Reynierse et al. 1972). Tables 6-9 indicate that the relationship among drinking variables remained constant and that regulation occurred through quantitative rather than qualitative adjustments. This is remarkable considering the physiological change that is incurred in each treatment.

III. Protein-Starved

The current energy balance of the blood of P. americana affects the metabolic state of the fat body

(Downer 1981). For example, excess glucose in the haemolymph (positive energy balance) may be synthesized into trehalose (favoured in excited animals) or glycogen and lipid (favoured in resting animals) by the fat body (Spring et al. 1977, 1986; Pond 1981). Energy required to perform behaviours, or in periods of starvation, favours the mobilization of fat body reserves (Cochran 1985; King et al. 1986).

Protein-starved cockroaches had access to sucrose and water only. Sucrose is readily converted into glucose which is synthesized into trehalose in the haemolymph and subsequently into glycogen or lipid in the fat body (Spring et al. 1977, 1986; Downer 1981; Pond 1981). Lipids contain twice as much energy by weight as carbohydrates, without strongly influencing osmotic pressure. When metabolized, lipids liberate water which may be valuable in water shortages (Pond 1981). The main disadvantage of lipids is that they are not readily transported and thus serve as long-term reserves only. Also, the lipid catabolic pathway yields ketone bodies which must be excreted (thereby affecting the water balance).

Unlike glycogen and lipids, trehalose is immediately accessible and fuels the thoracic muscles during foraging and buffers maintenance energy losses (King et al. 1986). If depleted, trehalose reserves can be replenished through the mobilization of fat body glycogen and lipids (Downer

and Matthews 1976a, b; Downer and Parker 1979; Pond 1981; King et al. 1986). Thus, a diet of unlimited sucrose should have at least filled the glycogen and trehalose reserves (lipid might be relatively open-ended) while allowing a protein deficiency to develop.

In normal cockroaches reared on a standard dog chow diet, the protein reserve is almost twice the size of the glycogen and trehalose reserves combined (Cochran et al. 1979). Therefore, if reserve size is tightly regulated, large increases in protein-feeding were expected in protein deprived animals. Also, if the feeding system is homeostatic, a rebound period following the feeding increase would be expected. Over the course of the experiment, it is possible that the treatment's peaks and troughs would average to levels almost identical to controls.

The initial days following the introduction of the protein pellets provided support for hypothesis 1. Consumption and feeding duration on protein were greater than controls over the first 8 days (compare Figs. 4 and 5 with 7 and 8). These results support the responses employed by blowflies when replenishing depleted protein reserves (Belzer 1970). This compensatory increase was immediately followed by a rebound period where consumption and duration were less than controls (Figs. 4, 5 and 7, 8).

Overall, there was little difference between the protein-starved treatment and controls. Block and bout number, feeding duration, daily consumption and feeding rate were all similar to controls (Tables 3 and 5). Thus the variables did average out to the control levels. These results strongly support a homeostatic system of feeding with reserves playing a key role in determining the set point.

A switch in preference from carbohydrate in controls to protein in protein-deprived animals indicates that cockroaches may be expanding specialists (explanation to follow) (Heller 1980; Richards 1983). The control results identified carbohydrate as the more desirable food. Thus carbohydrate is eaten more frequently as long as the deficit is low. With a high deficit, both foods are eaten (expanding specialist).

The key factor rationale (or limiting resource hypothesis, Pyke 1984) postulates that food choice is regulated by modifying the threshold of desirability of each food (Vickery 1984). For example, a cockroach deprived of protein becomes protein-sensitive, perhaps via sensory modification, and subsequently chooses more protein-bearing food. Optimal foraging theory does not allow for such a response. As outlined previously, optimization theory postulates that only energy reserves alter feeding, this resulting in only one optimizing

currency (energy). The protein-starved results clearly show that reserves do fluctuate in size (as evidenced by fluctuating feeding for both carbohydrate and protein, Fig. 8) and that there may be multiple optimizing currencies (depending on reserve depletion).

Possibly there was a bottleneck in protein consumption imposed by ingestion rate which lengthened the compensation period. Such a bottleneck would make motivation identification more difficult (cannot tell by feeding responses). In this case bout number, feeding duration and elicitation percentage should provide better indications of drive because they are not constrained.

The bottleneck may be related to the "ordering of events" argument posed in the introduction. If, as the literature suggests, protein digestion takes much longer than carbohydrate, increased protein-consumption during the compensation period would effectively limit carbohydrate consumption.

Regardless, the responses were adaptive as consumption rate increased resulting in enhanced protein consumption (supports findings by Simpson and Abisgold 1985). Cockroaches convert extra protein into uric acid and store it in the fat body. Consequently, the protein consumed during the compensation period probably repleted the reserve (Waldbauer et al. 1984; Cochran 1985). Thus

hypothesis 1 is accepted, protein-starved cockroaches initially prefer protein.

The transfer of dominance to carbohydrate consumption after the protein compensation period was expected because controls showed a preference for carbohydrate (see Table 10 bout size, feeding rate and consumption variables). This decline in protein intake reflects diminished demand as the protein-deficit was reduced (Lester 1984a). The very high sugar intake rate both during and after the compensation period was unexpected.

During the protein compensation period, carbohydrate consumption was similar to controls but duration was 6 times lower (this supports time minimization in optimization theory, Winterhalder 1983, but this also allowed more time for protein consumption). These results support the ordering of events argument presented earlier. With more time being spent on protein consumption, the need for carbohydrate could only be achieved by increasing consumption rate. This strategy is often employed in animals like cockroaches which encounter wide variations in levels of available energy (Hainsworth and Wolf 1983).

The increase in carbohydrate consumption probably arises since protein metabolism utilizes stored carbohydrates (Mullins and Cochran 1975a, b). Thus, Gordon's (1968) suggestion that both protein and carbohydrate reserves contribute to feeding regulation

seems likely, even though they may act through different mechanisms.

Carbohydrate consumption was greatest after the protein compensation period. Coupled with a feeding duration lower than controls, this response resulted in an increased intake rate. Thus, it appears that cockroaches switch feeding strategies depending on their physiological state and food type, just as foragers employ different patch-leaving strategies depending on the patch (McNair 1983; Green 1984) (Fig. 1a). The fact that overall consumption was significantly higher than controls (Tables 2 and 5) indicates that supplementary energy was probably required for increased protein metabolism.

The following scenario is proposed: the extensive protein-starvation severely depleted the urate stores which were mobilized for protein metabolism during the shortage (Cochran et al. 1979). The required energy was supplied by both energy stores and carbohydrate consumption. Thus both carbohydrate and water intake increased (Table 10). This scenario also presents the possibility that strategies employed during periods of deprivation may be "carried over" to periods of constant food supply.

Previous experience affects many kinds of rate functions and has been demonstrated by compensation in biochemical activity or behaviour in many invertebrates

(Faber 1975). Therefore, the starvation period experienced can affect compensatory behaviours following food reinstatement. A model has been proposed for such a mechanism and represents behaviour as a tradeoff between a food reward and feeding rate; the former affected by deprivation (Harley 1981; Lester 1984a, b). These findings lend support to the possibility that strategy carry-over, as outlined previously, occurred in this treatment.

The significant overall increase in carbohydrate consumption was probably facilitated by increasing the crop capacity. It has been reported that the digestive tract of P. americana can accomodate extra capacity specifically in times of starvation (Rollo 1986). The ramifications of this response can be followed in Fig. 16b.

Another factor may be addressed. It has been demonstrated that soft foods exit the crop faster than hard foods (Engelmann 1968). Thus cockroaches can eat more soft food per unit time (facilitated by decreased negative feedback, Fig. 16b). This makes the carbohydrate consumption responses difficult to interpret: was the increase due to the ease of eating or the depleted reserves? This dilemma might be dealt with in the future by making both food pellets similar in hardness.

Finally, alternation behaviour (Wilson and Fowler 1976) introduces an additional complicating factor. Did the cockroaches initially choose protein because of storage

depletion or because it was novel? Geissler and Rollo (1987) recently showed that poorly nourished cockroaches are more likely to sample novel foods compared to well nourished ones. A change in experimental protocol would be needed to separate these two mechanisms.

Uric acid mobilization from the fat body increases haemolymph K+ concentration (K+) (Mullins and Cochran 1974; Tucker 1977a, b) which in turn affects the Na+/K+ balance (Wharton and Lola 1970). Drinking is necessary to offset osmotic pressure disturbances associated with such ionic instability, even in starved cockroaches. It is hypothesized that water is stored in the haemolymph and this storage regulates drinking. As Figure 16b outlines, salts and sugars from the digestive tract and fat body alter the haemolymph osmotic pressure. This directly influences blood (body) volume which in turn affects drinking behaviour.

The protein-starved cockroaches showed overall increases in intake, bout size and drinking rate, while all the time-related variables decreased (elicitation percentage was 9%) compared to controls (Table 1). As evidence for the link between feeding and drinking: the drinking intake pattern corresponded to the intake feeding patterns (Fig. 8). Days 1-9 fluctuated around 75 uL/gm/day which was the period dominated by increased food

consumptions over controls (compare to Fig. 5). Interestingly, the imbibition rate was lower than controls during this compensation period. Carbohydrate consumption dominated the day 10-30 period, which paralleled an increase in water intake (up to 130 uL/gm/day) which ultimately increased the intake rate enough to result in an overall increase compared to controls. Also, carbohydrate and drinking peaks occurred together more frequently than protein/drinking occurrences (Figs. 6-8). The model predicts this as rapid infusion of sugar into the haemolymph would strongly influence osmotic pressure resulting in a need for immediate drinking (Fig. 16b).

It is likely that this imbibition aided carbohydrate ingestion by (a) lubrication and/or (b) dilution of the crop contents which would increase the rate of crop-emptying (Treherne 1957; Davey and Treherne 1963a, b, 1964). The latter effect is supported by an increased overall feeding rate compared to controls (Table 2). Complicating matters, the water intake pattern was linked to environmental humidity (see Equation 1 and Fig. 9).

In summary, the literature and this study's results suggest that drinking and feeding (protein and carbohydrate) are closely interdependent. On short time scales these behaviours are temporally mutually exclusive (McFarland 1977), but switching strategies are employed to obtain physiological homeostasis among various stores. The

main factor producing oscillations in regulated systems is time lags (see any standard ecology text). The mutual exclusivity of the various behaviours ensures the existence of time lags and consequently overshoot and undershoot characteristics of feeding. Because of these complex interactions, simple depletion-repletion models (e.g. Sibly and McCleery 1983, 1985) are not adequate to predict cockroach behaviour. Throughout this section, it is clear that cockroaches act homeostatically (feeding responds to offset reserve fluctuations) rather than maximally (animal is constant).

IV. Starved

Starvation has been found to alter food-search behaviour which in turn is affected by the state of energy reserves and food distribution (Barton-Browne 1975; Calow 1977; Jones 1977; Simpson and Bernays 1983). Initial increases in foraging effort may be followed by reduced activity and/or metabolism. Many animals reduce their metabolic rate (by suppression of behaviours) so that energy and nutrient demands are lowered (Reynierse *et al*. 1972; Barton-Browne 1975; Bernays and Simpson 1982). Even so, reserves are still depleted: lipids providing 66% of the metabolic energy used by starving cockroaches,

glycogen 22% and protein 12% (Cervenkora 1960; Calow 1977; Jones 1977). Such deprivation increases mortality and reproductive deficiences (Durbin and Cochran 1985; Cochran 1985).

Blattella germanica compensate for short-term food deprivation by eating more in the first and subsequent days following food reinstatement (Barton-Browne 1975; Rollo 1984), but this effect eventually levels off (Gordon 1968). Table 10 shows that starved P. americana increased overall consumption. This was most notable in the 4-day compensation period as mean total consumption approached 70 mg/gm/day compared to 38 mg/gm/day for controls (Figs. 5 and 12). Feeding duration also increased during this period which supports the correlation between these variables (Figs. 4 and 11, Table 8). The increased duration was associated with lower consumption rates compared to controls for both carbohydrate and protein. This violates optimization theory which assumes that energy intake is maximized and constant (see Pyke 1984). Others have noted violations as well (see Sih 1982; Pyke 1984) and this has led several researchers to conclude that most animals are not optimal (Sih 1982; Lester 1984b; Munger 1984). Thus, P. americana and B. germanica compensate for starvation in a similar adaptive (but non-maximal) manner.

Problems with optimization theory also stem from the

time scale over which maximization is to be carried out (Pyke et al. 1977; Maynard-Smith 1978; Pyke 1984). Behaviour which maximizes energy intake over a lifetime may not be the same strategy which maximizes over a year, month or day.

Assuming that the time scale for maximization could be identified (e.g. monthly maximization), optimal foraging theory predicts that feeding would be constant over this period. Instead, the results supported a homeostatic response dependent on the physiological state. For example, the compensation period for the protein-starved treatment was 9 days (seven month depletion, see Figs. 7 and 8) compared to only 4 days for the starved treatment (20 day depletion, see Figs.11 and 12). As alluded to earlier, this may be the result of food quality differences or differing digestive periods.

Significant increases over controls in bout number and feeding duration for for both foods (Table 5, Figs. 10 and 11) suggests that feeding in starved cockroaches is regulated by both reserves. The dynamic interrelationship between these reserves accounts for the differences between the protein-starved and starved treatments. Since basal maintenance must be upheld, a simple solution would be to break down and mobilize non-limiting nutrients. Such catabolic processes may contribute to the synthesis or liberation of precursors for the limiting nutrient.

Starved cockroaches faced a negative nutrient balance which forced them to draw upon their long-term energy stores (see Fig. 16b) (Cervenkora 1960). Reinstatement of both foods reflected the desire for protein pellets as protein intake was three times greater than controls during the 3-day compensation period (Fig. 12). The long feeding durations (Fig. 11) were accompanied by inefficient consumption rates. After the compensation period, protein consumption rate was only slightly greater than controls, probably due to the reduced drive (resulting from the replenished deficit). As the stores became repleted, the protein feeding drive and feeding duration decreased. This was accompanied by an improved rate of intake compared to controls.

Carbohydrate consumption did not differ from controls during the compensation period even though duration increased. The resulting slower consumption rate may reflect limitations due to protein ingestion (Figs. 4, 5, 11 and 12). The slower carbohydrate ingestion rate carried over past the compensation period even though an increase in carbohydrate consumption was observed (Figs. 5 and 12). The results for both foods show that compensatory intake following starvation was achieved by increased duration even though intake rate declined (Leir and Barlow 1982).

In summary, starved cockroaches spent more time eating

and ingesting protein than carbohydrate (overall and during the compensation period) suggesting that starvation may deplete protein reserves to a greater extent than energy reserves. This was surprising because most optimality models assume that energy reserves are the most important. Also, recall that control cockroaches preferred carbohydrate. Thus, opposite decisions are made depending on the relative state of the reserves. Such results are typical of a homeostatic (rather than a maximizing) system. Finally, the results clearly show that multiple currencies exist (carbohydrate, protein, water etc.) and that the value of these currencies vary according to internal state. Thus, hypothesis 2 was rejected, starved cockroaches do not initially prefer carbohydrate over protein.

The ramifications of these results and those of the protein-starved suggest that reserve depletion may be ordered. For example, in both treatments it appears that the protein reserve was utilized before the energy reserves. This initially encouraged protein consumption over carbohydrate once food was introduced.

It is difficult to separate the effects of starvation and subsequent carbohydrate and protein consumption on drinking. Starved animals generally require less water than those fed "ad libitum" (McFarland 1965). In cockroaches, this is due to increased reabsorption, retention and metabolic water production (Faber 1975;

Simpson 1982; Cochran 1985; King et al. 1986). Roper and Crossland (1982) suggested that when starved animals eat, the causal factors stimulating drinking are low. As feeding continues, the causal factors for drinking rise, eventually matching controls. Thus drinking was expected to increase proportionally with feeding and since total feeding increased compared to controls, drinking was expected to increase as well. This did not occur (see Table 10). This was likely due to high blood volumes (drinking would aggravate this, see Fig. 16b). Research has shown that starved cockroaches become overhydrated (Wharton et al. 1965, Rollo 1984) and this would reduce drinking. This large water reserve might be adaptive since the cockroach has a larger blood volume through which to absorb nutrients once food is found.

The decreased drinking duration indicates that thirst was low but this result may be interpreted three ways: (a) a large water reserve was accumulated during starvation (to maintain survival?) or (b) a carry-over of reduced drinking during starvation occurred (Wall 1970; Wharton and Lola 1970; Mullins and Cochran 1974, 1975a, b; Heit et al. 1973; Tucker 1977a, b), or (c) the production of metabolic water and water conservation provided homeostasis (Wall and Oschman 1970; Mullins 1974; Mullins and Cochran 1974, 1975a, b).

Uric acid metabolism has been implemented in the latter interpretation. Cockroaches consuming high protein diets store urate salts (especially with K+) (Mullins and Cochran 1974, 1975a, b; Tucker 1977a, b; Cochran 1985) (Fig. 16b). This process liberates hydrogen ions which are buffered by phosphate and bicarbonate. The latter buffer with H+ ultimately dissociates into carbon dioxide and water (Wall and Oschman 1970; Mullins and Cochran 1974, 1975a, b). This metabolic water may offset drinking if produced in adequate quantities. The data support such a mechanism in starved cockroaches as protein consumption was greater than controls and drinking was reduced.

The reduced drinking may have contributed to the reduction of carbohydrate consumption (especially during the compensation period). This postulate is based on the strong link between these behaviours: as presented in the protein-starved discussion, carbohydrate consumption paralleled water intake for 20 days (Fig. 8) and their peaks coincided more often than protein and water (see Figs. 6-8).

V. Agar-Fed

Poor food quality has been linked to reduced stores and this has a negative impact on adult performance (Rose 1972; Slansky 1982). Poorly fed animals can increase their

fitness by increasing their food intake (Sih 1982; Slansky and Scriber 1985), often through increased duration (McNair 1982). Changing foods is another response (Mattson 1980; McNair 1983; Vickery 1984; Simpson and Abisgold 1985; Geissler and Rollo 1987). Some animals specialize on one food type until satiation is approached. Then, in order to minimize the time required to reach satiation, they may consume low value foods that would normally be ignored (Pyke 1984; Sih 1984). By minimizing feeding time, animals lower the risk of predation.

Both responses were exhibited by agar-fed cockroaches: Overall protein consumption increased significantly from controls (Table 5), paralleling an increase in overall consumption rate (Table 3). During the compensation period, protein consumption rate was much greater than controls and this carried over until the end of experiment (Figs. 4, 5, 14 and 15). The low intake of agar during the compensation period was likely due to the lack of stimulation from the sense organs. Yet, overall agar consumption was virtually the same as control carbohydrate consumption (Table 2). This surprising result was due to large agar ingestion after the 9-day compensation period (Fig. 15). The fact that cockroaches ate indigestible agar at all seems inexplicable (especially in terms of optimality arguments). Not only would the sensory stimulus

be low for agar pellets, but Geissler and Rollo's (1987) research suggests that well-nourished cockroaches should avoid novel foods (agar). Hypothesis 3 is accepted: cockroaches initially prefer protein over agar pellets.

With no available carbohydrate, the cockroaches may have increased their protein consumption as a substitute for energy. This is based on evidence that protein may be metabolized for energy under certain conditions (Geissler, unpublished).

Feeding responses usually require nutrients to be present in the food. Nutritious food selection is important: it is obvious that cockroaches were "zeroing in" on protein (Table 9- only 3 correlations were significant) as opposed to the agar pellets. Wigglesworth (1974) states that the cockroach's gut microflora can digest cellulose thereby liberating glucose. Yet, it is unlikely that the gut microflora can derive any nutrients from indigestible agar pellets. Consequently, it appears that the responses represent compensatory feeding on non-nutritious food. This clearly opposes optimality theory as non-nutritious foods should be ignored.

The postulation that large protein consumption reduces the necessity for water is supported in this treatment as well. Large decreases in drinking duration compared to controls occurred even though rates were elevated during the compensation period (Table 1, Figs. 4 and 14). But

this did not increase intake over controls (Figs. 5 and 15).

VI. Summary

The control results indicated that protein pellets were less desirable and harder to process than carbohydrate. Reduced protein consumption was accompanied by reduced feeding duration but a greater rate of consumption resulted compared to carbohydrate. Thus, maximizing uptake rate does not necessarily reflect desirability or actual total intake.

Several results linked drinking to carbohydrate consumption. Drinking may have provided lubrication or dilution of crop contents. Increased protein consumption has been shown to increase metabolic water production. It is speculated that this may reduce the need to drink (depending on the amount of water needed for nitrogenous waste excretion).

The results of the protein-starved, starved and agar-fed treatments strongly indicate that behaviour is a reflection of reserves. This has far-reaching implications when studying animal behaviour. In the future, studies must analyze behaviour as a function of the animal's physiological reserves.

Protein-starved cockroaches initially increased protein consumption. Unexpectedly, carbohydrate consumption increased as well. It is speculated that increased protein metabolism utilized available carbohydrates, thus creating a need for dietary sugars (energy). Reiterating, it may be easier to use dietary sugars directly from the haemolymph rather than mobilizing energy from storage. In fact, it is possible that the energy reserves were not used at all.

The starved treatment tested the validity of optimality theory. The hypothesis was rejected: starved cockroaches do not initially prefer carbohydrate. This indicated that starving cockroaches use more of their protein reserves (at least initially) compared to energy reserves.

The agar-fed experiment showed that cockroaches choose nutrition (protein) over bulk (agar), but it was totally surprising that non-nutritious agar was consumed at all.

The starved and agar-fed experiments resulted in the strongest evidence opposing optimal foraging theory. This study revealed that three major reserves are monitored: fat body energy, fat body uric acid and blood water supply. The data showed that these reserves fluctuate in size and feeding responds strongly to offset these fluctuations. Optimality assumes that the animal's physiology is largely invariant over time. This study disclosed the apparent

instability of cockroach feeding. This instability was a direct result of peaks resulting from overshoot/undershoot dynamics as the cockroach attempted to maintain homeostasis. Also, cockroaches may focus on several currencies (carbohydrate, protein, water, etc.) and the value of these currencies may vary according to internal state. Optimality assumes one currency (energy) and its value remains constant. Cockroaches ate indigestible agar which also opposes optimality theory. Finally, this study consistently showed that cockroaches do not maximize intake nor do they minimize time. (However, the amount of time required to eat or drink was remarkably short). Rather, they eat to fulfill a motivation caused by a reserve deficit. This was often represented by longer feeding periods, usually at slower intake rates. Consequently, despite large initial compensatory responses, long-term intake was similar or only slightly greater than controls.

Thus cockroaches displayed flexible behavioural strategies linked to dynamics of storage reserves and food type. Adaptive (but non-maximal) responses exceeding controls were elicited frequently and were characterized by longer activity durations (which cannot be circumvented due to consumption constraints). Consequently, this necessitated longer compensation periods to attain physiological homeostasis.

The behavioural and physiological models (Fig. 16a and b) indicate that all parts are dynamically linked. Tradeoffs among components preclude optimization of any single part. Perhaps for this reason the structure of Figs. 16a and 16b is almost totally inconsistent with an optimality framework. Figures 16a and 16b are capable of predicting daily consumption, feeding duration and consumption rate. Future research is necessary to extend the resolution to the sub-components comprising these models and the dynamics of their interaction.

The overall findings of this thesis strongly support an experimental components framework underlying feeding regulation. This framework has a homeostatic nature and involves large reserve interactions. The hypotheses of optimal foraging theory are not supported and appear to be relatively irrelevant.

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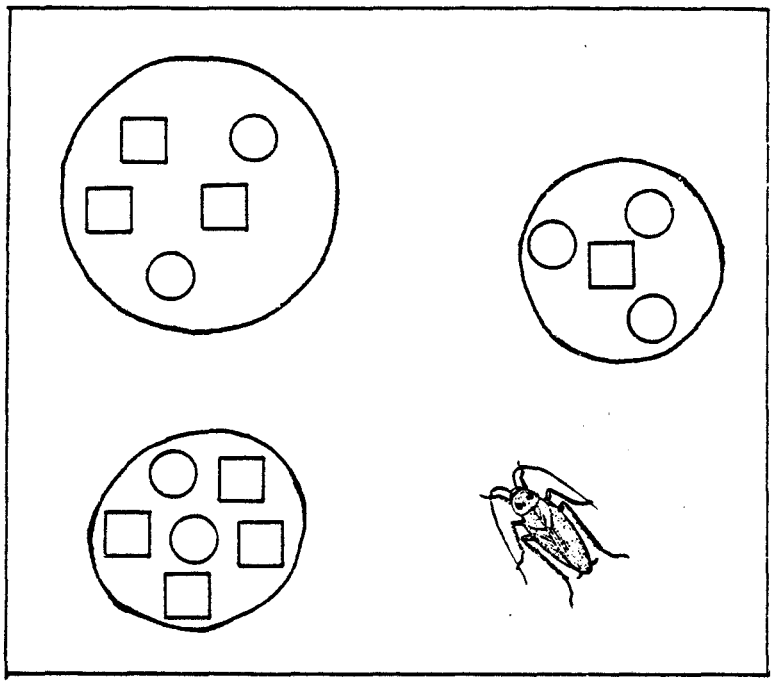
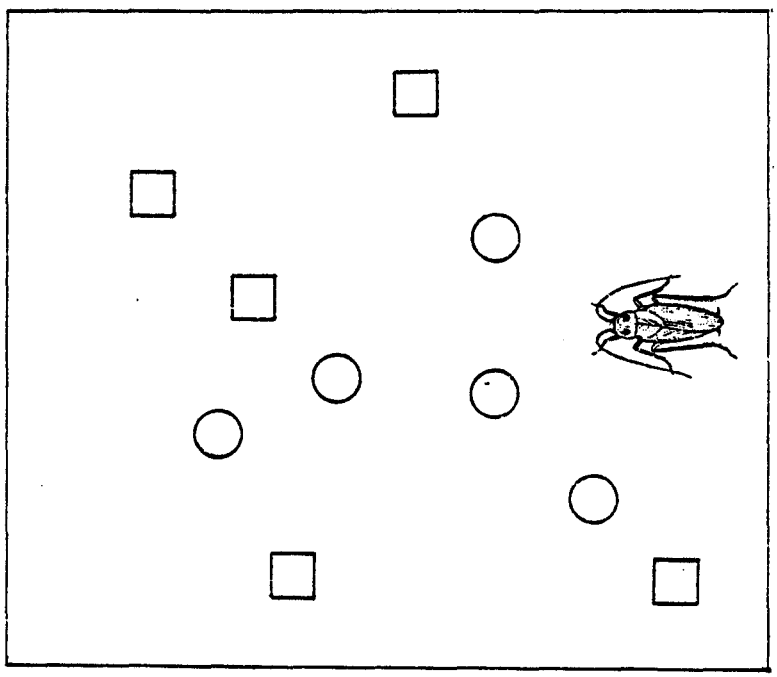
Figure 1a. The first level of optimal foraging theory considers choice of patches and decisions about changing patches. Patches contain food differing in quality, distribution and abundance. Note: the insert lists compounds which are (a) considered when choosing food and (b) subsequently altered quantitatively.

Figure 1b. Once in a patch, the animal must decide which food items to ingest. This is the second level of optimal foraging theory. This thesis is primarily concerned with choices between either protein (nutrients) or sugar (energy).





water
PROTEIN
CARBOHYDRATE
lipids
uric acid salts
vitamins / minerals
bulk

Figure 1c. Components of cockroach physiology involved in regulation of food and water balance showing the major types of interactions. The model was synthesized from the literature and provided a framework for investigating the behavioural effects resulting from fat body alteration. This represents a third level of foraging theory as well as the transition from the organism to physiological levels.

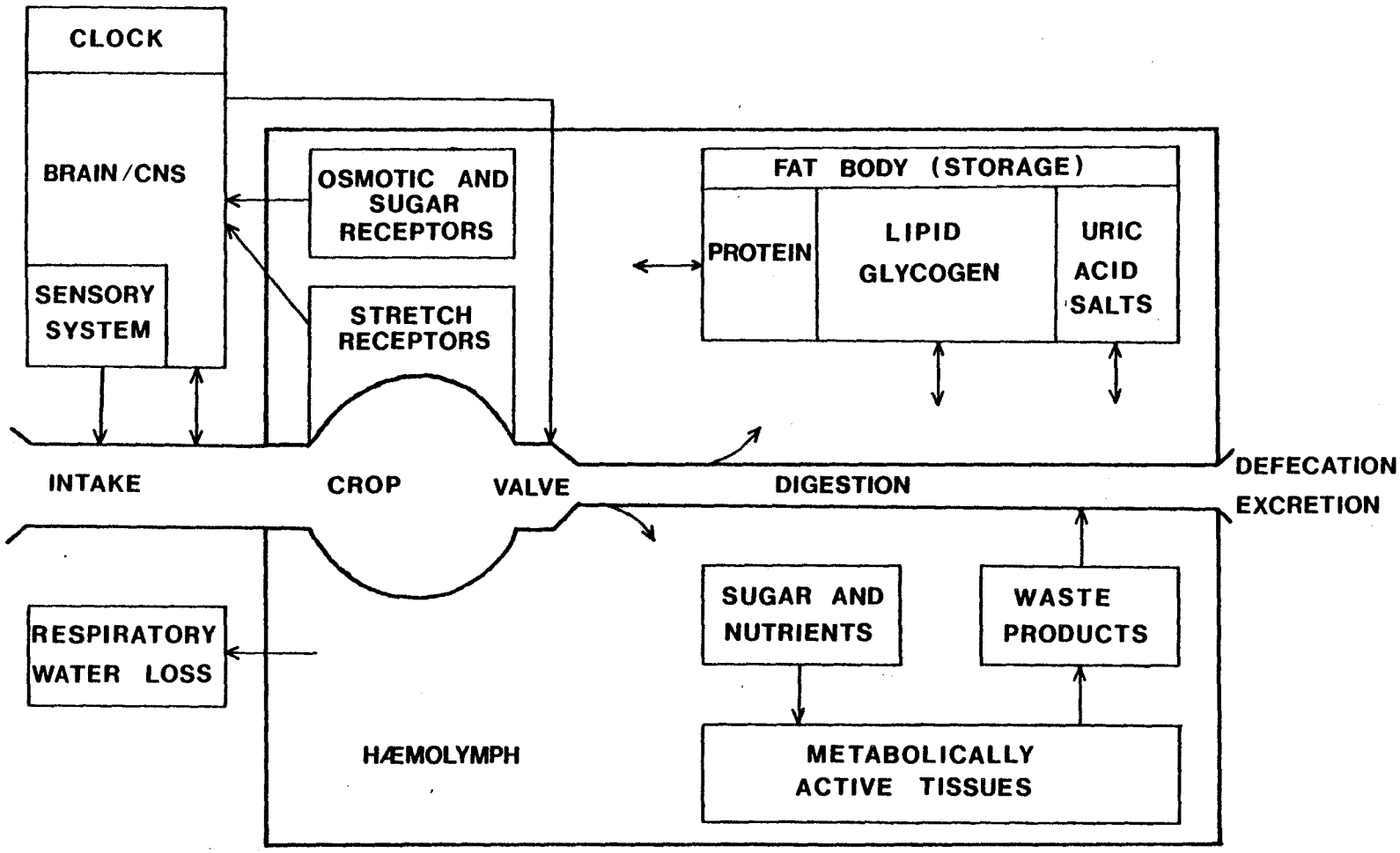

CLOCK
BRAIN/CNS
SENSORY SYSTEM
OSMOTIC AND SUGAR RECEPTORS
STRETCH RECEPTORS
FAT BODY (STORAGE)
PROTEIN
LIPID
GLYCOGEN
URIC ACID SALTS
INTAKE
CROP
VALVE
DIGESTION
DEFECATION
EXCRETION
RESPIRATORY WATER LOSS
SUGAR AND NUTRIENTS
WASTE PRODUCTS
HÆMOLYMPH
METABOLICALLY ACTIVE TISSUES

Figure 2. The experimental habitat.
PN- protein pellet
CHOH- sugar pellet
PIA- peripheral interface adaptor

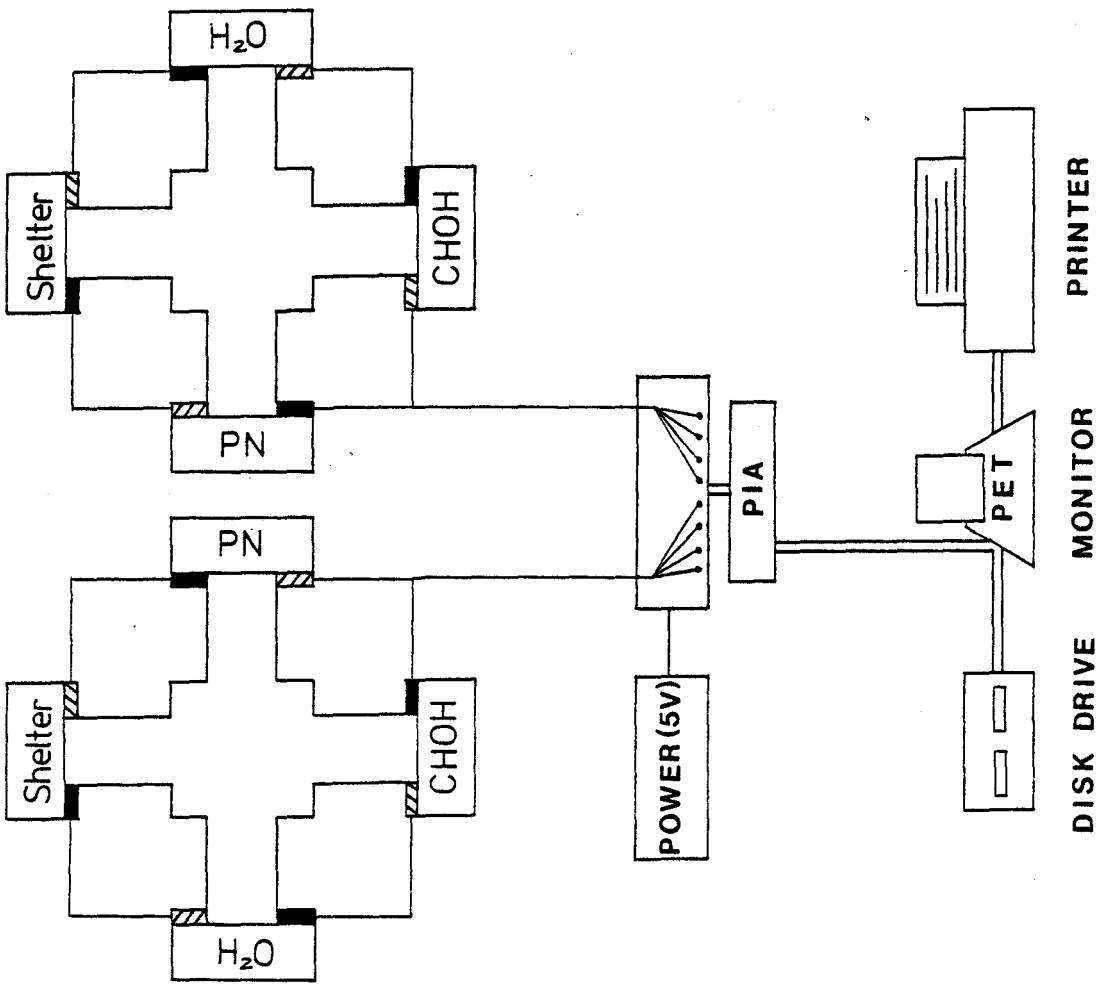
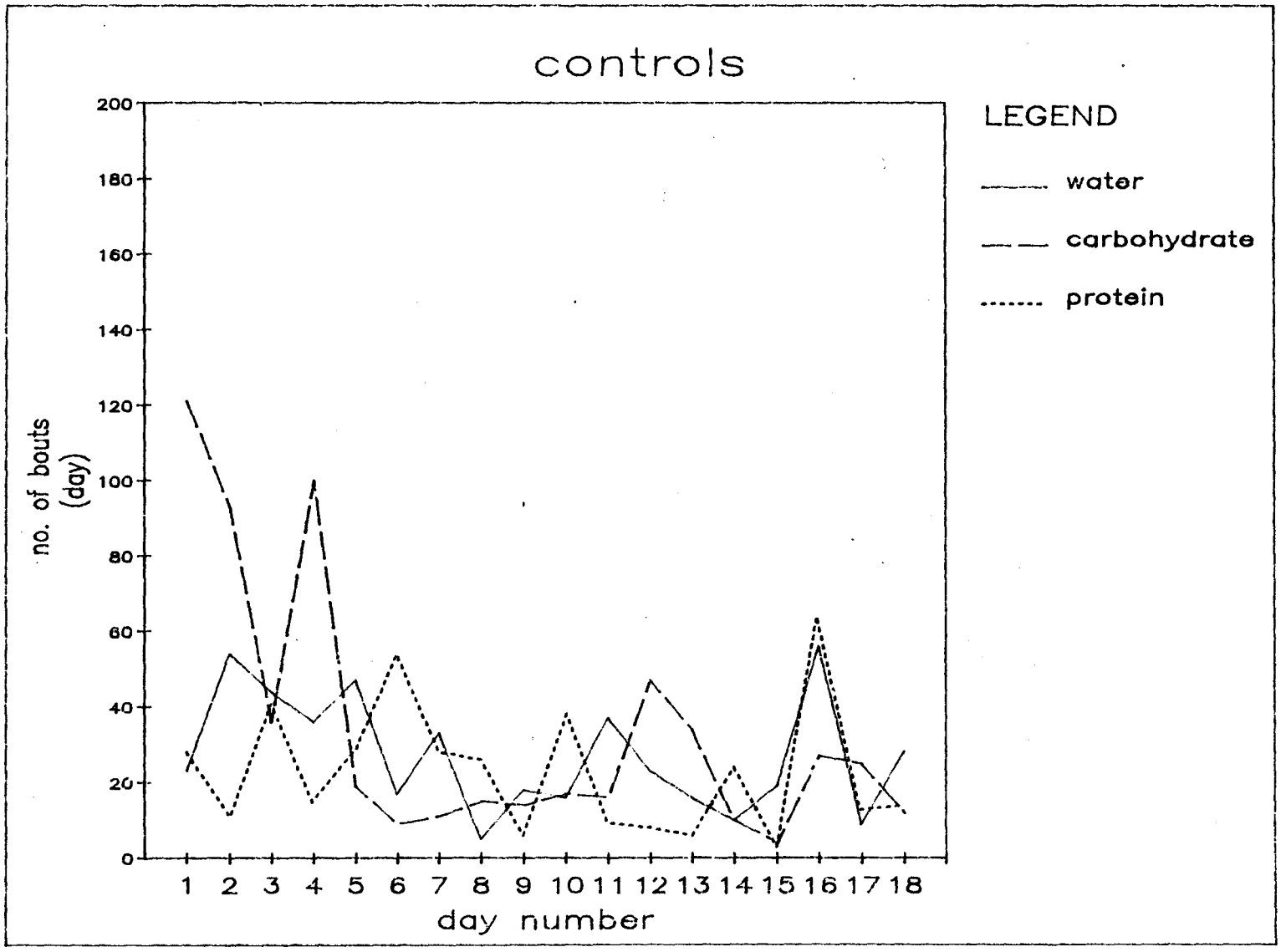
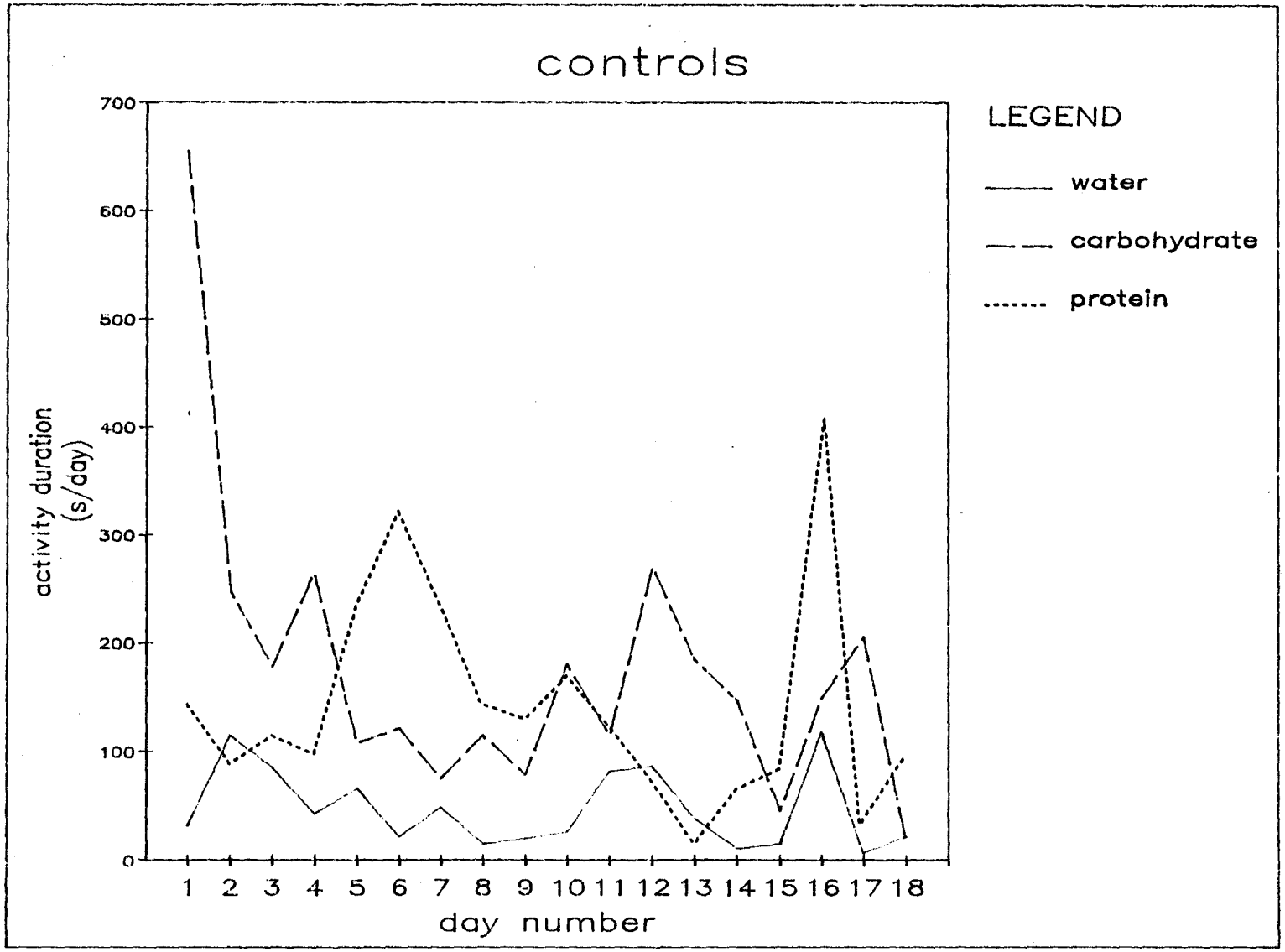

H₂O
Shelter
CHOH
PN
PN
Shelter
CHOH
H₂O
POWER(5V)
PIA
PET
PRINTER
MONITOR
DISK DRIVE

Figure 3. The overall patterns of mean bout number for water, carbohydrate and protein. Means were derived from 4 male control cockroaches. Observations were based on a total of 64 days (512 hours of scotophase).


controls
LEGEND
water
carbohydrate
protein
no. of bouts (day)
200
180
160
140
120
100
80
60
40
20
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
day number

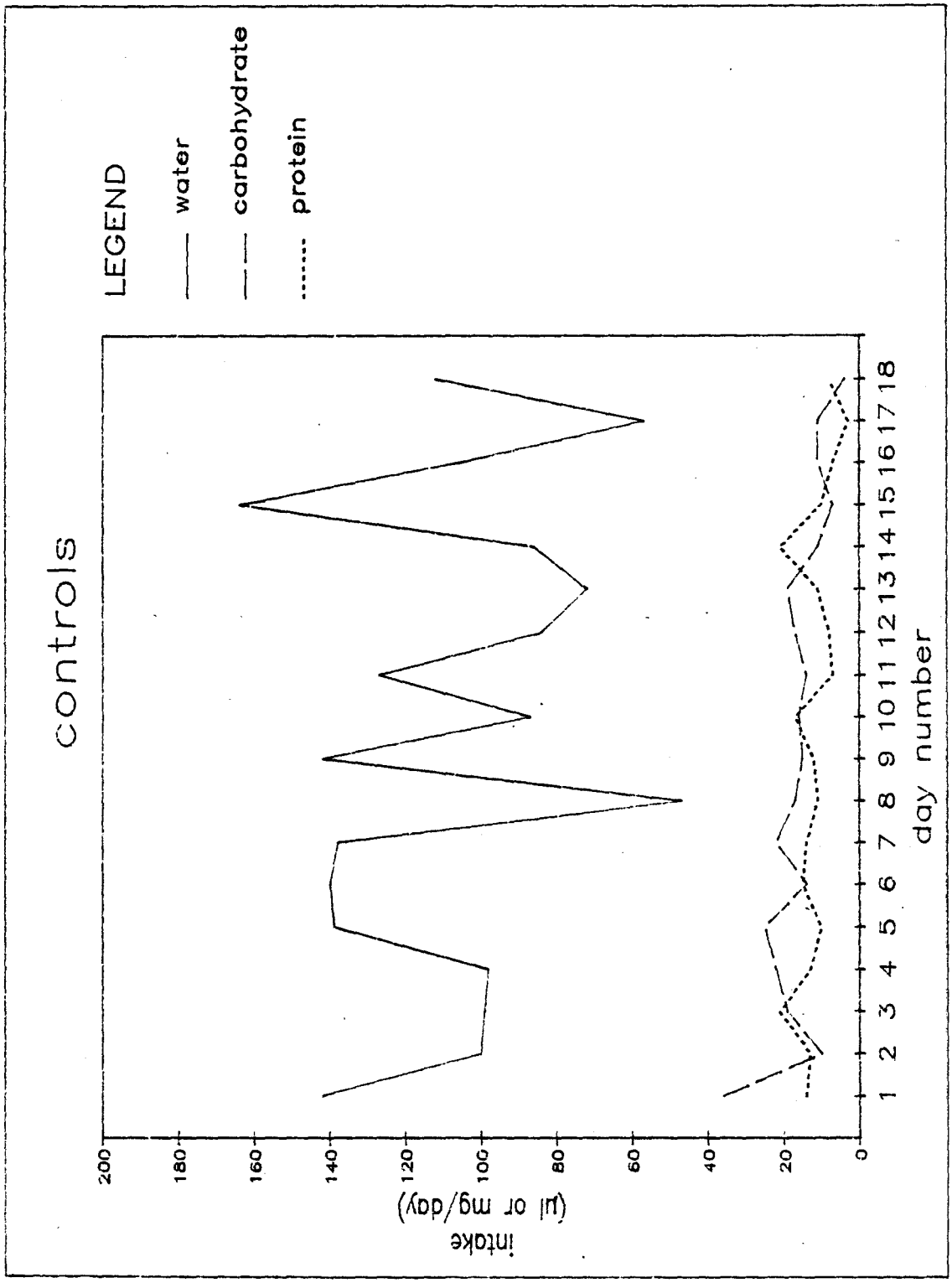
CONTROLS

Figure 4. The overall patterns of mean activity duration for water, carbohydrate and protein. Means were derived from 4 male control cockroaches. Observations were based on a total of 64 days (512 hours of scotophase).


controls
LEGEND
water
carbohydrate
protein
activity duration (s/day)
700
600
500
400
300
200
100
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
day number

CONTROLS

Figure 5. The overall patterns of mean intake for water, carbohydrate and protein. Means were derived from 4 male control cockroaches. Observations were based on a total of 64 days (512 hours of scotophase).


controls
LEGEND
water
carbohydrate
protein
intake
(ul or mg/day)
200
180
160
140
120
100
80
60
40
20
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
day number

PROTEIN-STARVED

Figure 6. The overall patterns of mean bout number for water, carbohydrate and protein. Means were derived from 4 male protein-starved cockroaches. Observations were based on a total of 96 days (768 hours of scotophase).

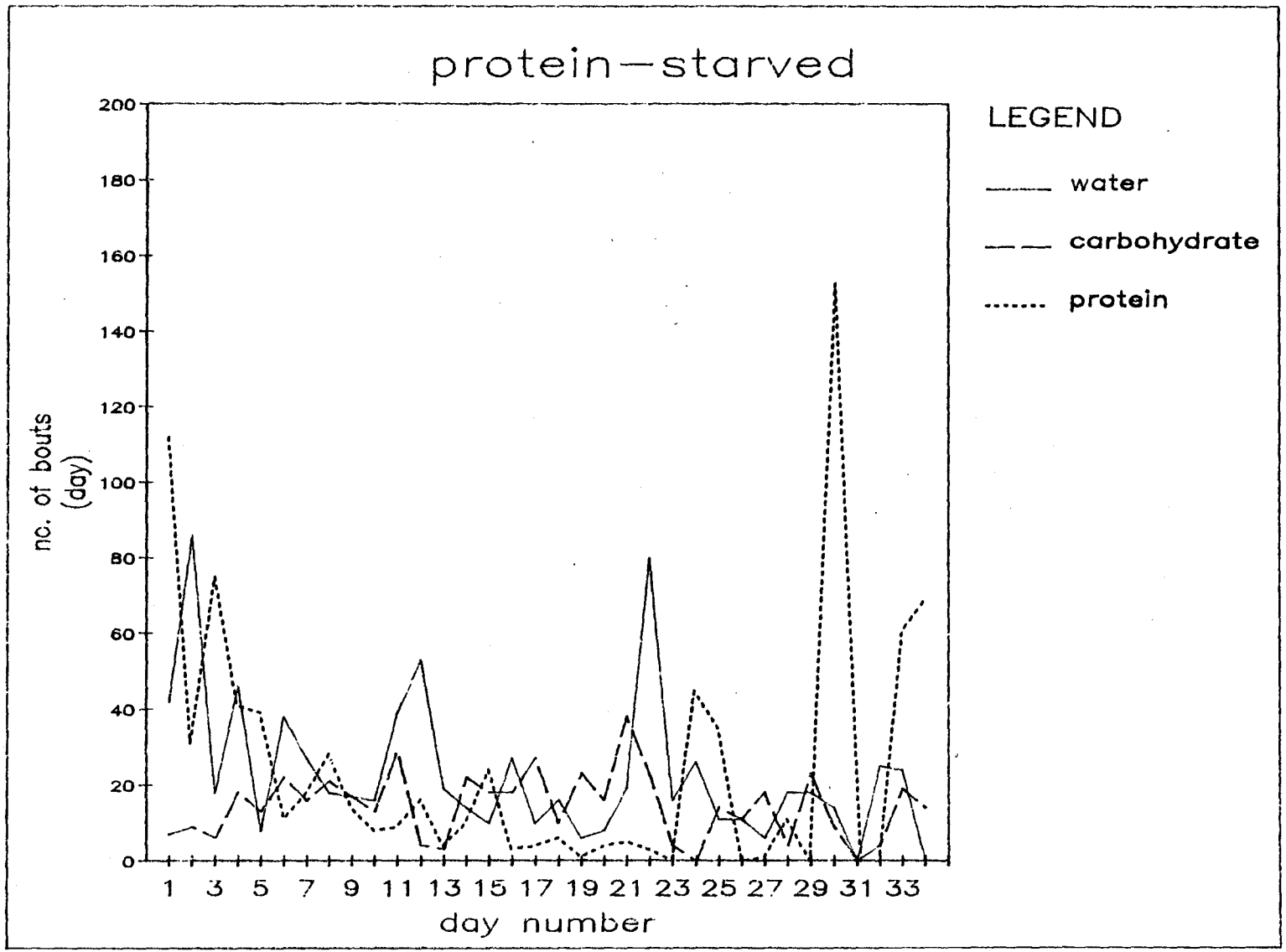
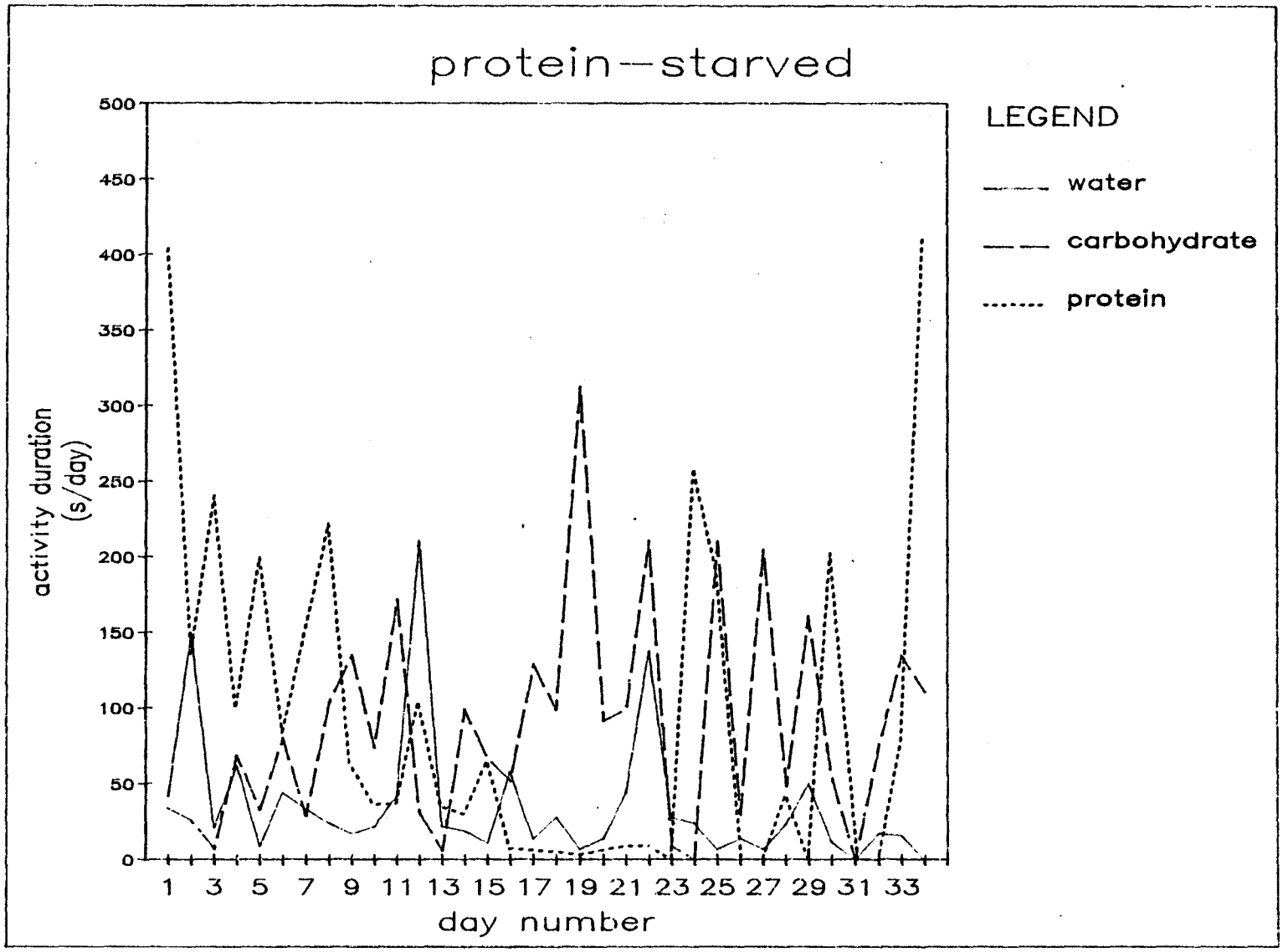
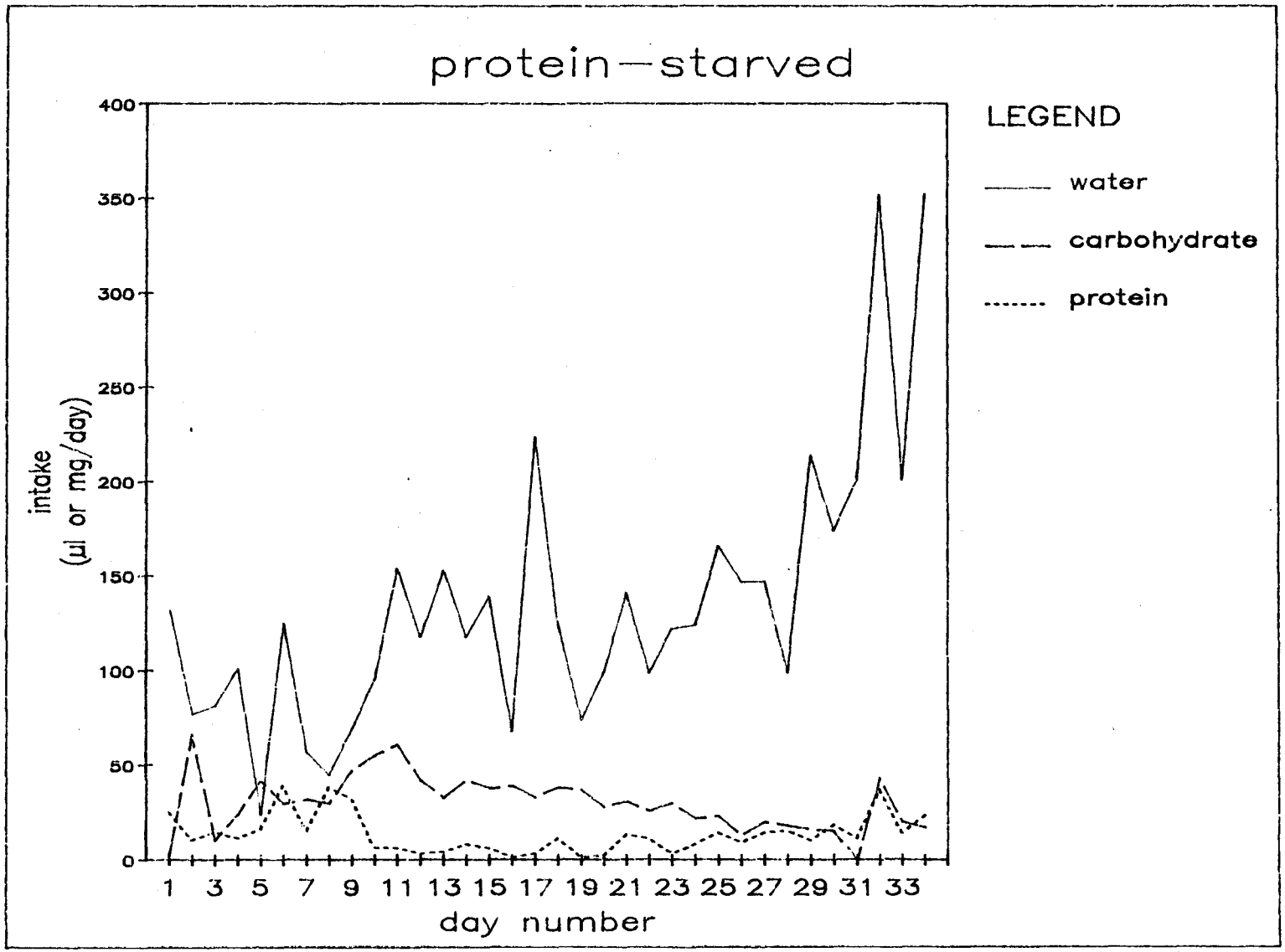

protein—starved
LEGEND
water
carbohydrate
protein
no. of bouts (day)
200
180
160
140
120
100
80
60
40
20
0
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33
day number

Figure 7. The overall patterns of mean activity duration for water, carbohydrate and protein. Means were derived from 4 male protein-starved cockroaches. Observations were based on a total of 96 days (768 hours of scotophase).


protein—starved
LEGEND
water
carbohydrate
protein
activity duration (s/day)
500
450
400
350
300
250
200
150
100
50
0
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33
day number

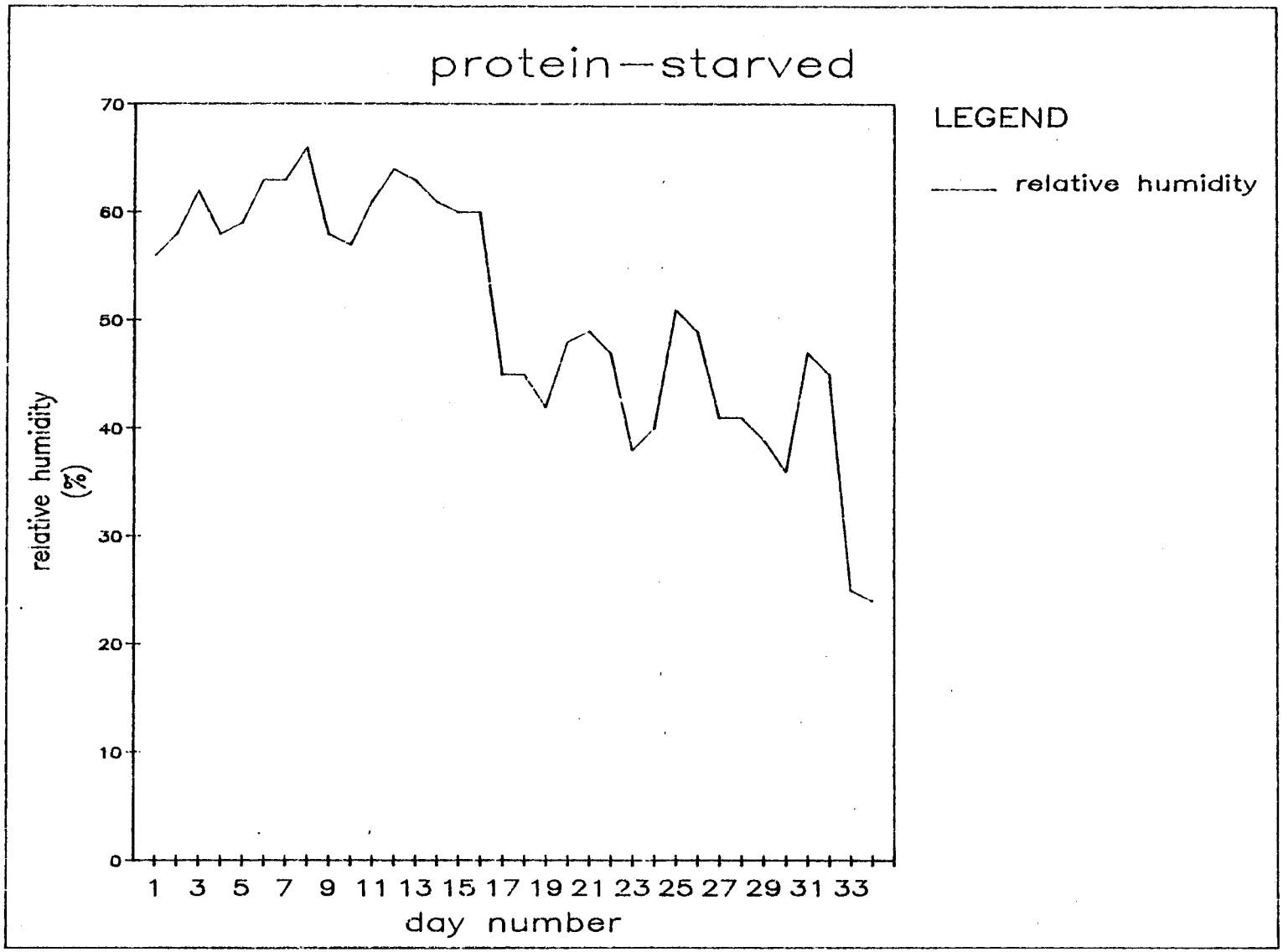
PROTEIN-STARVED

Figure 8. The overall patterns of mean intake for water, carbohydrate and protein. Means were derived from 4 male protein-starved cockroaches. Observations were based on a total of 96 days (768 hours of scotophase).


protein—starved
LEGEND
water
carbohydrate
protein
intake
(µl or mg/day)
400
350
300
250
200
150
100
50
0
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33
day number

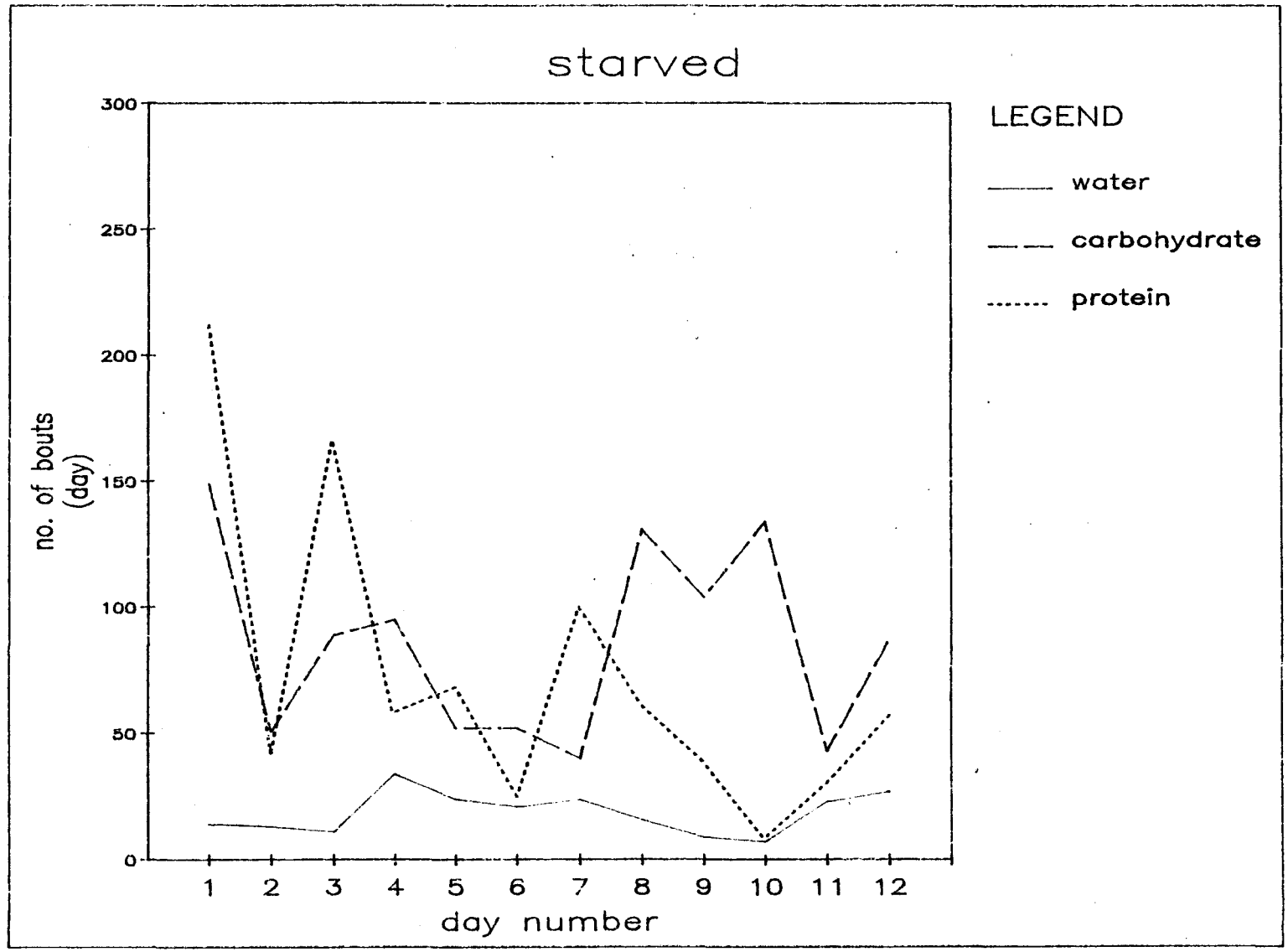
PROTEIN-STARVED

Figure 9. The overall pattern of mean relative humidity for the protein-starved treatment. Means are derived from 4 male cockroaches observed over 96 days.


protein—starved
LEGEND
relative humidity
relative humidity (%)
70
60
50
40
30
20
10
0
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33
day number

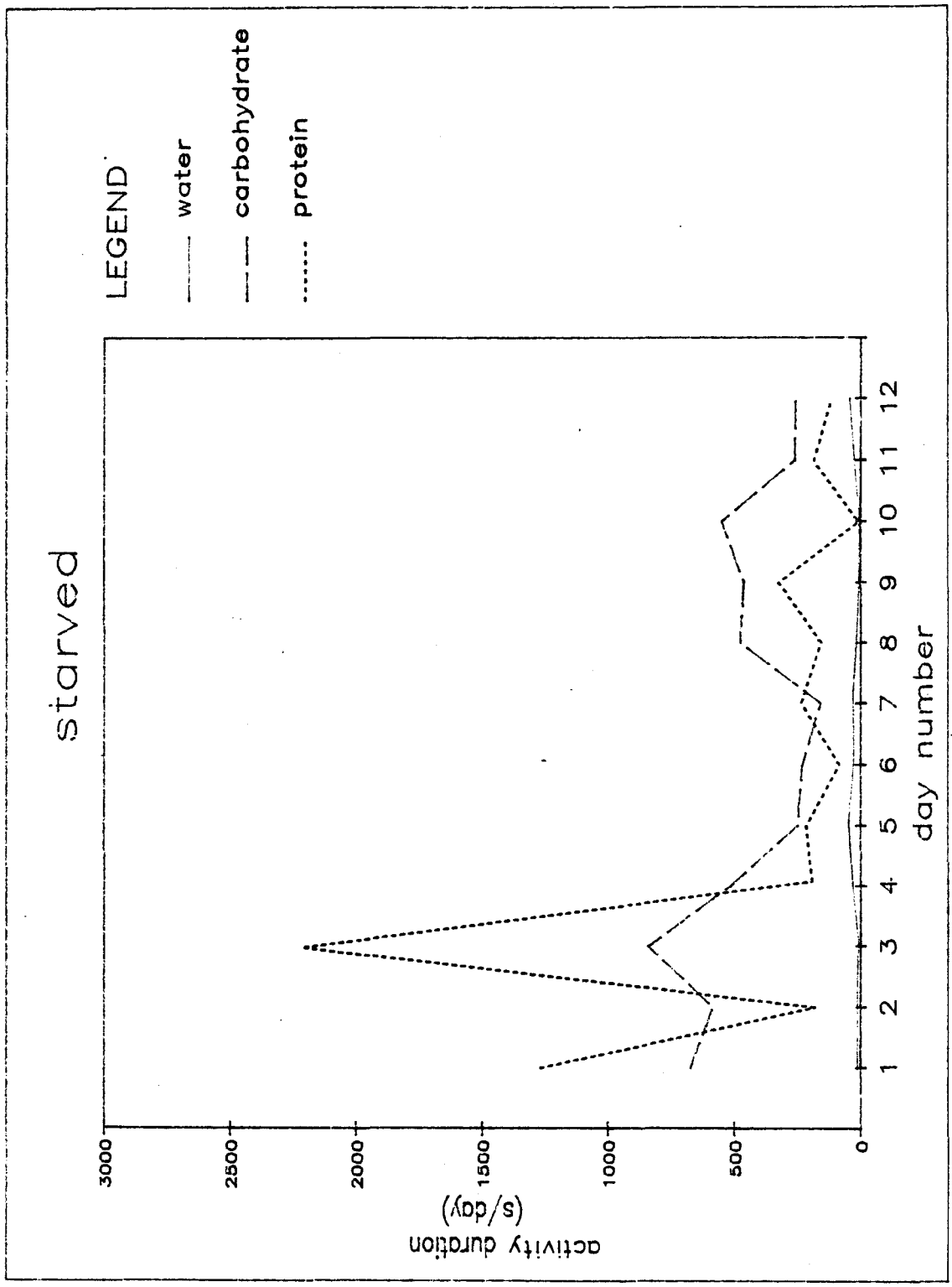
STARVED

Figure 10. The overall pattern of mean bout number for water, carbohydrate and protein. Means were derived from 2 male starved cockroaches. Observations were based on a total of 24 days (192 hours of scotophase).


starved
LEGEND
water
carbohydrate
protein
no. of bouts (day)
300
250
200
150
100
50
0
1
2
3
4
5
6
7
8
9
10
11
12
day number

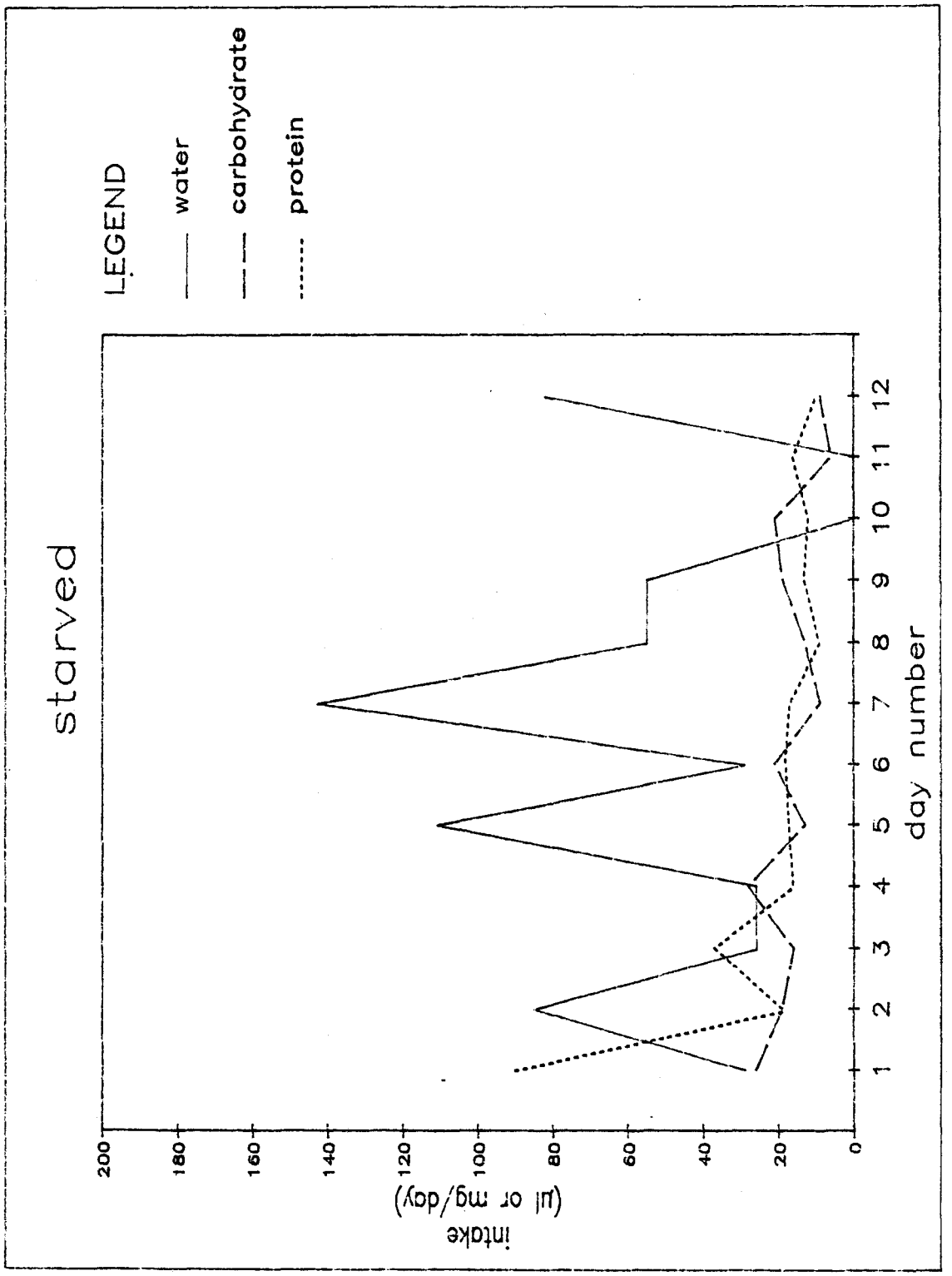
STARVED

Figure 11. The overall pattern of mean activity duration for water, carbohydrate and protein. Means were derived from 2 male starved cockroaches. Observations were based on a total of 24 days (192 hours of scotophase).


starved
LEGEND
water
carbohydrate
protein
activity duration
(s/day)
3000
2500
2000
1500
1000
500
0
1 2 3 4 5 6 7 8 9 10 11 12
day number

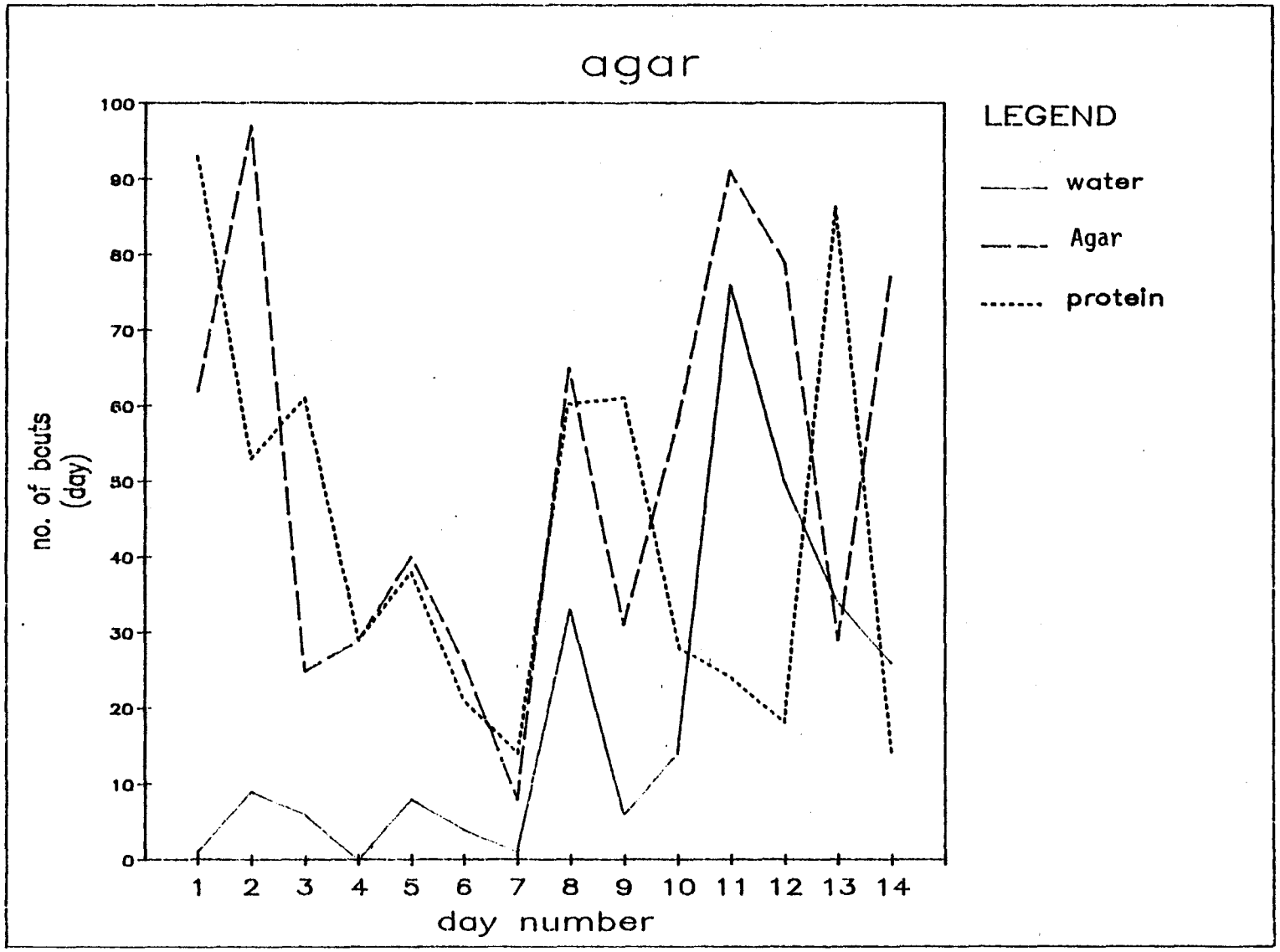
STARVED

Figure 12. The overall pattern of mean intake for water, carbohydrate and protein. Means were derived from 2 male starved cockroaches. Observations were based on a total of 24 days (192 hours of scotophase).


starved
LEGEND
water
carbohydrate
protein
intake
(µl or mg/day)
200
180
160
140
120
100
80
60
40
20
0
1 2 3 4 5 6 7 8 9 10 11 12
day number

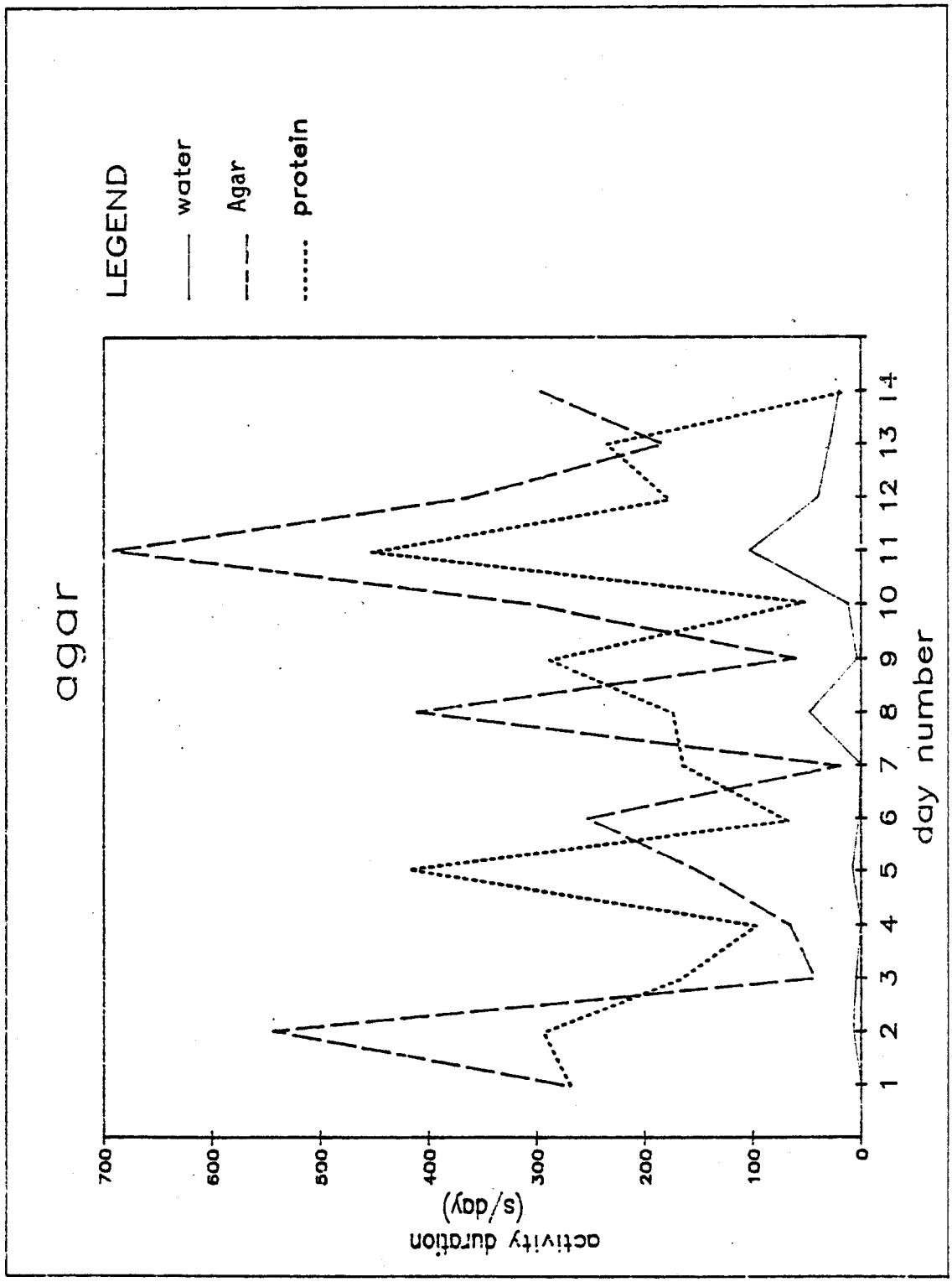
AGAR-FED

Figure 13. The overall pattern of mean bout number for water, carbohydrate and protein. Means were derived from 2 male agar-fed cockroaches. Observations were based on a total of 28 days (224 hours of scotophase).


agar
LEGEND
water
Agar
protein
no. of bouts (day)
day number
0
10
20
30
40
50
60
70
80
90
100
1 2 3 4 5 6 7 8 9 10 11 12 13 14

AGAR-FED

Figure 14. The overall pattern of mean activity duration for water, carbohydrate and protein. Means were derived from 2 male agar-fed cockroaches. Observations were based on a total of 28 days (224 hours of scotophase).


agar
LEGEND
water
Agar
protein
activity duration
(s/day)
700
600
500
400
300
200
100
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14
day number

AGAR-FED

Figure 15. The overall pattern of mean intake for water, carbohydrate and protein. Means were derived from 2 male agar-fed cockroaches. Observations were based on a total of 28 days (224 hours of scotophase).

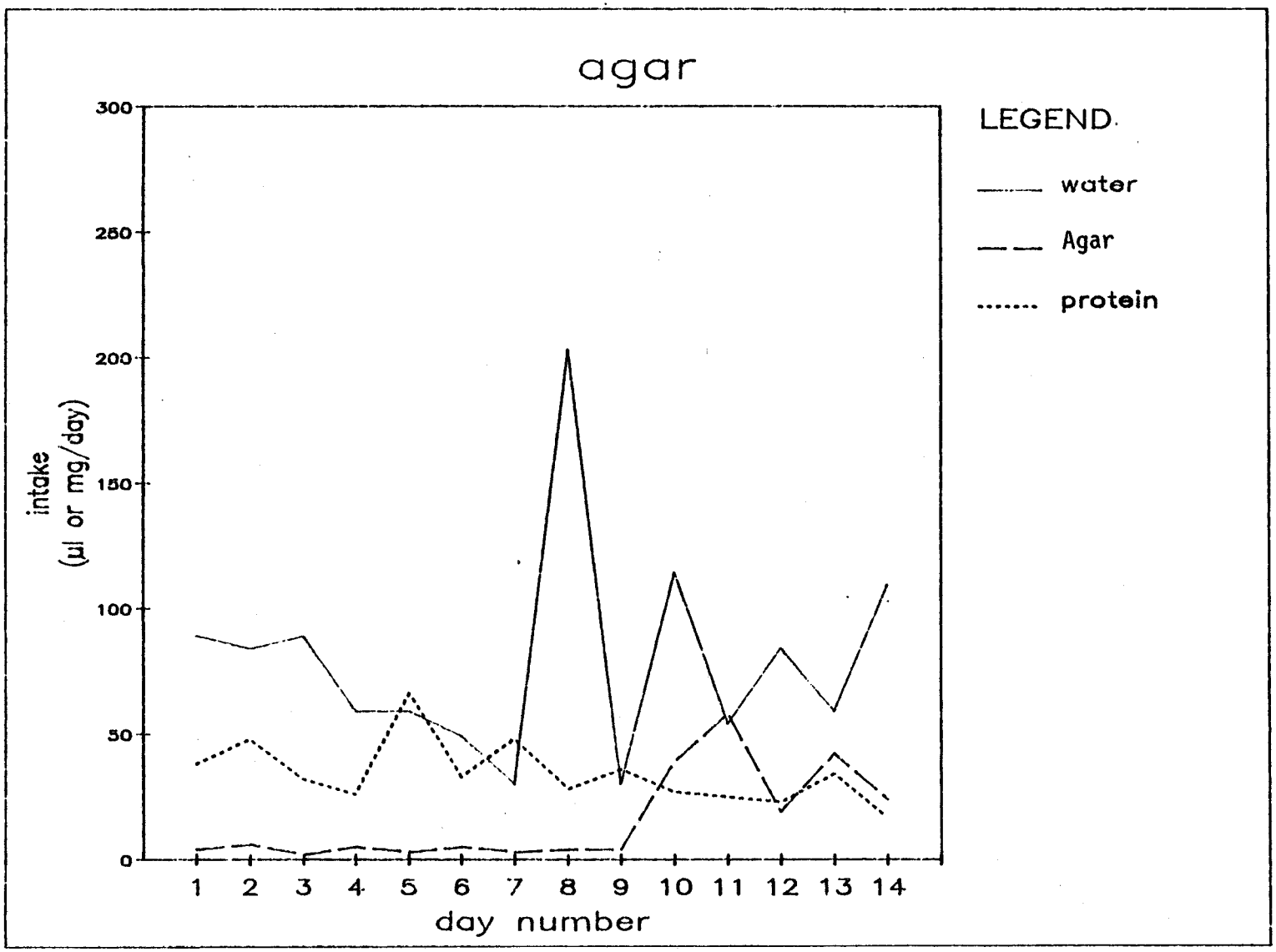

agar
300
250
200
150
100
50
0
intake
(µl or mg/day)
1 2 3 4 5 6 7 8 9 10 11 12 13 14
day number
LEGEND
water
Agar
protein

Figure 16a. The behavioural model. This model represents decision flow based on reserve status. The decision routine is influenced by feedback from the physiological model.

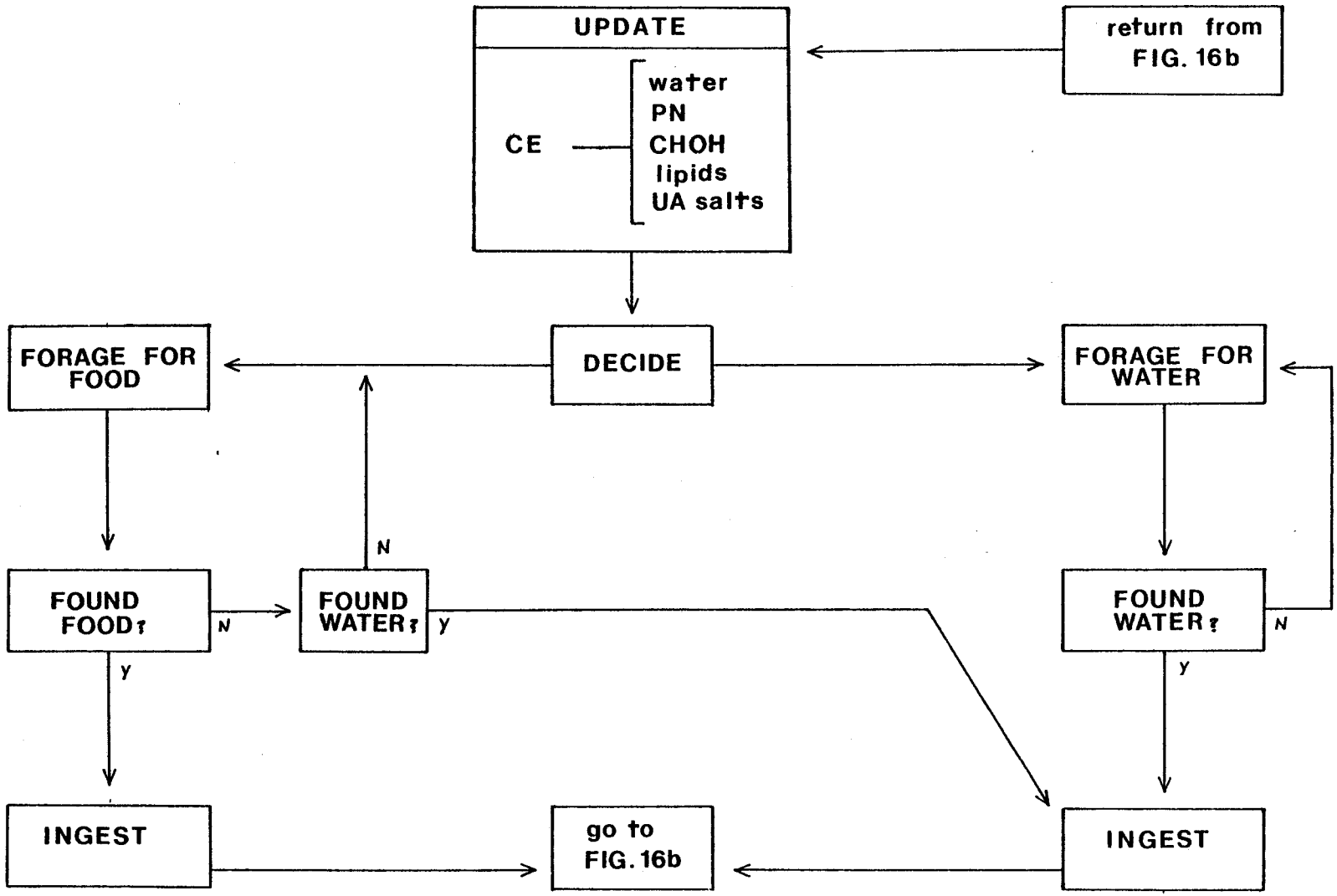
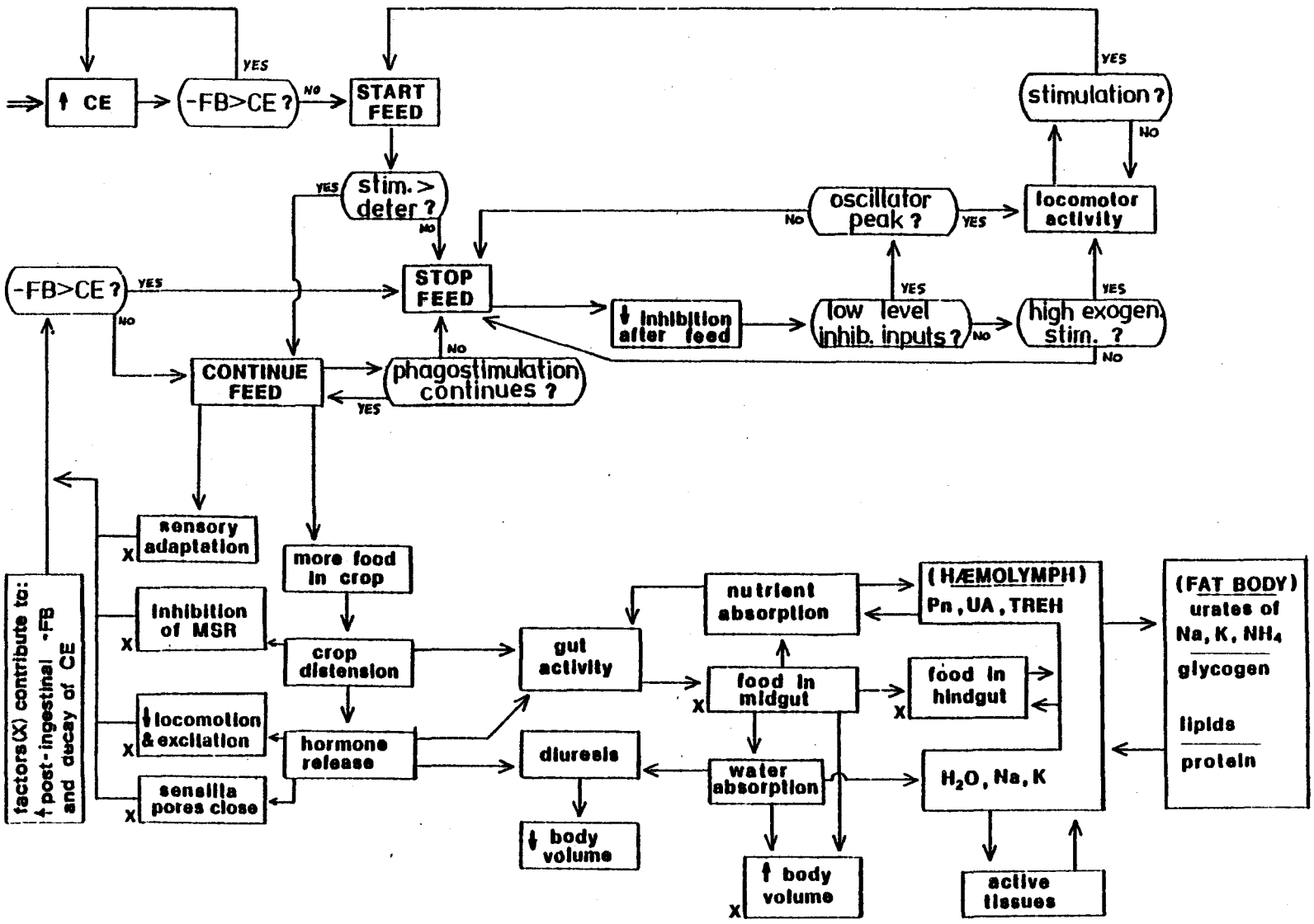

UPDATE
CE
water
PN
CHOH
lipids
UA salts
return from FIG. 16b
FORAGE FOR FOOD
DECIDE
FORAGE FOR WATER
FOUND FOOD?
FOUND WATER?
FOUND WATER?
N
N
N
y
y
y
INGEST
go to FIG. 16b
INGEST

Figure 16b. The physiological model. Speculations concerning physiological mechanisms were primarily based on food choice.

CE -central excitability
-FB -negative feedback
Pn -protein
UA -uric acid
TREH-trehalose
MSR -mechano/sensory receptors


↑ CE
-FB>CE ?
YES
NO
START FEED
stimulation ?
YES
NO
stim.> deter ?
YES
NO
oscillator peak ?
No
YES
locomotor activity
-FB>CE ?
YES
NO
STOP FEED
↓ inhibition after feed
low level inhib. inputs ?
YES
No
high exogen. stim. ?
YES
NO
CONTINUE FEED
phagostimulation continues ?
NO
YES
factors(X) contribute to: ↑post-ingestinal -FB and decay of CE
sensory adaptation
X
more food in crop
Inhibition of MSR
X
crop distension
↓locomotion & excitation
X
hormone release
sensilla pores close
X
gut activity
nutrient absorption
(HÆMOLYMPH) Pn, UA, TREH
(FAT BODY) urates of Na, K, NH4 glycogen lipids protein
food in midgut
X
food in hindgut
X
diuresis
water absorption
H2O, Na, K
↓ body volume
↑ body volume
X
active tissues

WATER

Table 1. Daily means (+/-SE) for each variable and treatment for drinking behaviour. These tables ignore the compensatory response.

Controls	n=64 days
Protein-starved	n=96 days
Starved	n=24 days
Agar-fed	n=28 days

WATER

Treatment		no. of Blocks (day)	Block Duration (s/day)	no. of Bouts (day)	Drinking Duration (s/day)	Non-Drinking Time (s/day)	Intake (uL/gm/ day)	Bout length (s)	Bout size (uL/gm)	Drinking Rate (uL/gm/s)
Control	mean	1.7656	393.3606	27.0469	48.3733	344.9873	107.6420	1.2312	6.2778	6.8641
	± SE	0.1694	107.3558	3.3080	9.3003	103.7183	9.1417	0.1304	1.2701	1.3453
Protein-	mean	1.5104	462.3889	25.6250	41.8205	420.5683	117.0855	1.2192	7.9206	8.3403
Starved	± SE	0.1607	169.6388	3.5361	7.4570	166.8603	9.5896	0.1252	1.1774	1.6921
Starved	mean	1.5000	194.1571	18.4583	23.8171	170.3400	53.4283	1.0079	3.1529	4.0200
	± SE	0.2125	111.5076	3.6020	5.5037	108.0314	11.1410	0.1056	1.2382	2.3079
Agar	mean	1.1429	316.6443	18.8571	19.9018	296.7425	79.4136	0.7450	7.5332	11.9189
	± SE	0.2002	175.2778	6.0110	6.1033	172.0493	15.0704	0.1999	2.7387	5.1955

CARBOHYDRATE

Table 2. Daily means (+/-SE) for each variable and treatment for carbohydrate feeding behaviour. hese tables ignore the compensatory response.

Controls	n=64 days
Protein-starved	n=96 days
Starved	n=24 days
Agar-fed	n=28 days

Note: carbohydrate was replaced by agar for the agar-fed treatment.

CARBOHYDRATE

Treatment		no. of Blocks (day)	Block Duration (s/day)	no. of Bouts (day)	Feeding Duration (s/day)	Non-Feeding Time (s/day)	Consumption (mg/gm/day)	Bout length (s)	Bout size (mg/gm)	Feeding Rate (mg/gm/s)
Control	mean	1.8281	446.0323	35.9688	184.4331	261.5992	17.1045	7.6523	0.8883	0.1578
	± SE	0.2008	101.2644	7.9330	29.9533	77.9433	1.7172	1.3386	0.1524	0.0512
Protein-Starved	mean	1.2813	168.4768	14.7396	80.3090	88.1678	32.9459	5.1416	3.8606	3.0836
	± SE	0.1069	26.2466	1.5710	10.0644	22.5369	2.9695	0.7157	0.9054	1.4167
Starved	mean	2.7083	2417.3158	85.3333	439.2508	1978.0650	16.7529	5.8967	0.2433	0.0550
	± SE	0.2601	671.5601	12.7210	81.7223	664.4867	2.4025	1.6006	0.0464	0.0068
Agar	mean	2.2857	2036.4379	51.0714	261.9086	1774.5293	15.5629	4.8664	0.3714	0.1146
	± SE	0.2806	890.6374	9.4410	61.8063	859.7027	4.6860	0.8339	0.0808	0.0287

PROTEIN

Table 3. Daily means (+/-SE) for each variable and treatment for protein feeding behaviour. These tables ignore the compensatory response.

Controls	n=64 days
Protein-starved	n=96 days
Starved	n=24 days
Agar-fed	n=28 days

PROTEIN

Treatment		no. of Blocks (day)	Block Duration (s/day)	no. of Bouts (day)	Feeding Duration (s/day)	Non-Feeding Time (s/day)	Consumption (mg/gm/day)	Bout length (s)	Bout size (mg/gm)	Feeding rate (mg/gm/s)
Control	mean	1.5781	369.4216	23.0313	142.0358	227.3858	12.5420	6.5820	1.2145	0.8381
	± SE	0.1479	84.7514	4.4748	25.9324	73.8754	1.1230	1.2114	0.3389	0.3749
Protein-Starved	mean	1.5417	312.1231	25.2292	100.0110	212.1121	13.3340	2.7451	0.7995	0.7624
	± SE	0.2234	80.0335	4.7717	16.0612	74.7634	1.7664	0.4225	0.2041	0.3682
Starved	mean	2.7083	997.7237	72.0417	432.5925	565.1313	22.8587	4.7700	0.7008	0.3912
	± SE	0.2318	321.9209	18.1138	177.0723	176.8153	5.5542	1.0611	0.1803	0.1286
Agar	mean	2.5000	2307.5993	42.6429	205.3771	2102.2221	34.3029	5.2989	3.0818	2.4175
	± SE	0.2967	970.6679	8.1580	40.9250	970.5387	2.9259	1.0325	1.0367	1.6277

Table 4. Analysis of variance for each behaviour. Variables which differed significantly between treatments were further analyzed by Duncan's multiple range test (see Table 5).

		F-ratio	D.F.	r	Significance
WATER					
Treatment	vs BTS	0.828	3,208	0.109	0.480
Treatment	vs DUR	1.703	3,208	0.155	0.167
Treatment	vs INTK	4.642	3,208	0.250	0.004 *
Treatment	vs RATE	1.100	3,208	0.125	0.350
CARBOHYDRATE					
Treatment	vs BTS	17.177	3,208	0.446	0.001 *
Treatment	vs DUR	17.174	3,208	0.446	0.001 *
Treatment	vs INTK	8.647	3,208	0.333	0.001 *
Treatment	vs RATE	1.740	3,208	0.156	0.160
PROTEIN					
Treatment	vs BTS	6.828	3,208	0.299	0.001 *
Treatment	vs DUR	6.463	3,208	0.292	0.001 *
Treatment	vs INTK	14.304	3,208	0.414	0.001 *
Treatment	vs RATE	1.307	3,208	0.136	0.273

* Significant difference at 5% level of probability - see Duncan analysis (Table 5).

Table 5. Duncan's multiple range test of variables which differed significantly between treatments for each behaviour.

* indicates a significant difference between the two treatments involved. For example, water intake differed significantly between controls and starved, protein-starved and starved and protein-starved and agar-fed.

Note: carbohydrate was replaced by agar for the agar-fed treatment.

WATER

-Intake-

Mean	Group	Starved	Agar	Control	Pn-starved
53.4283	Starved				
79.4136	Agar				
107.6420	Control	*			
117.0855	Protein-starved (Pn-starved)	*	*		

CARBOHYDRATE

-no. of bouts-

Mean	Group	Pn-starved	Control	Agar	Starved
14.7396	Pn-starved				
35.9688	Control	*			
51.0714	Agar	*			
85.3333	Starved	*	*	*	

-feeding duration-

Mean	Group	Pn-starved	Control	Agar	Starved
80.3090	Pn-starved				
184.4331	Control	*			
261.9086	Agar	*			
439.2508	Starved	*	*	*	

-Intake-

Mean	Group	Agar	Starved	Control	Pn-starved
15.5629	Agar				
16.7529	Starved				
17.1045	Control				
32.9459	Pn-starved	*	*	*	

PROTEIN

-no. of bouts-

Mean	Group	Control	Pn-starved	Agar	Starved
23.0313	Control				
25.2292	Pn-starved				
42.6429	Agar				
72.0417	Starved	*	*	*	

-feeding duration-

Mean	Group	Pn-starved	Control	Agar	Starved
100.0110	Pn-starved				
142.0358	Control				
205.3771	Agar				
432.5925	Starved	*	*	*	

-Intake-

Mean	Group	Control	Pn-starved	Starved	Agar
12.5420	Control				
13.3340	Pn-starved				
22.8587	Starved	*	*		
34.3029	Agar	*	*	*	

Table 6. Regression analysis applied to all variables for each behaviour for controls. Only significant pairs ($P<0.05$) are tabulated. See methods for definitions of variables.

-CONTROLS (n=64)-

Behaviour	y	A	b	X	multiple r	F	P < 0.05 Significance
Drinking	BLKD	33.8526	13.2920	BTS	0.4096	12.4966	0.001
	BLKD	154.4788	4.9383	DUR	0.4278	13.8891	0.000
	BLKD	37.4490	1.0317	NAT	0.9967	9376.4428	0.000
	BTS	12.6452	0.2977	DUR	0.8370	145.0939	0.000
	BTS	23.2082	0.0111	NAT	0.3489	8.5922	0.005
	DUR	37.4490	0.0317	NAT	0.3531	8.8336	0.004
	AINT	0.6643	0.8178	RATE	0.8663	186.3961	0.000
Carbohydrate	BLKD	124.1438	8.9491	BTS	0.7011	59.9268	0.000
	BLKD	− 75.7453	2.8291	DUR	0.8368	144.8565	0.000
	BLKD	− 112.7534	32.6689	INTK	0.5540	27.4527	0.000
	BLKD	113.7684	1.2701	NAT	0.9776	1338.6761	0.000
	BTS	− 2.9684	0.2111	DUR	0.7971	108.0611	0.000
	BTS	− 7.3815	2.5344	INTK	0.5486	26.6942	0.000
	BTS	19.8738	0.0615	NAT	0.6045	35.7019	0.000
	DUR	− 22.9824	12.1263	INTK	0.6952	57.9898	0.000
	DUR	113.7684	0.2701	NAT	0.7029	60.5501	0.000
	INTK	14.4962	0.0100	NAT	0.4526	15.9704	0.000
	ADUR	1.4183	7.0181	AINT	0.7989	109.3653	0.000
	AINT	0.7398	0.9409	RATE	0.3159	6.8739	0.011
Protein	BLKD	53.2393	13.7284	BTS	0.7249	68.6372	0.000
	BLKD	116.2131	1.7827	DUR	0.5455	26.2620	0.000
	BLKD	33.4332	26.7890	INTK	0.3550	8.9391	0.004
	BLKD	120.1052	1.0964	NAT	0.9557	654.2872	0.000
	BTS	3.6087	0.1367	DUR	0.7925	104.6635	0.000
	BTS	1.0288	1.7543	INTK	0.4403	14.9080	0.000
	BTS	15.4094	0.0335	NAT	0.5534	27.3671	0.000
	DUR	47.6601	7.5248	INTK	0.3259	7.3660	0.009
	DUR	120.1052	0.0964	NAT	0.2748	5.0625	0.028
	INTK	11.5297	0.0045	NAT	0.2929	5.8160	0.019
	AINT	0.5493	0.7937	RATE	0.8779	208.3628	0.000

Table 7. Regression analysis applied to all variables for each behaviour for protein- starved cockroaches. Only significant pairs ($P<0.05$) are tabulated. See methods for definitions of variables.

-PROTEIN STARVED (n=96)-

Behaviour	y	A	b	X	multiple r	F	P <0.05 Significance
Drinking	BLKD	-133.9748	23.2727	BTS	0.4851	28.9309	0.000
	BLKD	89.9028	8.9068	DUR	0.3915	17.0183	0.000
	BLKD	35.1791	1.0158	NAT	0.9992	55492.6829	0.000
	BTS	10.9998	0.3497	DUR	0.7375	112.0829	0.000
	BTS	21.5230	0.0098	NAT	0.4602	25.2624	0.000
	DUR	35.1791	0.0158	NAT	0.3534	13.4114	0.000
	AINT	2.6194	0.6356	RATE	0.9134	473.5144	0.000
Carbohydrate	BLKD	35.4505	9.0251	BTS	0.5402	38.7340	0.000
	BLKD	56.5818	1.3933	DUR	0.5343	37.5505	0.000
	BLKD	101.5335	2.0319	INTK	0.2299	5.2448	0.024
	BLKD	73.3934	1.0784	NAT	0.9260	565.6392	0.000
	BTS	6.7388	0.0996	DUR	0.6382	64.6082	0.000
	BTS	10.9800	0.1141	INTK	0.2157	4.5867	0.035
	BTS	12.6248	0.0240	NAT	0.3441	12.6249	0.001
	DUR	43.2568	1.1246	INTK	0.3318	11.6303	0.001
	AINT	2.1470	0.5558	RATE	0.8697	291.7103	0.000
Protein	BLKD	166.7608	5.7617	BTS	0.3435	12.5769	0.001
	BLKD	103.9776	2.0812	DUR	0.4177	19.8624	0.000
	BLKD	89.4268	1.0499	NAT	0.9808	2373.1845	0.000
	BTS	1.7426	0.2348	DUR	0.7905	156.5375	0.000
	BTS	17.8393	0.5542	INTK	0.2052	4.1301	0.045
	DUR	57.3850	3.1968	INTK	0.3516	13.2574	0.000
	DUR	89.4268	0.0499	NAT	0.2323	5.3608	0.023
	ADUR	2.2465	0.6237	AINT	0.3013	9.3836	0.003
	AINT	0.4439	0.4664	RATE	0.8415	228.0699	0.000

Table 8. Regression analysis applied to all variables for each behaviour for starved- cockroaches. Only significant pairs ($P<0.05$) are tabulated. See methods for definitions of variables.

-STARVED (n=24)-

Behaviour	y	A	b	X	multiple r	F	P<0.05 Significance
Drinking	BLKD	-125.1971	17.3014	BTS	0.5589	9.9931	0.005
	BLKD	-117.7781	13.0971	DUR	0.6464	15.7933	0.001
	BLKD	18.4688	1.0314	NAT	0.9992	14539.2755	0.000
	BTS	4.0307	0.6058	DUR	0.9256	131.5429	0.000
	BTS	15.4498	0.0177	NAT	0.5297	8.5809	0.008
	DUR	18.4688	0.0314	NAT	0.6163	13.4736	0.001
	AINT	1.0508	0.5229	RATE	0.9747	418.3734	0.000
Carbohydrate	BLKD	433.0420	1.0031	NAT	0.9926	1464.6015	0.000
	BTS	37.7455	0.1083	DUR	0.6960	20.6686	0.000
	BTS	25.8869	3.5484	INTK	0.6702	17.9366	0.000
	DUR	43.3056	23.6344	INTK	0.6948	20.5353	0.000
	ADUR	- 1.4007	29.9890	AINT	0.8688	67.7028	0.000
Protein	BLKD	-141.0270	15.8068	BTS	0.8894	83.2954	0.000
	BLKD	282.1949	1.6540	DUR	0.9098	105.7212	0.000
	BLKD	15.2943	42.9783	INTK	0.7415	26.8732	0.000
	BLKD	61.8942	1.6560	NAT	0.9095	105.3508	0.000
	BTS	34.4347	0.0869	DUR	0.8498	57.1944	0.000
	BTS	8.5547	2.7774	INTK	0.8516	58.0755	0.000
	BTS	27.5629	0.0787	NAT	0.7683	31.6896	0.000
	DUR	- 50.8952	21.1511	INTK	0.6635	17.2972	0.000
	DUR	61.8942	0.6560	NAT	0.6550	16.5305	0.001
	INTK	10.6869	0.0215	NAT	0.6857	19.5184	0.000
	AINT	0.2463	1.1617	RATE	0.8287	48.2399	0.000

Table 9. Regression analysis applied to all variables for each behaviour for agar-fed cockroaches. Only significant pairs ($P<0.05$) are tabulated. See methods for definitions of variables.

-AGAR (n=28)-

Behaviour	y	A	b	X	multiple r	F	P<0.05 Significance
Drinking	BLKD	- 5.9816	17.1089	BTS	0.5867	13.6495	0.001
	BLKD	7.1414	15.5515	DUR	0.5415	10.7874	0.003
	BLKD	14.4679	1.0183	NAT	0.9996	29207.3677	0.000
	BTS	1.0585	0.8943	DUR	0.9081	122.2079	0.000
	BTS	12.9941	0.0198	NAT	0.5655	12.2254	0.002
	DUR	14.4679	0.0183	NAT	0.5162	9.4447	0.005
	AINT	1.3299	0.5205	RATE	0.9874	1009.5171	0.000
Agar	BLKD	-894.6160	57.3913	BTS	0.6084	15.2767	0.001
	BLKD	49.2943	7.5872	DUR	0.5265	9.9722	0.004
	BLKD	201.4927	1.0340	NAT	0.9981	6933.8099	0.000
	BTS	16.8372	0.1307	DUR	0.8557	71.1017	0.000
	BTS	37.3284	0.8831	INTK	0.4383	6.1829	0.020
	BTS	39.9884	0.0062	NAT	0.5687	12.4307	0.002
	DUR	129.7885	8.4895	INTK	0.6437	18.3908	0.000
	DUR	201.4927	0.0340	NAT	0.4736	7.5167	0.011
	AINT	0.2399	1.1469	RATE	0.4075	5.1757	0.031
Protein	BLKD	206.9663	0.9992	NAT	0.9991	14605.1104	0.000
	BTS	19.7841	0.1113	DUR	0.5584	11.7770	0.002
	AINT	1.7083	0.5681	RATE	0.8920	101.2490	0.000

Table 10. Combined feeding means (+/-SE) including the percentage of each food type (P= protein, C= carbohydrate, A= agar) and drinking for each variable and treatment.

Treatment	no. of Blocks (day)	no. of Bouts (day)	Block Duration (s/day)	Activity Duration (s/day)	Non-Activity Time (s/day)	Intake (mg or uL/ gm/day)	Bout length (s)	Bout size (mg or uL/gm)	Intake rate (mg or uL/ gm/s)	
CONTROL										
Feeding	3.4062	59.0001	815.4539	326.4689	488.9850	29.6465	14.2343	2.1028	0.9959	
± SE	0.3487	12.4078	186.0158	55.8857	151.8187	2.8402	2.5500	0.4913	0.4261	
% Foods	54C 46P	61C 39P	55C 45P	56C 44P	53C 47P	58C 42P	54C 46P	42C 58P	16C 84P	% of Protein (P) Carbo (C)
Drinking	1.7656	27.0469	393.3606	48.3733	344.9873	107.6420	1.2312	6.2778	6.8641	
± SE	0.1694	3.3080	107.3558	9.3003	103.7183	9.1417	0.1304	1.2701	1.3453	
PROTEIN-STARVED										
Feeding	2.8230	39.9688	480.5999	180.3200	300.2799	46.2799	7.0867	4.6603	3.8460	
± SE	0.3303	6.3427	106.2801	26.1256	97.3003	4.7359	1.1382	1.1095	1.7849	
% Foods	45C 55P	37C 63P	35C 65P	45C 55P	29C 71P	71C 29P	65C 35P	83C 17P	80C 20P	% of Protein (P) Carbo (C)
Drinking	1.5104	25.6250	462.3889	41.8205	420.5683	117.0855	1.2192	7.9206	8.3403	
± SE	0.1607	3.5361	169.6388	7.4570	166.8603	9.5896	0.1252	1.1774	1.6921	
STARVED										
Feeding	5.4166	157.3750	3415.0395	871.8433	2543.1963	39.6116	10.6667	0.9441	0.4462	
± SE	0.4919	30.8348	993.4810	258.7946	841.3020	7.9567	2.6617	0.2267	0.1354	
% Foods	50C 50P	54C 46P	71C 29P	50C 50P	78C 22P	42C 58P	55C 45P	26C 74P	12C 88P	% of Protein (P) Carbo (C)
Drinking	1.5000	18.4583	194.1571	23.8171	170.3400	53.4283	1.0079	3.1529	4.0200	
± SE	0.2125	3.6020	111.5076	5.5037	108.0314	11.1410	0.1056	1.2382	2.3079	
AGAR										
Feeding	4.7857	93.7143	4344.0372	467.2857	3876.7514	49.8658	10.1653	3.4532	2.5321	
± SE	0.5773	17.5990	1861.3053	102.7313	1830.2414	7.6119	1.8664	1.1175	1.6564	
% Foods	48A 52P	54A 46P	47A 53P	56A 44P	46A 54P	31A 69P	48A 52P	11A 89P	5A 95P	% of Protein (P) Agar (A)
Drinking	1.1429	18.8571	316.6443	19.9018	296.7425	79.4136	0.7450	7.5332	11.9189	
± SE	0.2002	6.0110	175.2778	6.1033	172.0493	15.0704	0.1999	2.7387	5.1955	