To the Graduate Council:

I am submitting herewith a thesis written by James L. Jenkins, Jr. entitled "The Predatory Behavior of Male Anolis carolinensis carolinensis: Effects of Hunger and Prey Distance on Involvement Time." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

A. C. Echternacht, Major Professor

We have read this thesis
and recommend its acceptance:

Accepted for the Council:

Vice Chancellor
Graduate Studies and Research

B

THE PREDATORY BEHAVIOR OF MALE *ANOLIS CAROLINENSIS CAROLINENSIS*: EFFECTS OF HUNGER AND PREY DISTANCE ON INVOLVEMENT TIME

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

James L. Jenkins, Jr.

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DEDICATION

I dedicate this thesis to my parents,

Lawrence "Dock" and Marie Jenkins,

who have provided encouragement along the way.

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I would like to extend appreciation to those individuals responsible for contributing to the completion of this study.

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ABSTRACT

The essential qualities of optimal foraging are time and energy. These are the items that are being optimized either by maximizing energy uptake for a particular foraging bout, or by restricting the diet for a certain energy uptake while minimizing foraging time.

Most models have several factors in common when approaching how the optimal diet (the diet which maximizes the net rate of energy or mass intake) in a fine grain situation (an area in which resources are distributed in a random manner) is obtained. One of these factors is that each food type has an associated food value measured in calories or units of weight and an associated involvement time. This does not take into consideration either distance between predator and prey or the hunger state of the animal. Previous studies have suggested that hunger may affect involvement time and that pursuit time may be a function of distance. Therefore, it is possible that either one or the other or both are capable of modifying involvement time. In light of this hypothesis, the present study was designed to determine if either distance and/or hunger state has an effect on involvement time or its components in male Anolis carolinensis carolinensis.

A 4 x 4 factorial arrangement was used with four progressive distances and four progressive hunger states. Ten replications were completed in the laboratory, each composed of the 16 combined states. In each trial a lizard in a specific hunger state was given an opportunity to pursue, capture, and consume a fly tethered at a set distance.

The results show that involvement time was influenced by both distance and hunger state. The effect of hunger was not significant at the 0.05 alpha level, but was borderline at 0.06. The subcomponent handling time was not affected by the distance traveled or the hunger state of the individual. Differences found in involvement time can be traced directly to the subcomponent pursuit time. Pursuit time is affected by both distance and hunger. Pursuit time is composed of move time and stop time. Move time is affected by the distance a predator has to travel for a prey item, but not the hunger state of the predator. Stop time is affected by both distance and hunger. Both sub-variables of stop time (wait and survey time) are affected by these sources of variation.

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I. INTRODUCTION

> Feeding is such a universal and commonplace business that we are inclined to forget its importance. The primary driving force of all animals is the necessity of finding the right type of food and enough of it (Elton, 1927).

Optimal diet is but one of four categories included in optimal foraging theory; patch choice, allocation of time to patches, and the foraging path complete this body of theory. These elements constitute a microecological approach to population dynamics. Population dynamics are presently modeled using large scale population phenomena such as predation and competition which are included in macroecological theory. The microecological approach could provide valuable parameters and coefficients for population modeling. The elements of optimal foraging theory when combined with factors such as prey distribution (spatial and temporal) determine small scale events, the sum of which is the very core of predation and competition (Pyke, et al., 1977).

Why an organism should forage optimally or have an optimal diet is a question that can be looked at in terms of long range goals. The long term goal would seem to be increased fitness. Natural selection favors any animal whose genetic constitution predisposes it to forage such that its expected genetic contribution to subsequent generations is maximized (Estabrook and Dunham, 1976). Positive selection would be made for those individuals (phenotypes) responding properly to the appropriate environmental clues (Stenseth and Hansson, 1979). Since evolutionary optima are approximated to varying degrees of success,

and while one never expects perfection, neither is there any reason to suspect that this hypothesized behavior (optimal diet) is "too difficult" for an organism to have evolved (Wilson, 1976).

Long term goals, such as increased fitness, are met by achieving short term goals. These short term goals may be of separate duration and require different indicators to substantiate their fulfillment. Short time scale investigations have been conducted by Katz (1974) and Craig, et al. (1979). Craig, et al. (1979) investigated long and short term dynamic optimization models concerning feeding strategy in the California loggerhead shrike (Lanius ludovicianus gambeli). These two models had scale lengths of 1 year and 1 day, respectively. The long term model optimizes handling time and weight of the organism simultaneously. The short term model tries to account for prey diversity in the diet and the occurrence of uneconomical prey. Both models agree fairly well with data, indicating that no one model or time scale is likely to depict accurately all aspects of feeding behavior of an organism.

The essential qualities of optimal foraging are time and energy. These are the items that are being optimized either by maximizing energy uptake for a particular foraging bout, or by restricting the diet for a certain energy uptake while minimizing foraging time (Cody, 1974). When modeling optimal foraging energy maximizing or time minimizing is accomplished through a game with rules and constraints or confines (Charnov, 1973; Wilson, 1976). And the "model" assumes rewards and will allow the predator some choice of actions; of the possible actions, some set will maximize the value of the reward

(an optimal set). This then needs to be compared to the real behavior. The currency or food value used can be elementary food types (proteins, fats, carbohydrates), special nutriments, or caloric density. If the foraging models are to express the gain to the predator in terms of net gain, the food value for the prey items must be in the same units as the cost of the activity. This requires the calorie to be used as the food unit (Charnov, 1973). It has been noted that there may be nutrient restraints, such as calcium and other minerals and vitamins (Pulliam, 1975; Westoby, 1978), but these are usually not included in models.

Most models have several factors in common when approaching how the optimal diet (the diet which maximizes the net rate of energy or mass intake) in a fine grain situation (an area in which resources are distributed in a random manner) is obtained (Pyke, et al., 1977).

(1) Each food type has an associated food value measured in calories or units of weight and an associated handling time. Food types are first ranked by their ratios of the food value to handling time.

(2) In addition to time spent handling food items, time must be spent searching for them. These times are assumed to be mutually exclusive and to account for all the time available for foraging. Taking into account the handling times, food values, and search time (which is a function of the diet of the animal), it is then possible to calculate the net rate of food gain for any possible diet.

(3) Finally, the optimal diet is determined by beginning with the highest value of the ratios of food value to handling time, and then adding food types to the diet in their rank order. This process is continued so long as the ratio of food value to handling time for each addition to the diet is greater than the net rate of food intake for the diet without the addition. When this inequality reverses, the optimal diet has been obtained.

Another aspect of optimal foraging is that a size-distance relationship exists. Schoener (1971) predicted that the relationship does exist and made the following predictions based on theory:

1. Food sizes should decrease with decreasing predator size, but asymptotically. This has been shown to occur in insectivorous lizards (Davis, 1967; Hirth, 1963; Inger, 1959; Kennedy, 1956; Schoener, 1967, 1968; Schoener and Gorman, 1968; Simon, 1976) and hawks (Storer, 1966) but not in tropical terns (Ashmole, 1968).
2. A predator at a given distance should take prey both larger and smaller than any at a greater distance, but the large size limit should decline less with increasing distance than the small limit should increase. This has been found in Anolis (Schoener, 1969), trout (Brawn, 1969), and oilbirds (Snow, 1962). It is also felt that this is why certain birds bring their nestlings larger food than they themselves eat (Royama, 1966; Verner, 1965).
3. Distributions of prey size eaten by a predator from a uniform size-abundance distribution of available prey should be more negatively skewed (longer left tail) if the predator pursues its prey over greater distances or is relatively large than if the predator pursues its prey less or is relatively small. Ivlev (1961) found this to be true in fish.

Charnov (1976) found that the mantid Hierodula crassa, a sit and wait predator, does express a size-distance relationship as a

function of hunger. Holling's (1966) data were used to test his model. It had been found that the mantids could measure the rate of food intake. The measure of hunger was found by satiating the predator and at differing time intervals again testing to see how much food matter would be consumed. The prey consumed was the house fly (Musca domestica). By subtracting the quantity fed at a later time period from the initial satiation total the level of hunger as a function of the amount of food in the stomach was measured. By seeing if the mantids would stalk prey items at different distances while being in different states of satiation, Charnov concluded that the ratio

$$\frac{\text{expected net energy from one item of type i}}{\text{expected handling time for an item of type i}}$$

is a decreasing function of pursuit distance. Therefore, the mantid adds to or drops prey items from the diet in order or rank based on a measure (food in the gut) of the rate of food intake.

Using size as a measure of energy content, with the larger prey item being profitable and the smaller item not profitable, Krebs, et al. (1977) tested predictions of optimal foraging using five captive great tits (Parus major). Results showed that great tits can select prey on the basis of reward per unit handling time and that the degree of prey selection depends on the encounter rate with profitable prey, rather than with unprofitable prey.

Werner and Hall (1974) found that the bluegill sunfish became more selective as the encounter rate with profitable prey increased, and further that small prey were selectively ignored at the predicted

density of large prey. However, Pyke, et al. (1977) noted that Werner and Hall did not test whether the degree of prey selection was independent of the availability of the small prey. It is possible that the fish always scan for the next visible prey, and if large prey are more abundant and more conspicuous, one could expect selection.

The effect of satiation of the predator on handling times has been examined in several studies. Krebs, et al. (1977) did not find that overall handling times varied with hunger with one notable exception; there was a slight increase in handling time with satiation using the large prey item, an eight segmented mealworm, as opposed to the four segmented mealworm. Smith and Dawkins (1971), also working with great tits, used larger prey items and found that a slight increase in handling time did occur with satiation. In fish it has been noted that handling times vary with hunger (Ware, 1971; Werner, 1974).

At this point it is uncertain what part hunger plays in the overall question of optimal foraging. Hunger will cause an animal, such as Anolis carolinensis, to take risks otherwise not taken. Greenberg and Noble (1944) noted that at times hunger led to brief intrusions by one male Anolis into another male's territory to snatch flies from a jar; after feeding, the intruder always retreated into his own territory. Schoener (1969) suggests that hunger also functions to monitor fluctuations in the food supply, "telling" the predator when it must eat low energy yielding items and when it can confine itself to the very best. This is supported by Craig (1978) who

argues that on cool mornings the relative lack of food in a loggerhead shrike's stomach will cause it to feed on suboptimal prey because its hunger threshold will be exceeded. This seems to occur even though a superabundance of desired prey might be available later in the day.

As previously mentioned most models of optimal foraging have an underlying assumption that with each prey type there is a constant handling time (time from point of recognition to ingestion) (Hughes, 1979; Pyke, et al., 1977). This does not take into consideration either distance between predator and prey or the hunger state of the animal. As previously noted, evidence suggests that hunger may affect handling time and Schoener (1979) states that pursuit time or provisioning time must be a function of distance. Therefore, it is possible that either one or the other or both are capable of modifying the "handling time," henceforth termed involvement time (Hughes, 1979). In light of this hypothesis, the present study was designed to determine if either distance and/or hunger state has an effect on involvement time or its components in male Anolis carolinensis carolinensis.

II. METHODS AND MATERIALS

TERMINOLOGY

Prior to 1979, handling time was regarded as including recognition time, pursuit time, attack time, and eat time (+ digestive time) (Charnov, 1976). This can basically be seen as the time from point of recognition to the point of ingestion (Pyke, et al., 1977; Hughes, 1979). However, Hughes (1979) separates recognition time from "handling time" and refers to both as involvement time. Schoener (1979) in his prey profitability ratio of e_i/t_i, has t_i standing for (handling-swallowing time) + (pursuit or provisioning time). He offers no standard definitions for these terms; however, this author assumes that handling time would include eat time, i.e., time from point of capture through swallowing. Pursuit time would include everything from point of recognition to the beginning of eat time. When Schoener is dealing with central place foraging, provisioning time would include the time required to return to the point being provisioned with the prey item, and handling would not occur until actual eating of that item.

In the present study "involvement time," the total time dedicated to an individual prey item, is composed of pursuit time and handling time. Pursuit time is the time from point of first movement toward the prey item until the moment of capture. Handling time is the time from the instant of capture through the last swallow. Recognition time is assumed to be instantaneous or at least constant for a prey type and will not be included.

The variable pursuit time is composed of two sub-variables, move time and stop time. Move time is the time devoted to actual movement by the predator from the instant he first moved toward the prey item until the moment of capture. Stop time is the amount of time spent in a stationary position after initially starting toward the prey item until the instant of capture.

The sub-variable stop time is composed of two component variables, wait time and survey time. Wait time is the stationary time that the predator's head was straight (aligned with body) and parallel with the substrate. Survey time occurred when the lizard's head moved, cocked, angled, scanned the surroundings, or in some way departed from the wait position.

PREDATOR

Forty adult male Anolis carolinensis carolinensis with snout-vent lengths of 57-62 mm were selected for use in this study from a group of 400 animals purchased from the Snake Farm, Laplace, Louisiana. Anolis carolinensis from this general area have been previously studied in their natural habitat (Gordon, 1956), and are frequently used in laboratory experimentation. Lizards were received from December 1978 to February 1979. Animals were maintained on a diet of mealworms, crickets, and flies. Mealworms and/or crickets were given weekly while approximately five flies per lizard were provided daily.

PREY

The common housefly (Musca domestica) was the prey item used in these experiments. King (1966) found that prey of the Order Diptera made up a substantial part of the diet of Anolis carolinensis and Burghardt (1964) found that movement is a necessary characteristic of items preyed upon by this species of lizard. Musca domestica has sufficient size, was easily raised, and was capable of almost constant movement.

PHOTOPERIOD AND TEMPERATURE

Natural light was admitted into the laboratory through two north-facing windows. The main source of light was a controlled artificial lighting system. This system contained five 2 F40CW bulb fluorescent fixtures, two 75 W reflector flood lights, and one 250 W reflec-infrared bulb. The artificial light cycle was controlled by a timer. A 13 L/11 D photoperiod was maintained throughout the study since Fox and Dessauer (1957) found that appetite in male Anolis carolinensis was enhanced by exposure to longer photoperiods.

Laboratory temperatures were maintained within the range of 23.0° to 36.0° C throughout the experimental period. A narrower range was maintained during testing (29.0° to 31.0° C). Diurnal temperature cycles were not kept under constant or preferred conditions because Wilhoft (1958) showed that constant housing of lizards at their "preferred" temperature may lead to thyroid hypertrophy and eventually death. Maximum temperatures were controlled by a wall

mounted cooling unit. Minimum temperatures were controlled by two portable space heaters. Minimum and maximum temperature readings were recorded daily. Test temperatures were taken prior to each trial.

EXPERIMENTAL DESIGN

The factorial experiment, originally referred to as the "complex experiment," is an experiment containing all combinations of several levels of several factors.

The experimental design for this study was a 4 x 4 factorial arrangement, having two main effects, distance and hunger, with four levels of each factor. The 4^2 factorial may be considered either as a 4^2 or as a 4 x 4. The latter consideration is necessary if two factors, each at four levels, are tested in all combinations (Federer, 1955).

The advantages of a factorial experiment are (Federer, 1955):

1. All experimental units are utilized in evaluating effects, resulting in the most efficient use of resources.
2. The effects are evaluated over a wider range of conditions with the minimum outlay of resources.
3. The interaction of the factors can be estimated.
4. Unbiased estimates of effects are obtained whether or not time trends are present.
5. A factorial set of treatments is optimum for estimating main effects and interactions.

The disadvantages of a factorial experiment are (Federer, 1955):

1. The factorial arrangement may turn out to be an inefficient procedure to obtain the answer for a specific question. However, information on a number of effects and interactions is usually preferable to information on a specific combination.
2. One real disadvantage of factorial arrangements is the large and prohibitive number of combinations necessary to study several factors at several levels.

Distance was used as one main effect; it was composed of four fixed levels, with equal separation between any two neighboring distances. The four levels were 20, 40, 60, and 80 cm. Each progressive distance extended the space a predator had to travel to obtain food.

The main effect, hunger, was also composed of four fixed levels, with equal periods of deprivation between any two adjacent states. The four levels were 24, 48, 72, and 96 hours. Each progressive hunger state temporally extended the period since last feeding.

One replicate was composed of 16 cells, each cell representing one of the combined states. A total of 10 replicates was conducted. Due to time considerations each replicate was divided into two tests, each test consisting of eight trials.

Preliminary design testing was accomplished during May and June, 1979. It was found that the best hours of testing were between 1000 and 1600 hours and that approximately four hours were required to perform eight trials. Therefore, each replicate was conducted over

a period of two consecutive days. Experimentation was conducted from July 11, 1979 through October 4, 1979.

Sequence selection of the arrangement of treatment states within each replicate was at random. A randomly assorted digit table (Snedecor and Cochran, 1967) was used to determine each position. Selection of individuals was also at random. So as not to bias the data each lizard was used approximately the same number of times. Therefore, due to the number of lizards (40) and the number of required trials (160), each lizard was available for initial selection four times. This was accomplished by dividing the trials into four groups, with each lizard represented once in each group. The lizard chosen for any trial within each grouping was at random, the only exception being that an individual was not allowed to participate in two tests of the same replicate. If for any reason an individual chosen for a particular trial was unable to participate (i.e., eyes swollen shut or death) another individual was randomly selected as a replacement prior to hunger state preparation.

HUNGER STATE PREPARATION

Hunger state preparation and testing required an eight day period for each replicate. Designated individuals were removed from their respective aquaria and housed in separate one gallon glass containers. Sand was placed in the bottom of each container to a depth of 1.5 cm. Two small petri dishes were placed inside, one for water, the second for prey items. A semicircular opening was cut in the upper half of the container lid. Wire screening was cut to

size and glued to the inside of the lid. Each unit was shelved in a rack providing isolation from neighboring units. A 250 W infrared reflect light provided illumination for the units. Placement into the jars occurred six days prior to testing. Therefore, eight lizards were placed in the housing units on day 1 and those participating in test 2 were placed in the units on day 2. All lizards were given five flies per day for their first three days of confinement. Feeding on the last three days prior to a test was dependent on the hunger state required. Those requiring hunger state 4 were not fed after day 3, thus depriving them of food for 96 hours. Those placed in hunger state 3 were not fed after day 4, thus being deprived of food for 72 hours. Individuals in hunger state 2 were not fed after day 5, hence being deprived of food for 48 hours. Individuals in hunger state 1 were not fed the day of testing, thus being deprived of food 24 hours. At the beginning of any deprivation period jars were checked for prey items not consumed; if any remained they were counted and removed. Upon completion of a replicate, lizards were returned to their respective aquaria and each housing jar cleaned.

TEST APPARATUS

Trials were conducted in a feeding apparatus (Figure 1), the bottom, two ends, extended hood, and back of which were constructed from 1.9 cm plywood. The hood extended 30 cm from the perch end of the apparatus. An opening existed at the perch end to allow fitting of individual jars into the apparatus. A platform 11.0 cm in height was placed inside the hood to elevate the mouth of the jar to match

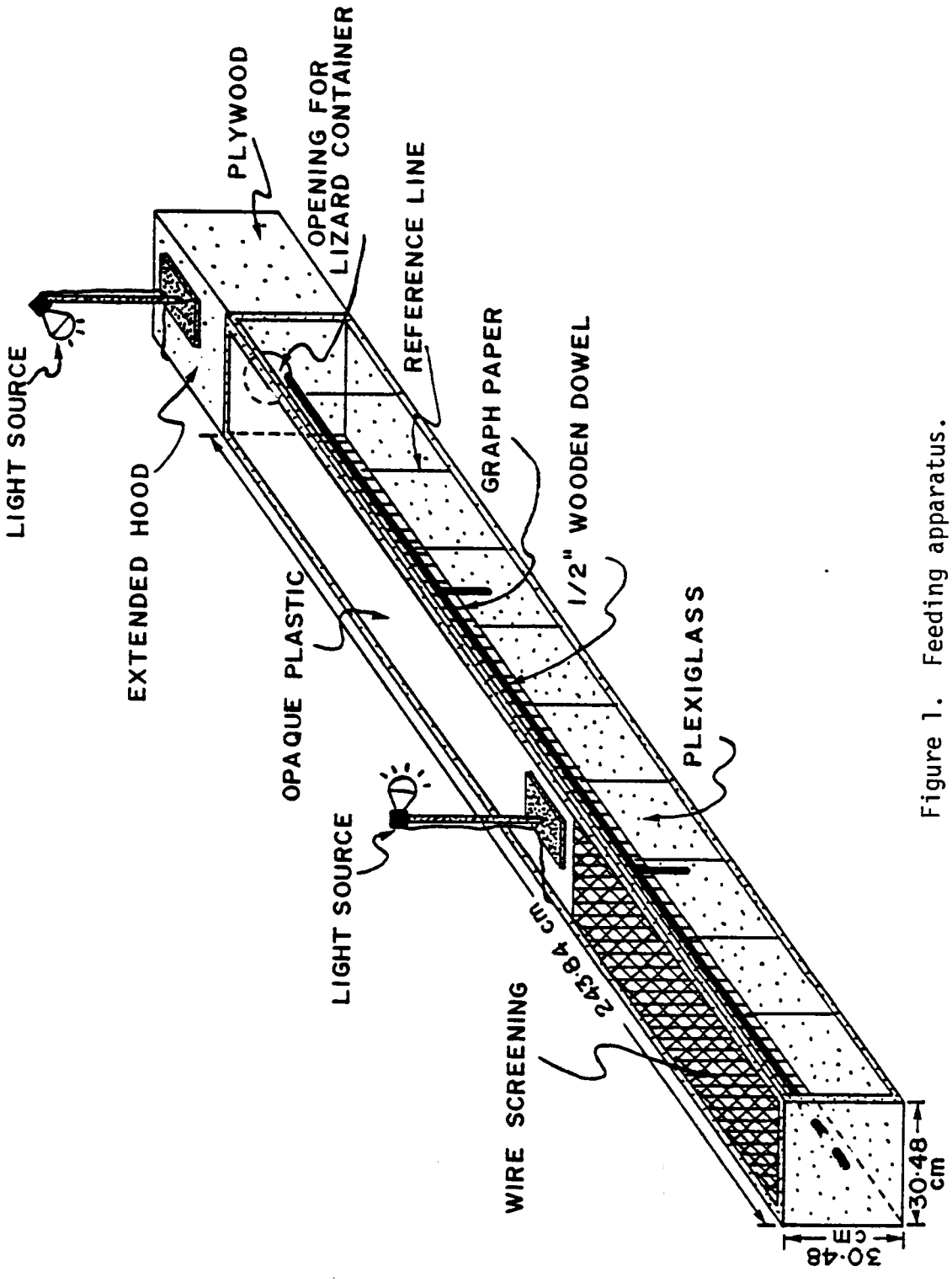


Figure 1. Feeding apparatus.

the opening. The front of the apparatus was 0.7 cm plexiglass and the top was of hinged construction with a screen wire covering. Two sections of opaque plexiglass 70.4 x 21.1 x 0.3 cm were placed over the screening to diffuse light and reduce heating in the feeding area. Two 75 W reflector flood lights were used for lighting the apparatus. One, located at the perch end, was at a height of 22.5 cm and an angle of 45°. The second light source was placed 110 cm from the perch opening at a height of 27.2 cm and a 60° angle. The area of best illumination was from 0 to 95 cm. A round wooden dowel, 1.3 cm in diameter, extended the length of the apparatus with supports at 57 and 188 cm. The top of the dowel was at a height of 14.6 cm above the apparatus floor. The rear wall was covered with graph paper and increments of 5 cm and 1 cm were denoted with vertical solid black lines and numerals and vertical dashed black lines, respectively. The plexiglass side was marked every 25 cm with solid black lines; this was necessary for proper distance alignment. A cardboard barrier 236 x 177.5 x 0.4 cm, behind which the observer stood, was located parallel with and 210 cm from the apparatus. Five observation windows, measuring 17 x 2 cm each, were located 97.8 cm from the bottom of the barrier. Black fiberglass screening was placed over each opening; this did not hinder the observer's ability to accurately see all facets of involvement time. However, during the swallowing portion of handling time the screening was lifted in order to obtain exact times of completion.

TEST PROCEDURES

Prior to testing, temperature of the room and apparatus was checked and recorded to insure testing within a range of 28° - 31° C.

Prefacing each trial was a 15 minute introduction period and a 15 minute wait period. The introduction period was used to minimize inhibition and help familiarize the lizard with the test feeding apparatus. After removal of the jar lid, the container was placed on the platform inside the extended hood. If the lizard had not left the jar and actually entered the feeding area after one minute, a slight tap was delivered to the end of the jar; this action was not taken during an actual trial. The introduction period conditions paralleled those of an actual trial with the exception that no prey item was present in the apparatus and the jar was not tapped as previously mentioned. At expiration of the introduction period, the lizard was returned to his jar. This was followed by a 15 minute wait period. The wait period was used to minimize any handling effect incurred during removal after the introduction period. All subjects tested were in the green color phase and did not have dark patches posterior to the eyes, indicating a tonic condition in which the lizard was alert and not disturbed.

At the beginning of each testing day 12-15 flies were anesthetized with ether. A thin black polyester string was attached with glue to the posterior portion of the head and the anterior portion of the thorax. The flies were then taped by the string to a piece of paper where they remained until required for a trial.

To begin a trial a fly was picked at random and secured to the dowel at the test distance with a strip of masking tape. The tethered fly had approximately 6.35 mm of string after attachment.

When the prey item was in place the lizard container was positioned in the apparatus; thereafter, all events of importance were voice recorded on tape. The following events were immediately noted:

1. Time jar was placed in the apparatus.
2. Time at which the lizard appeared at the mouth of the jar (distance 0).
3. When the lizard started moving.
4. When the lizard stopped moving.
5. The distance from 0 at which the lizard stopped.
6. Status during each stop, according to the following categories:
   a. Wait
   b. Survey
   c. Prey handling

Data were transcribed from the tapes to data sheets through repeated play-backs. Time for any one event was recorded to the nearest 1/10 second using a stopwatch.

A trial was terminated when any one of the following criteria were met:

1. A capture was made and handling time ended.
2. The lizard ran past the fly.

3. No capture occurred within 15 minutes of placing the jar into the feeding apparatus.
4. The lizard jumped to the substrate or climbed the wall after moving onto the dowel.
5. If the lizard jumped to the substrate or climbed the wall upon entering the feeding area and prior to moving onto the dowel, he was removed, put in wait for one minute and placed back into the apparatus. The trial was terminated if this occurred a second time.

DATA ANALYSIS

The data sets for involvement time, handling time, pursuit time, move time, stop time, wait time and survey time were analyzed using analysis of variance (ANOVA) strategies.

Two major criteria govern the reliability of results derived from the use of analysis of variance. The use of randomization of treatments within replicates insures a reliable test of significance of treatment effects (Kempthorne, 1952). The second, and perhaps most important criterion is the estimation of the treatment effects. The reliability of such a point estimate can be improved if the data conform to standard assumptions concerning the use of ANOVA (Little and Hills, 1978). Therefore, a log $(y + 1)$ transformation was performed to correct for the lack of homogeneity of variance in the data. A second potential problem obviated when preliminary analysis deemed that within lizard variation was not significantly different from between lizard variation.

The 4 x 4 factorial proved to be an unbalanced design because of missing values. Missing values are data points that were unobtainable in a replicate for one or more cells (treatment combinations). In the present study missing values were generated when a capture was not made by a lizard for the reasons already given. Least squares analysis, which can handle unequal subclass numbers, thus was deemed appropriate.

Data were analyzed using the General Linear Model (GLM) subprogram (Helwig and Council, 1979) in the experimental Statistical Analysis System (SAS) programs. The data were analyzed with replicate, distance, hunger state, and distance x hunger state included as classes of effects in the mathematical model. Since disproportionate and unequal subclass numbers were present, tests for overall class effects were based on partial sum of squares, parenthetically GLM type III. From the same analysis marginal and subgroup least squares means were calculated. Least squares means have the same expected values as do arithmetic means with proportionate subgroup numbers (Goodnight and Harvey, 1978).

Since distance and hunger state are both quantitative factors, differences within classes of effects were partitioned with polynomials. Complete third order polynomials were fitted and ordered from simple to complex. A sequential test of hypotheses was based on sequential sums of squares, parenthetically GLM type I.

All non-significant terms were deleted from the model and the data were refitted to the resulting reduced model. From this model a three dimensional projection of the response surface was drawn and is presented in the RESULTS section.

The untransformed variables of temperature at time of trial, lizard weight, and snout-vent length were graphically analyzed to access any difference in these factors at all levels of distance and hunger for when a capture was made. Figures 2 and 3 show mean temperatures for all distances and hunger states, respectively. Mean lizard weights are graphed for all distances and hunger states in Figure 4 and 5. The mean snout-vent lengths are depicted in Figures 6 and 7, representing distance and hunger state, respectively. It is apparent, without the use of statistical test, that these factors did not have significant effects on involvement time or its components.

The mean Anolis weight was ($\bar{x}$ = 4.48 gm, s.d. = 0.60) with a mean snout-vent length of $\bar{x}$ = 59.3, s.d. = 1.42. Prey items were of a mean length $\bar{x}$ = 6.54 mm, s.d. = 0.64 and width $\bar{x}$ = 2.28 mm, s.d. = 0.29. Their mean live weight was 0.012442 gm with a standard deviation of 0.000009.

The overall capture rate (trials within which the lizard captured and ate the prey item) was 65%. The percentage is only slightly different from experimental results of Sexton (1964) when working with differential predation in Anolis carolinensis.

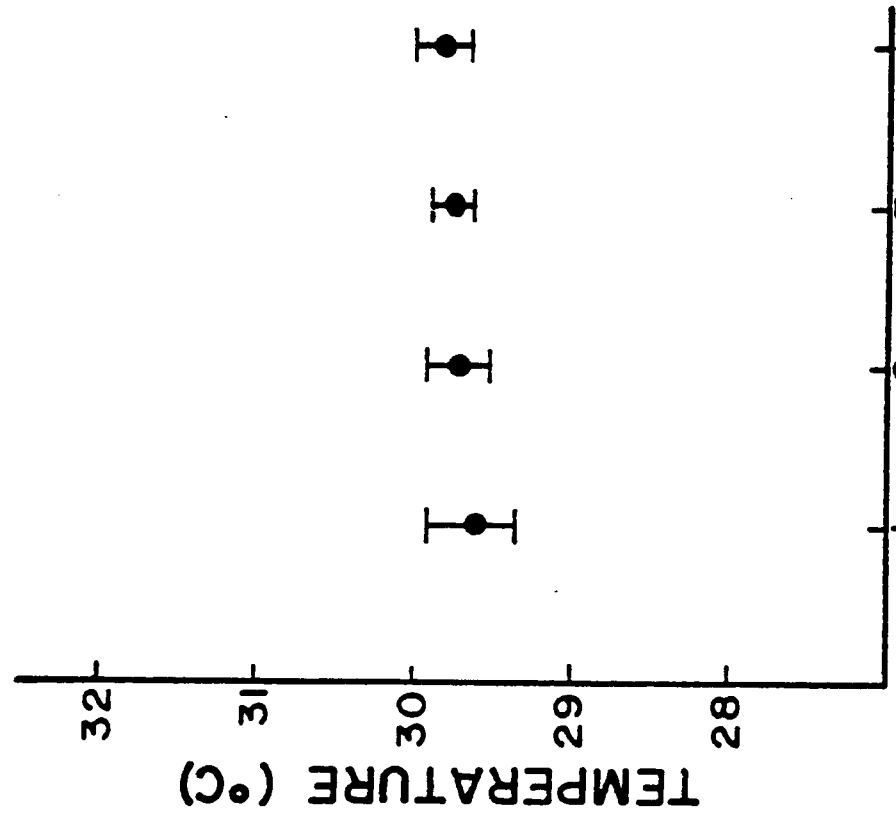


Figure 3. Trial temperature vs. hunger state for when a capture was made: mean ± 2 S.E.

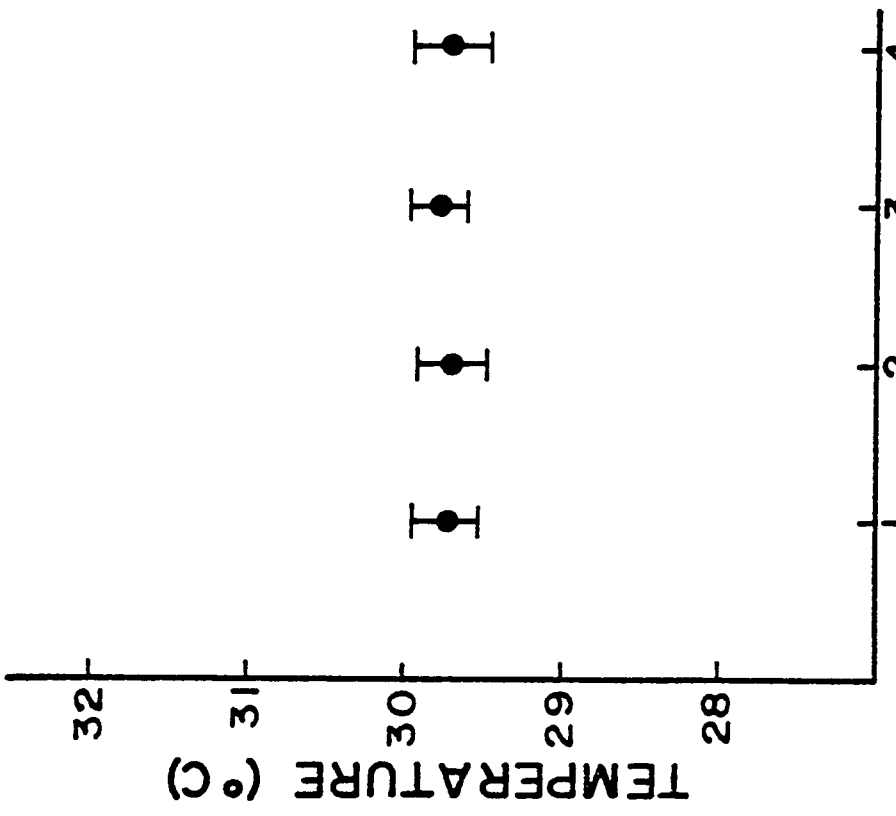


Figure 2. Trial temperature vs. distance for when a capture was made: mean ± 2 S.E.

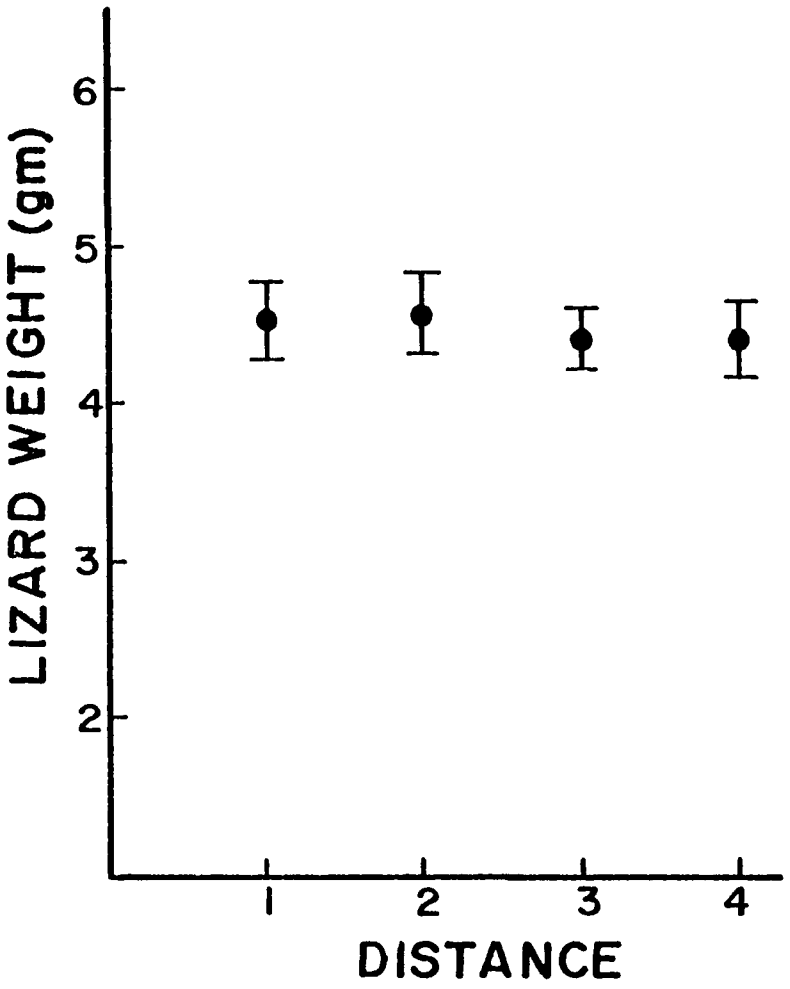


Figure 4. Weight of lizard vs. distance for when a capture was made: mean ± 2 S.E.

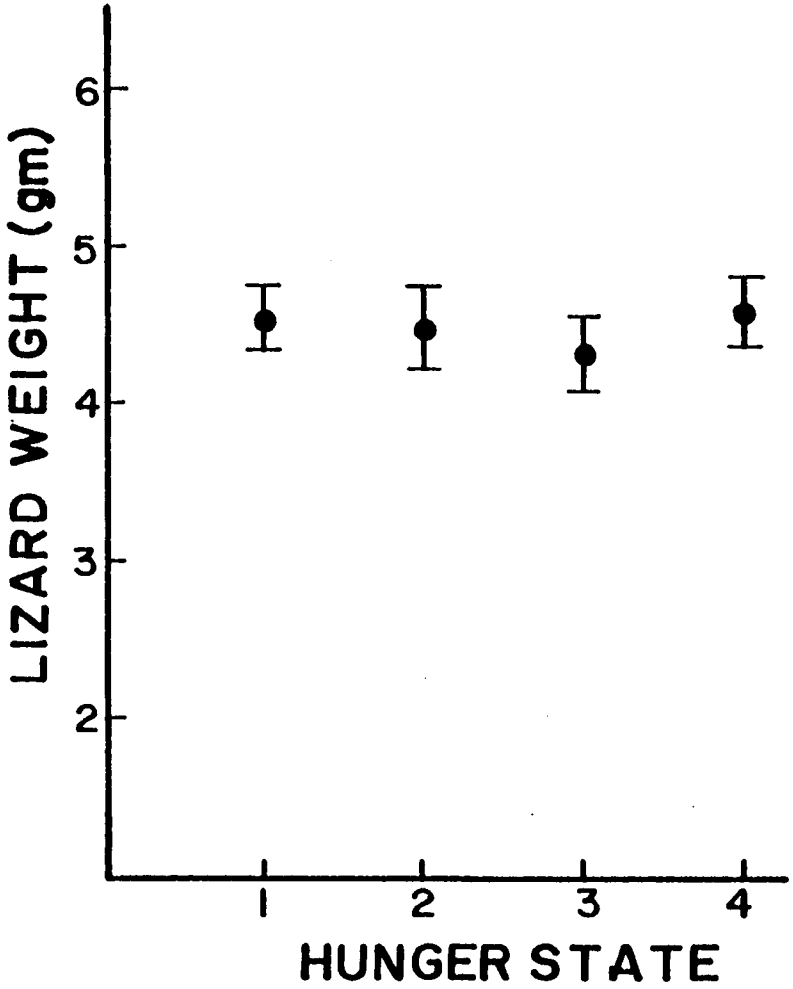


Figure 5. Weight of lizard vs. hunger state for when a capture was made: mean ± 2 S.E.

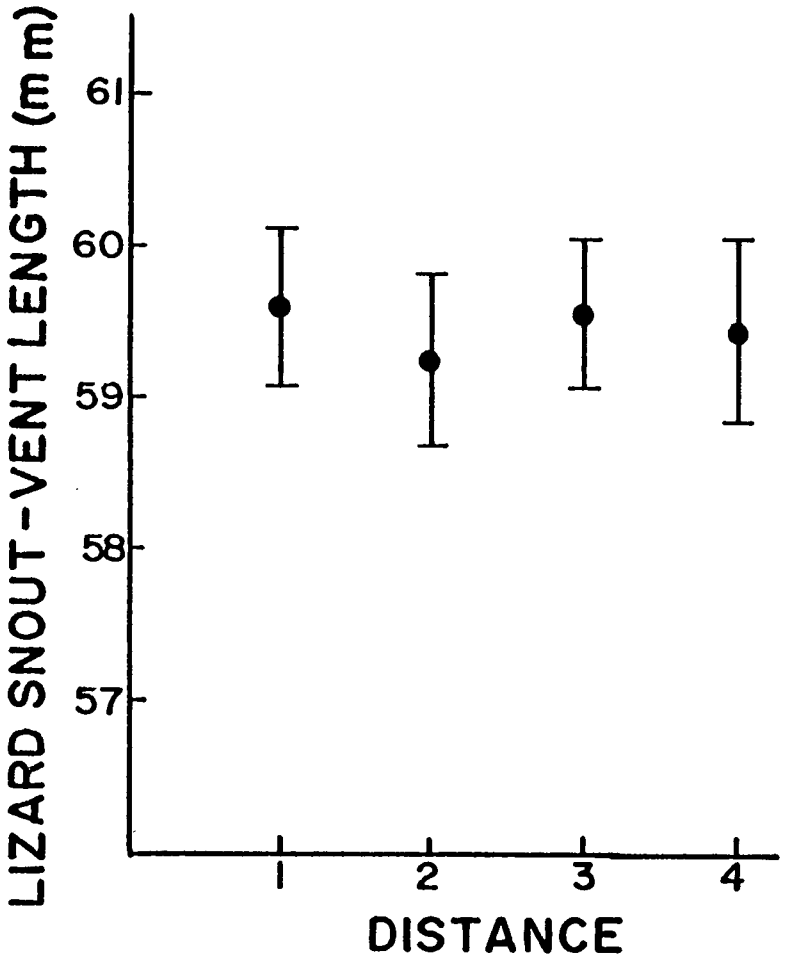


Figure 6. Snout-vent length of lizard vs. distance for when a capture was made: mean ± 2 S.E.

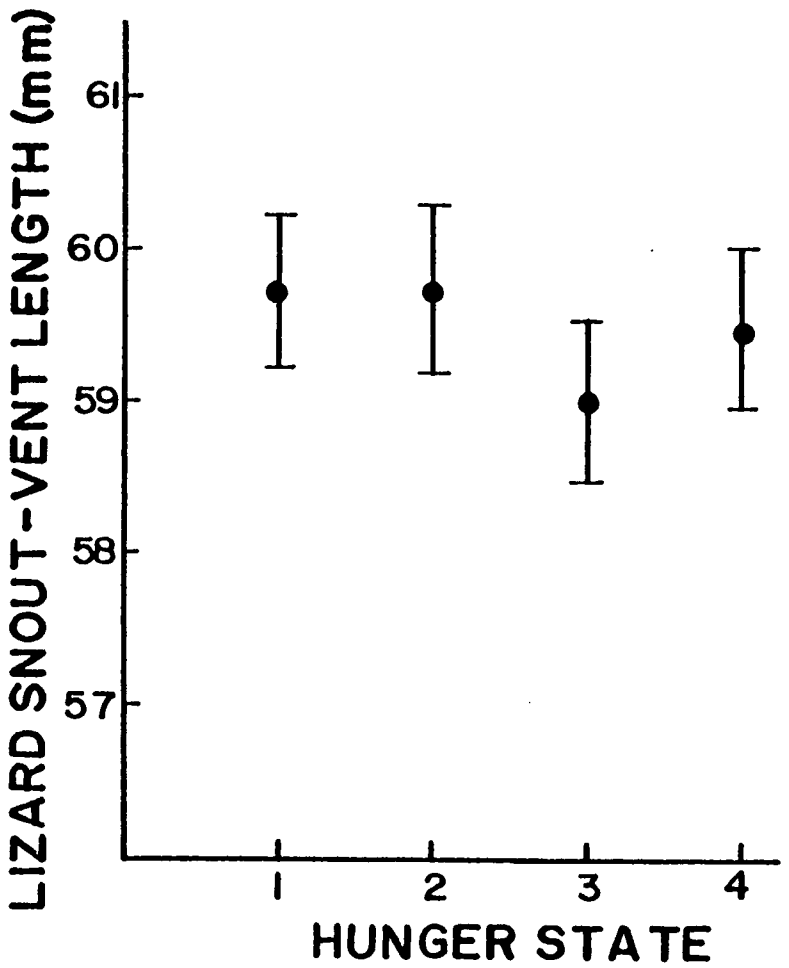


Figure 7. Snout-vent length of lizard vs. hunger state for when a capture was made: mean ± 2 S.E.

III. RESULTS

INVOLVEMENT TIME ANALYSIS

Involvement time is the total time dedicated to one prey item. It consists of the variables handling and pursuit time. Recognition time is inherent and understood to be instantaneous; there was no way to objectively evaluate it. The range for transformed values of involvement time was 2.48 to 5.83 seconds.

The results of the analysis of variance for involvement time can be found in Tables 1 and 2. In each table the major effects, distance and hunger, are broken down into their linear, quadratic, and cubic components. Since none of the interactions (see Table 1) were significant at the 0.05 level, they were included in the error term and the appropriate tests were run and tabulated in Table 2. The only effects statistically significant at the 0.05 level were replicate and linear distance. However, linear hunger was significant at the 0.06 level.

A three dimensional representation of the response surface is depicted in Figure 8. The linear model for involvement time utilizes the following parameters: replicate, distance, and hunger and mathematically appears as Involvement time = 3.75484 + 0.34221D - 0.10220H.

Comparison of least squares means are given in Table 3. Comparisons between level 1 of each effect and levels 2, 3, and 4 were made. Comparisons were also made between level 2 vs. 3 and 4

Table 1. Analysis of variance for involvement time with interactions in the model.

Source of Variation	df	ss	ms	F Value	PR>F
REPLICATE	9	9.201	1.022	2.65	*
TREATMENT	15				
DISTANCE	3				
D	1	14.829		38.50	*
D^2	1	0.406		1.05	
D^3	1	0.006		0.02	
HUNGER	3				
H	1	1.313		3.41	*
H^2	1	0.455		1.18	
H^3	1	0.337		0.87	
DISTANCE*HUNGER	9				
D*H	1	0.666		1.73	
$D*H^2$	1	0.001		0.00	
$D*H^3$	1	0.000		0.00	
D^2*H	1	0.019		0.05	
D^2*H^2	1	0.880		2.28	
D^2*H^3	1	0.216		0.56	
D^3*H	1	0.015		0.04	
D^3*H^2	1	0.000		0.00	
D^3*H^3	1	0.006		0.01	
Corrected total	101				
Error	77	29.658	0.385		

*=significance at the alpha 0.05 level.

Table 2. Analysis of variance for involvement time with interactions in the error term.

Source of Variation	df	ss	ms	F Value	PR>F
REPLICATE	9	9.201	1.022	2.79	*
TREATMENT	15				
DISTANCE	3				
D	1	14.829		40.36	*
D^2	1	0.406		0.77	
D^3	1	0.006		0.06	
HUNGER	3				
H	1	1.313		3.59	*
H^2	1	0.455		1.24	
H^3	1	0.337		0.92	
Corrected total	101				
Error	86	31.461	0.366		

*=significance at the alpha 0.05 level.

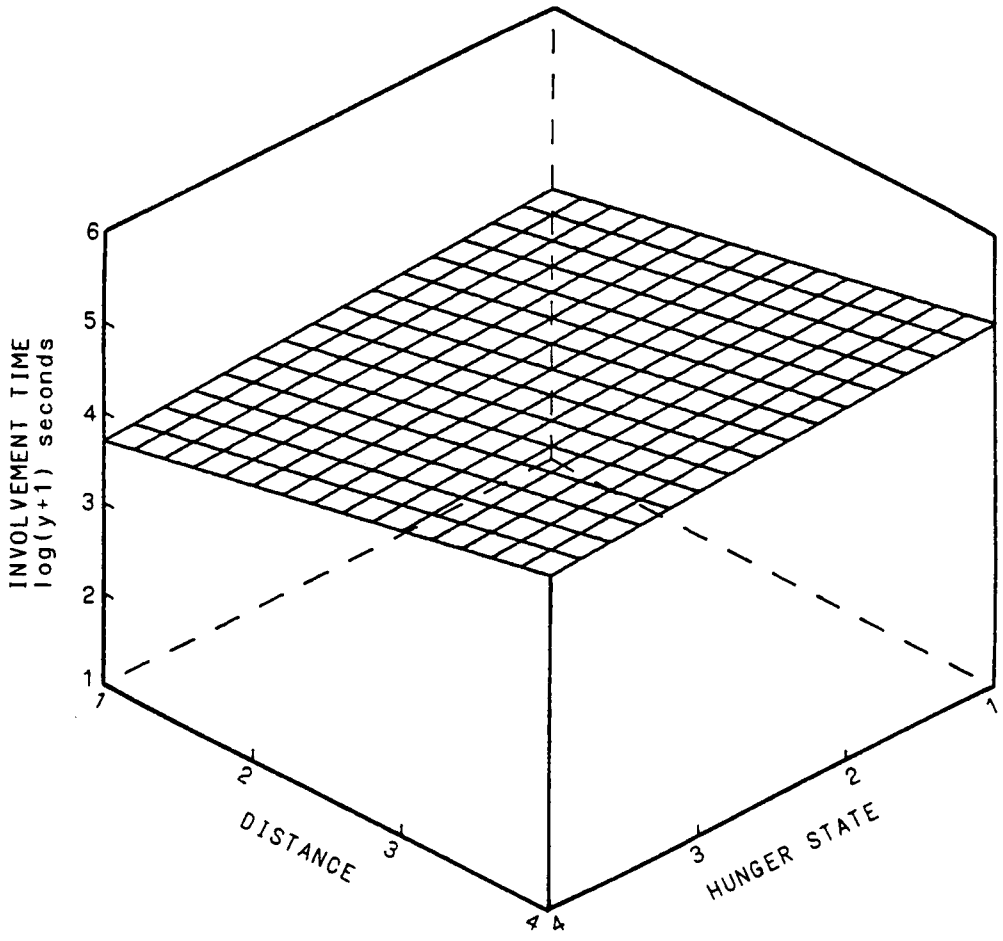


Figure 8. Three dimensional response surface for involvement time as affected by distance and hunger state.

Table 3. Least squares means, standard errors, and least squares mean comparisons for involvement time.

Variable		LSMEAN	Std. Err.	Ho: LSMEAN (I) = LSMEAN (J) 2	3	4
Distance	1	3.79	0.12	*	*	*
	2	4.19	0.14		*	*
	3	4.58	0.12			
	4	4.79	0.14			
Hunger	1	4.59	0.14	*		*
	2	4.21	0.13			
	3	4.31	0.12			
	4	4.23	0.13			

*=significance at the alpha 0.05 level.

and level 3 vs. 4. Least squares means and standard errors are also shown. Results show a significant difference in the levels of distance 1 vs. 2, 3, 4 and 2 vs. 3, 4; there were no significant differences between distance 3 and 4. There was a significant difference between levels 1 and 2, but not between 1 and 3, 4 in the effect of hunger. No significant differences were apparent in comparisons 2 vs. 3, 4 or 3 vs. 4.

Figure 9 depicts involvement time versus distance with plotting of the least squaresmean $\pm$ 2 standard errors. Figure 10 represents involvement time versus hunger state.

It appears that distance has a definite effect on involvement time. Hunger, while having an effect, does not have a significant one if a strict alpha level of 0.05 is adhered to.

HANDLING TIME ANALYSIS

Handling time, a component of involvement time, is the time from moment of capture until the last swallow. Since deprivation states were used instead of satiation states a digestive pause time was not required. Preliminary experimentation showed lizards in all hunger states tested would readily attack another prey after swallowing the first. The range for transformed values of handling time were 2.27 to 3.98 seconds.

The analyses of variance tables for handling times are in Tables 4 and 5. The organization of these tables is the same as those for involvement time. No component (linear, quadratic, or cubic) was significant for either distance or hunger. However, the replicate effect was significant.

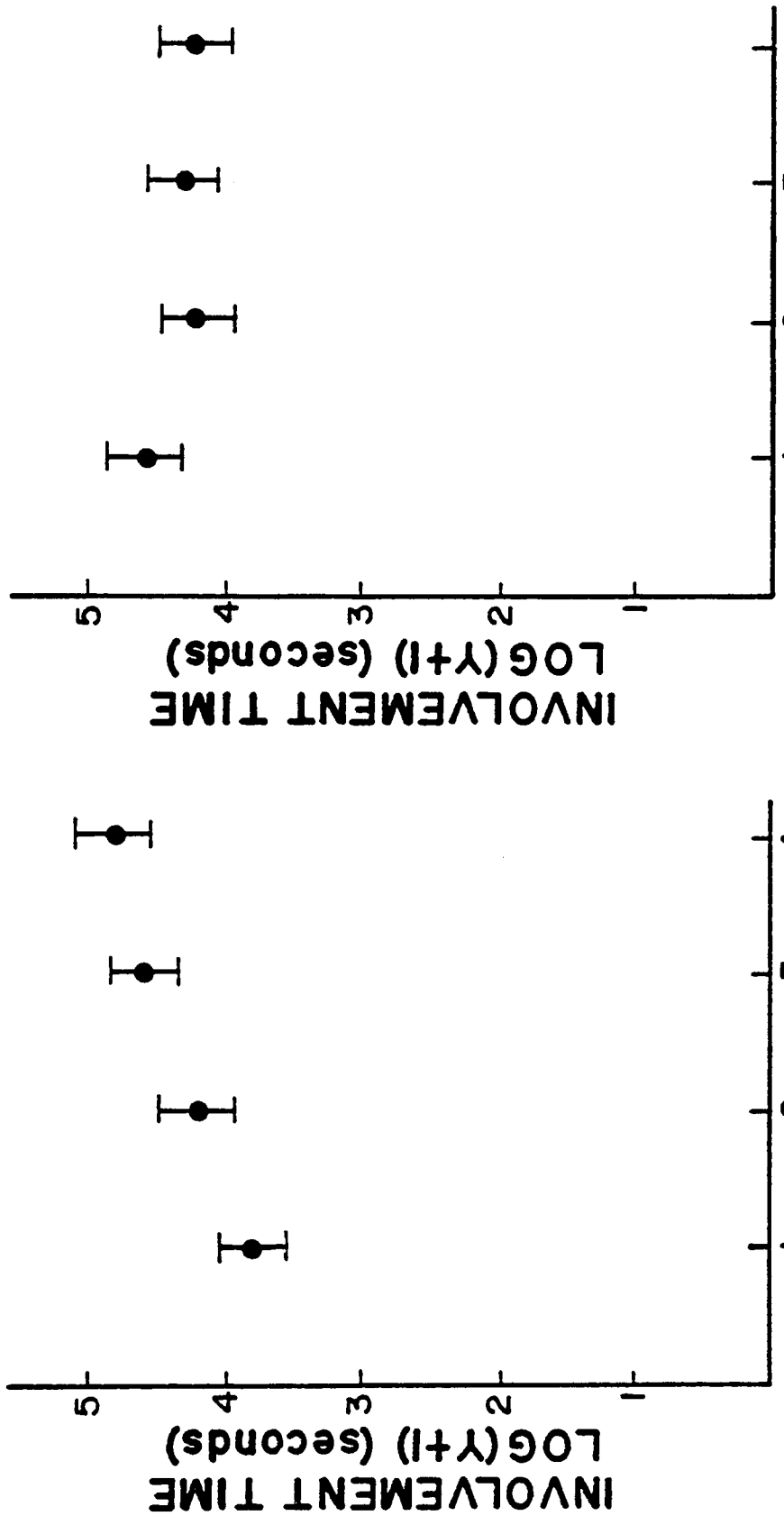


Figure 9. Least squares mean ± 2 S.E. for involvement time vs. distance.

Figure 10. Least squares mean ± 2 S.E. for involvement time vs. hunger state.

Table 4. Analysis of variance for handling time with interactions in the model.

Source of Variation	df	ss	ms	F Value	PR>F
REPLICATE	9	2.023	0.225	2.78	*
TREATMENT	15				
DISTANCE	3				
D	1	0.012		0.15	
D^2	1	0.000		0.00	
D^3	1	0.006		0.07	
HUNGER	3				
H	1	0.013		0.15	
H^2	1	0.059		0.73	
H^3	1	0.011		0.13	
DISTANCE*HUNGER	9				
D*H	1	0.088		1.08	
$D*H^2$	1	0.087		1.08	
$D*H^3$	1	0.030		0.37	
D^2*H	1	0.212		2.62	
D^2*H^2	1	0.055		0.68	
D^2*H^3	1	0.116		1.43	
D^3*H	1	0.044		0.54	
D^3*H^2	1	0.025		0.31	
D^3*H^3	1	0.050		0.62	
Corrected total	102				
Error	78	6.312	0.081		

*=significance at the alpha 0.05 level.

Table 5. Analysis of variance for handling time with interactions in the error term.

Source of Variation	df	ss	ms	F Value	PR>F
REPLICATE	9	2.023	0.225	2.79	*
TREATMENT	15				
DISTANCE	3				
D	1	0.119		0.15	
D^2	1	0.000		0.00	
D^3	1	0.006		0.07	
HUNGER	3				
H	1	0.013		0.15	
H^2	1	0.059		0.74	
H^3	1	0.011		0.13	
Corrected total	102				
Error	87	7.018	0.081		

*=significance at the alpha 0.05 level.

The response surface for handling time shown in Figure 11 is modeled linearly using the parameters of replicate, distance, and hunger. Beta values for this equation are 3.17519 - 0.00898D + 0.01152H, respectively.

Least squares means, standard errors, and comparisons are given in Table 6. The same level comparisons were made as with involvement time and at the same alpha level. With the a priori chosen comparisons no significant differences exist between levels of distance or of hunger.

Plotting of the LSMEANS for handling time vs. distance is shown in Figure 12. Handling time vs. hunger state is shown in Figure 13. Handling time, as defined in this study, is just about as constant as one could expect dealing with biological data. Therefore, handling time should not be affected by either the distance a predator must go for a prey item or the length of time it has been without food. However, this conclusion is limited to the confines of the levels under investigation in this study.

PURSUIT TIME ANALYSIS

Pursuit time, a component of involvement time, is the time from point of first movement toward the prey item until the moment of capture. The range for transformed values of pursuit time were 0.26 to 5.76 seconds.

Tables 7 and 8 contain the analysis of variance tables. The organization of those tables is the same as for the analysis of variance tables for involvement time. The analysis of variance shows

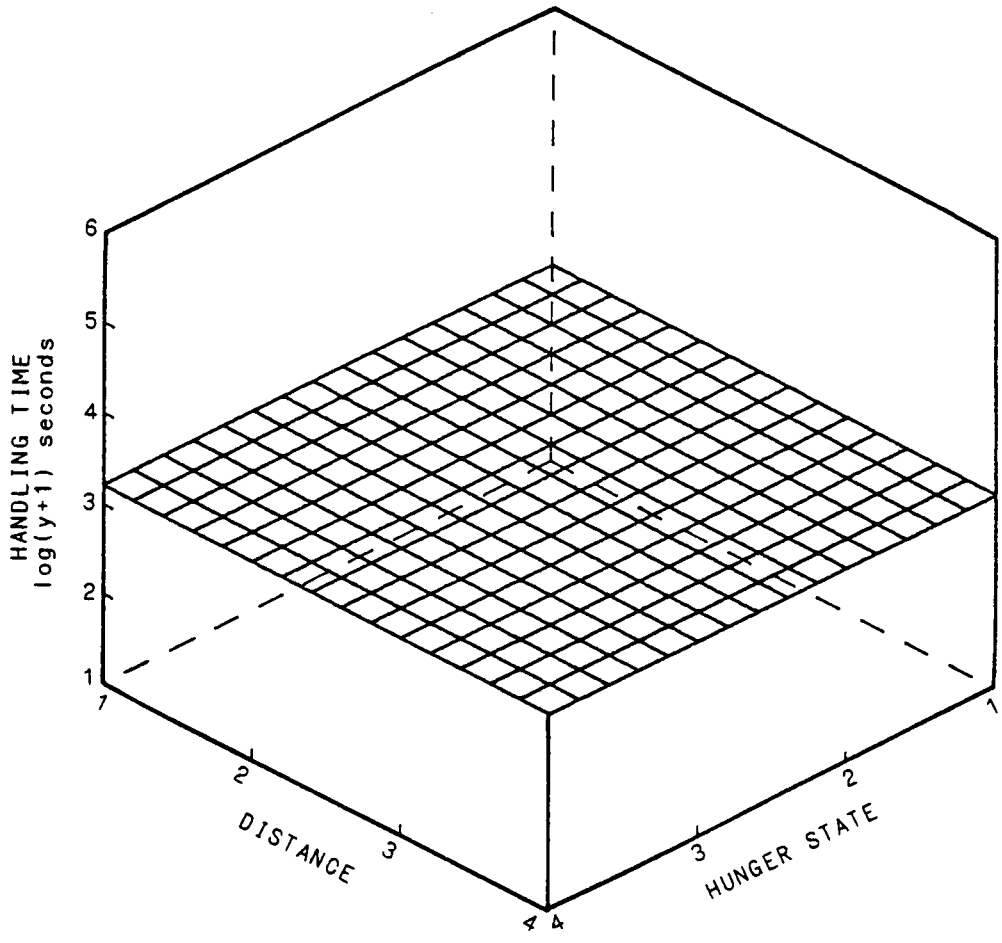


Figure 11. Three dimensional response surface for handling time as affected by distance and hunger state.

Table 6. Least squares means, standard errors, and least squares mean comparisons for handling time.

Variable		LSMEAN	Std. Err.	Ho: LSMEAN (I) = LSMEAN (J) 2	3	4
Distance	1	3.21	0.06			
	2	3.16	0.06			
	3	3.16	0.06			
	4	3.16	0.06			
Hunger	1	3.12	0.06			
	2	3.21	0.06			
	3	3.19	0.06			
	4	3.16	0.06			

*=significance at the alpha 0.05 level.

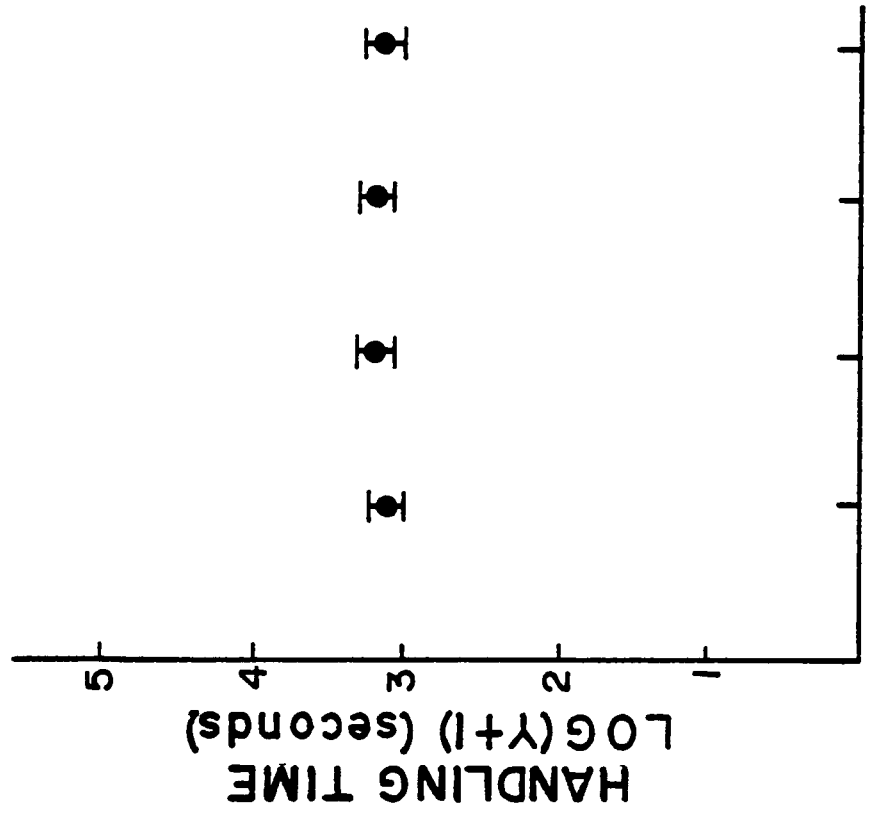


Figure 13. Least squares mean $\pm$ 2 S.E. for handling time vs. hunger state.

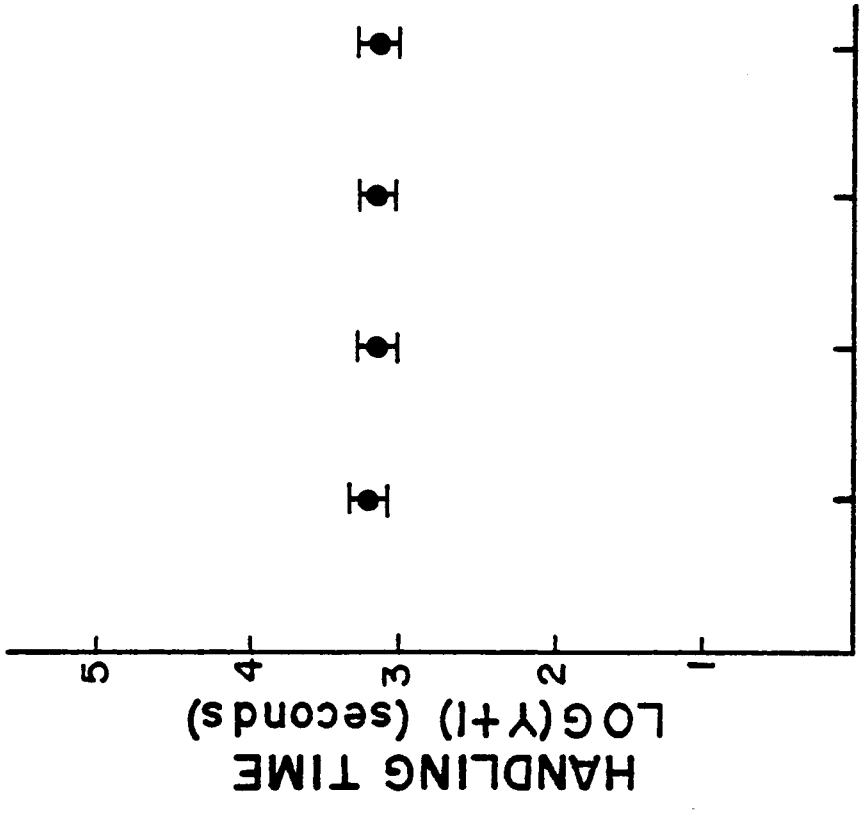


Figure 12. Least squares mean $\pm$ 2 S.E. for handling time vs. distance.

Table 7. Analysis of variance for pursuit time with interactions in the model.

Source of Variation	df	ss	ms	F Value	PR>F
REPLICATE	9	30.593	3.399	2.96	*
TREATMENT	15				
DISTANCE	3				
D	1	52.211		48.70	*
D^2	1	3.797		3.54	
D^3	1	0.007		0.01	
HUNGER	3				
H	1	5.840		5.09	*
H^2	1	1.536		1.34	
H^3	1	2.393		2.09	
DISTANCE*HUNGER	9				
D*H	1	0.388		0.34	
$D*H^2$	1	0.620		0.54	
$D*H^3$	1	0.048		0.04	
D^2*H	1	0.102		0.09	
D^2*H^2	1	1.371		1.20	
D^2*H^3	1	0.479		0.42	
D^3*H	1	0.300		0.26	
D^3*H^2	1	0.327		0.29	
D^3*H^3	1	0.138		0.12	
Corrected total	103				
Error	79	90.571	1.147		

*=significance at the alpha 0.05 level.

Table 8. Analysis of variance for pursuit time with interactions in the error term.

Source of Variation	df	ss	ms	F Value	PR>F
REPLICATE	9	30.593	3.399	3.17	*
TREATMENT	15				
DISTANCE	3				
D	1	52.211		48.70	*
D^2	1	3.797		3.54	
D^3	1	0.007		0.01	
HUNGER	3				
H	1	5.840		5.45	*
H^2	1	1.536		1.43	
H^3	1	2.393		2.23	
Corrected total	103				
Error	88	94.344	1.072		

*=significance at the alpha 0.05 level.

a significant effect for replicate, linear distance, and linear hunger. Quadratic distance is borderline ($P < 0.06$).

The response surface in Figure 14 for pursuit time was modeled linearly using the following parameters: replicate, distance, and hunger. Beta values are 2.63437 + 0.63287D - 0.207438H, respectively.

Least squares means, standard errors, and selected comparisons are shown in Table 9. The comparisons made are the same as for involvement time and at the same alpha level. A significant difference was shown between distance level 1 and the other levels. A significant difference was also evident between distance 2 and 4, but not between 2 and 3 ($P < 0.06$). The least squares means for pursuit time vs. distance are graphically presented in Figure 15. A significant difference was shown between hunger state 1 and 2 and 4; however, the significance level between 1 and 3 was 0.07. No further comparisons were shown to be statistically different. The least square means for pursuit time vs. hunger state are shown in Figure 16.

Pursuit time is affected by both distance and hunger state.

MOVE TIME ANALYSIS

Move time, a component of pursuit time, represents the time devoted to actual movement by the predator from the instant it first moved toward the prey item until moment of capture. Transformed values for move time ranged from 0.262 to 3.292 seconds.

Tables 10 and 11 contain the analysis of variance results. These tables are arranged the same as previous ones. The linear component of distance is the only significant effect.

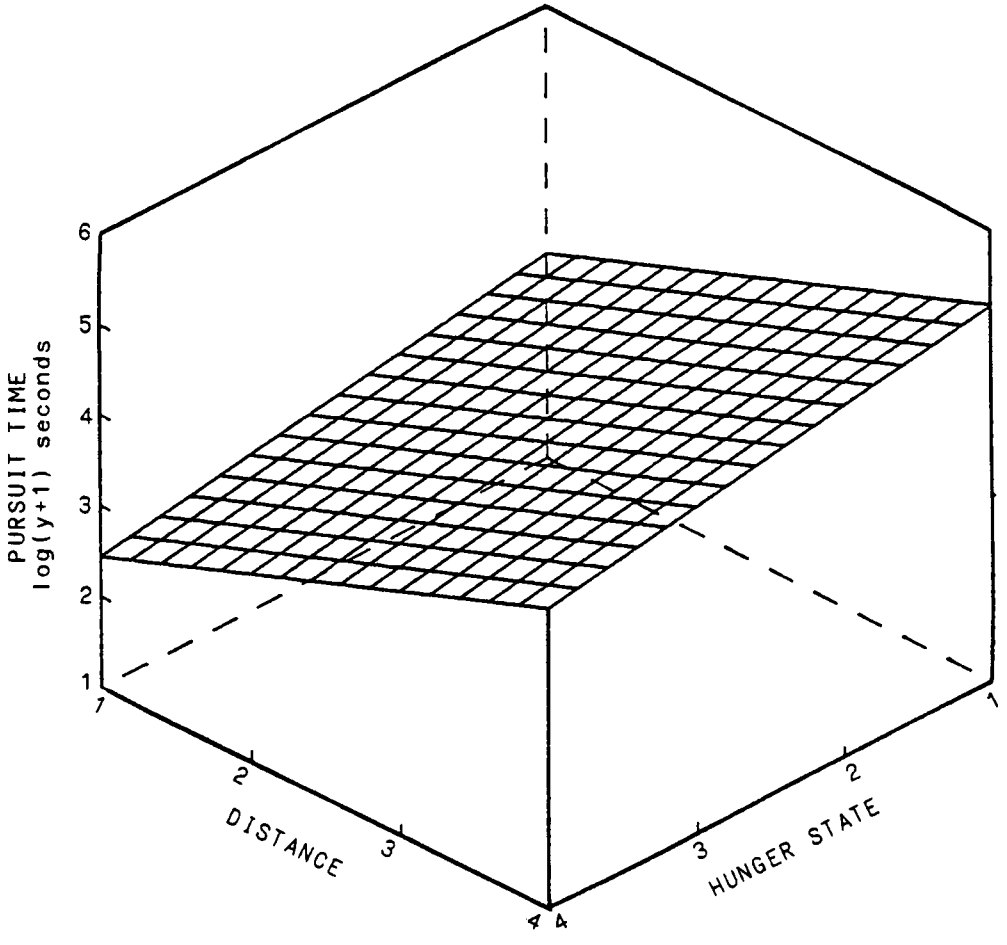


Figure 14. Three dimensional response surface for pursuit time as affected by distance and hunger state.

Table 9. Least squares means, standard errors, and least squares mean comparisons for pursuit time.

Variable		LSMEAN	Std. Err.	Ho: LSMEAN (I) = LSMEAN (J) 2	3	4
Distance	1	2.59	0.21	*	*	*
	2	3.55	0.24			*
	3	4.17	0.21			
	4	4.39	0.23			
Hunger	1	4.24	0.23	*		*
	2	3.40	0.23			
	3	3.66	0.21			
	4	3.40	0.22			

*=significance at the alpha 0.05 level.

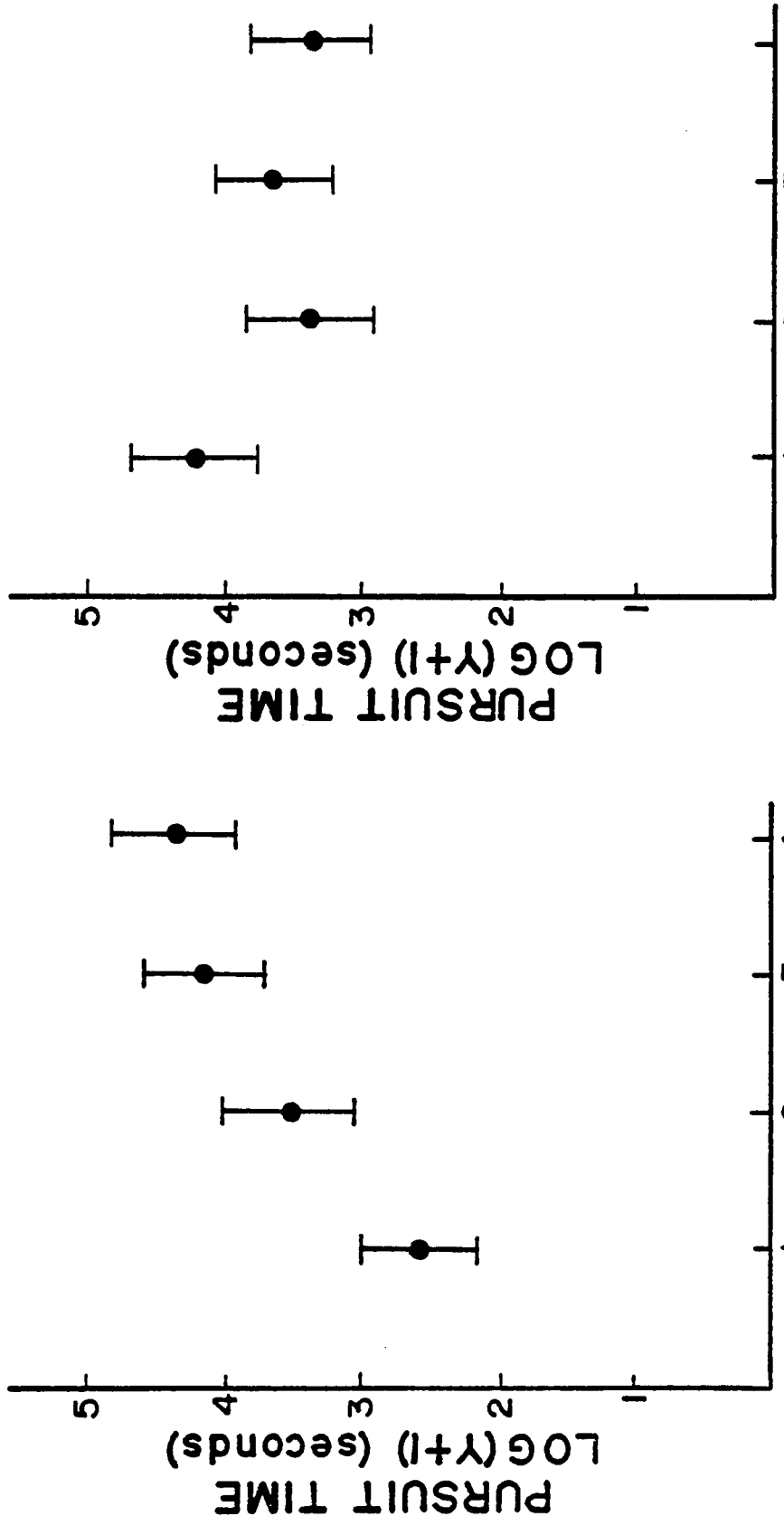


Figure 15. Least squares mean ± 2 S.E. for pursuit time vs. distance.

Figure 16. Least squares mean ± 2 S.E. for pursuit time vs. hunger state.

Table 10. Analysis of variance for move time with interactions in the model.

Source of Variation	df	ss	ms	F Value	PR>F
REPLICATE	9	4.019	0.447	1.43	
TREATMENT	15				
DISTANCE	3				
D	1	14.584		46.79	*
D^2	1	0.237		0.76	
D^3	1	0.330		1.06	
HUNGER	3				
H	1	0.218		0.70	
H^2	1	0.681		2.18	
H^3	1	0.226		0.72	
DISTANCE*HUNGER	9				
D*H	1	0.253		0.81	
$D*H^2$	1	0.130		0.42	
$D*H^3$	1	0.279		0.90	
D^2*H	1	0.892		2.86	
D^2*H^2	1	0.503		1.61	
D^2*H^3	1	0.065		0.21	
D^3*H	1	0.134		0.43	
D^3*H^2	1	0.284		0.91	
D^3*H^3	1	0.356		1.14	
Corrected total	102				
Error	78	24.312	0.312		

*=significance at the alpha 0.05 level.

Table 11. Analysis of variance for move time with interactions in the error term.

Source of Variation	df	ss	ms	F Value	PR>F
REPLICATE	9	4.019	0.447	1.43	
TREATMENT	15				
DISTANCE	3				
D	1	14.584		46.63	*
D^2	1	0.237		0.76	
D^3	1	0.330		1.06	
HUNGER	3				
H	1	0.218		0.70	
H^2	1	0.681		2.18	
H^3	1	0.226		0.72	
Corrected total	102				
Error	87	27.208	0.313		

*=significance at the alpha 0.05 level.

The response surface in Figure 17 was modeled linearly using beta values of 1.1893 + 0.33837D - 0.03343H. These values were estimated by the following parameters: replicate, distance, and hunger.

Least squares means, standard errors, and comparisons are shown in Table 12. The comparisons made are the same as with pursuit time and based on the same probability level. A significant difference exists between distance 1 and distances 3 and 4. The difference between 1 and 2 is non-significant at $P < 0.07$. There is a significant difference between distance 2 and distances 3 and 4. The least squares means for move time vs. distance can be found in Figure 18. The comparisons between the levels of hunger provided one difference that was significant, that being between hunger state 1 and 2. The means for move time vs. hunger state are shown in Figure 19.

Move time is affected by the distance a predator must travel to obtain a prey item, but not the state of deprivation it is experiencing.

STOP TIME ANALYSIS

Stop time, the second subcomponent of pursuit time, is the amount of time the lizard spent in a stationary position after initially starting toward the prey item until the instant of capture. Transformed values ranged from 0.0 to 5.70 seconds with 13 values at 0.

Analysis of variance results are shown in Tables 13 and 14. Significance was shown by the replicate effect and the linear

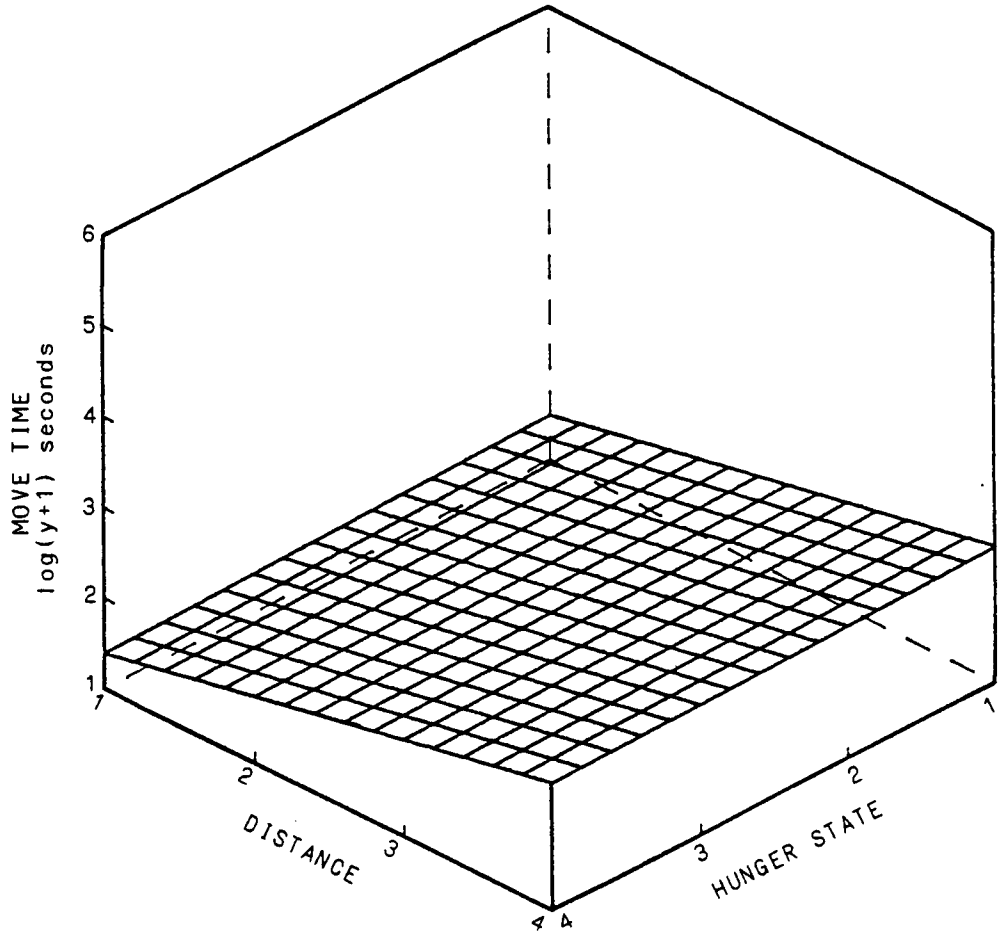


Figure 17. Three dimensional response surface for move time as affected by distance and hunger state.

Table 12. Least squares means, standard errors, and least squares mean comparisons for move time.

Variable		LSMEAN	Std. Err.	Ho: LSMEAN (I) = LSMEAN (J) 2	3	4
Distance	1	1.42	0.11		*	*
	2	1.72	0.12		*	*
	3	2.20	0.11			
	4	2.34	0.12			
Hunger	1	2.12	0.12	*		
	2	1.78	0.12			
	3	1.85	0.11			
	4	1.93	0.12			

*=significance at the alpha 0.05 level.

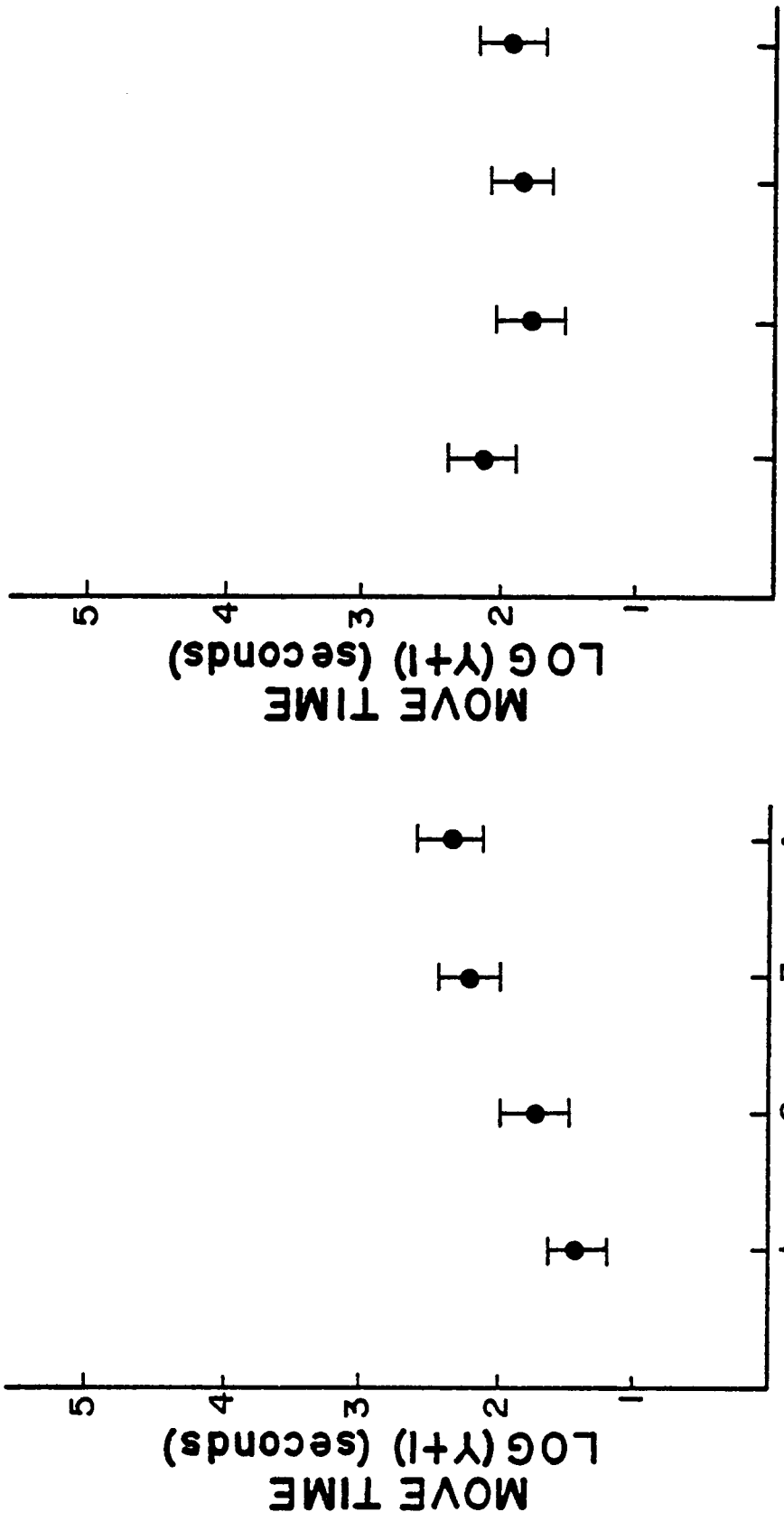


Figure 18. Least squares mean ± 2 S.E. for move time vs. distance.

Figure 19. Least squares mean ± 2 S.E. for move time vs. hunger state.

Table 13. Analysis of variance for stop time with interactions in the model.

Source of Variation	df	ss	ms	F Value	PR>F
REPLICATE	9	40.289	4.477	2.33	*
TREATMENT	15				
DISTANCE	3				
D	1	74.153		38.59	*
D^2	1	6.089		3.17	
D^3	1	0.072		0.04	
HUNGER	3				
H	1	12.912		7.17	*
H^2	1	1.368		0.76	
H^3	1	4.636		2.58	
DISTANCE*HUNGER	9				
D*H	1	0.762		0.40	
$D*H^2$	1	0.011		0.01	
$D*H^3$	1	1.573		0.82	
D^2*H	1	0.924		0.48	
D^2*H^2	1	0.680		0.35	
D^2*H^3	1	2.008		1.04	
D^3*H	1	0.003		0.00	
D^3*H^2	1	0.792		0.41	
D^3*H^3	1	0.024		0.01	
Corrected total	102				
Error	78	149.869	1.921		

*=significance at the alpha 0.05 level.

Table 14. Analysis of variance for stop time with interactions in the error term.

Source of Variation	df	ss	ms	F Value	PR>F
REPLICATE	9	40.289	4.477	2.49	*
TREATMENT	15				
DISTANCE	3				
D	1	74.153		41.18	*
D^2	1	6.089		3.38	
D^3	1	0.072		0.04	
HUNGER	3				
H	1	12.912		7.17	*
H^2	1	1.368		0.76	
H^3	1	4.636		2.58	
Corrected total	102				
Error	87	156.645	1.801		

*=significance at the alpha 0.05 level.

components of both distance and hunger. The quadratic component of distance was non-significant at $P < 0.07$.

The three dimensional representation shown in Figure 20 was linearly modeled using beta values derived from the equation Stop time = REPLICATE DISTANCE HUNGER. Beta values are 2.26464 + 0.75538D - 0.31699H, respectively.

Least squares means, standard errors, and comparisons are shown in Table 15. The comparisons made are the same as for pursuit time and evaluated at the same alpha level. A significant difference exists between distance 1 and distances 2, 3, and 4. A significant difference was shown between distances 2 and 4 with the difference between 2 and 3 equal to $P < 0.07$. No significant difference exists between distances 3 and 4. Figure 21 illustrates stop time vs. distance. The comparisons between the levels of hunger show significant differences between 1 and 2, 4. The difference between 1 and 3 was $P < 0.10$. The means of stop time vs. hunger are plotted in Figure 22.

Stop time is affected by both distance and hunger.

WAIT TIME ANALYSIS

Wait time, one of two components of stop time, is the stationary time that the lizard's head was in line with the body and aligned parallel with the dowel. Transformation values ranged from 0.0 to 5.35 seconds with 13 values of 0.

Analysis of variance results are presented in Tables 16 and 17. These tables are arranged the same as previous analysis of variance

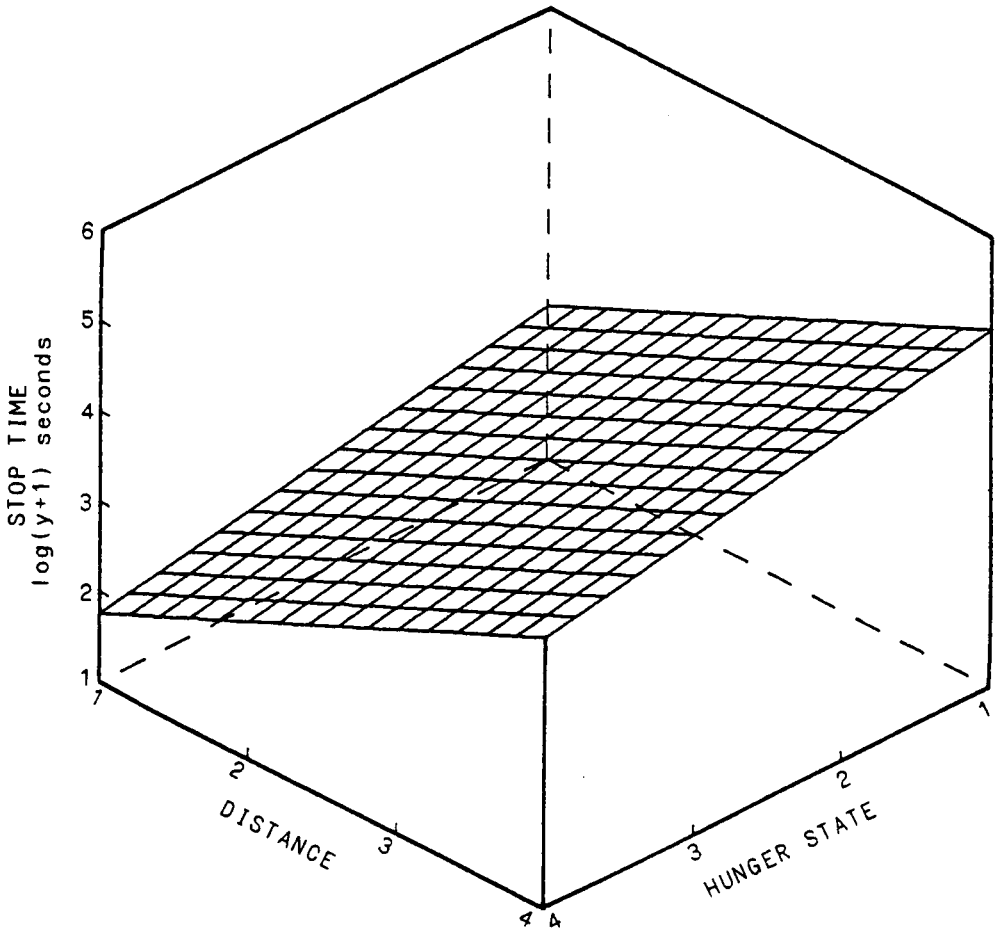


Figure 20. Three dimensional response surface for stop time as affected by distance and hunger state.

Table 15. Least squares means, standard errors, and least squares mean comparisons for stop time.

Variable		LSMEAN	Std. Err.	Ho: LSMEAN (I) = LSMEAN (J) 2	3	4
Distance	1	2.04	0.27	*	*	*
	2	3.20	0.31			*
	3	3.95	0.28			
	4	4.14	0.30			
Hunger	1	4.07	0.30	*		*
	2	3.05	0.30			
	3	3.38	0.28			
	4	2.83	0.29			

*=significance at the alpha 0.05 level.

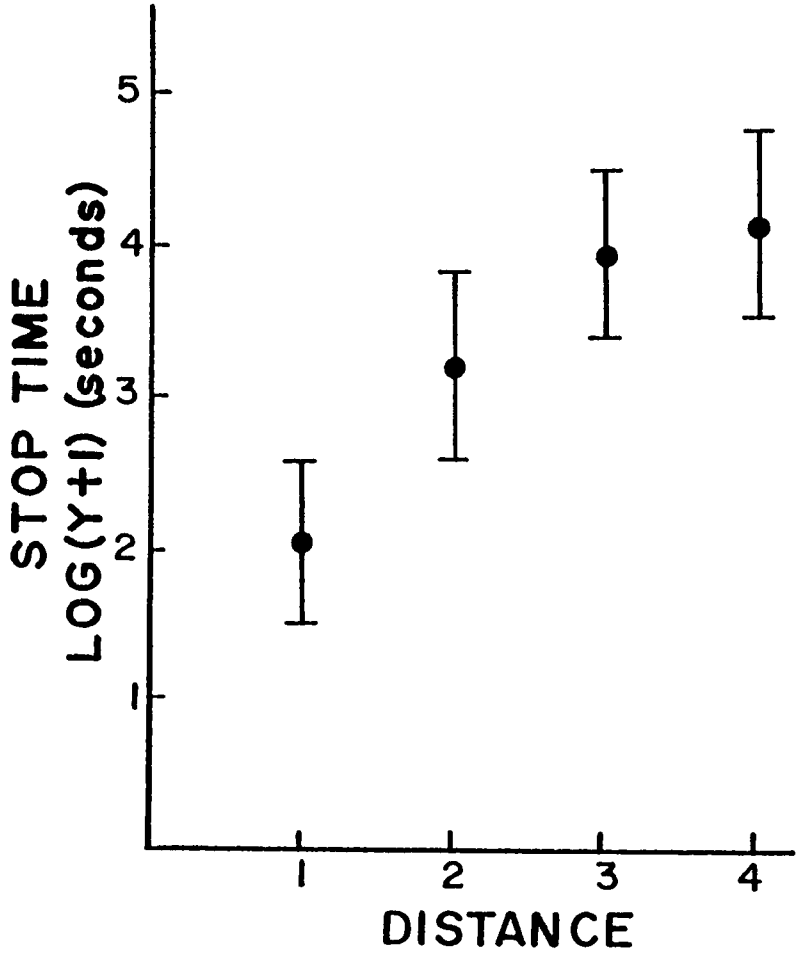


Figure 21. Least squares mean ± 2 S.E. for stop time vs. distance.

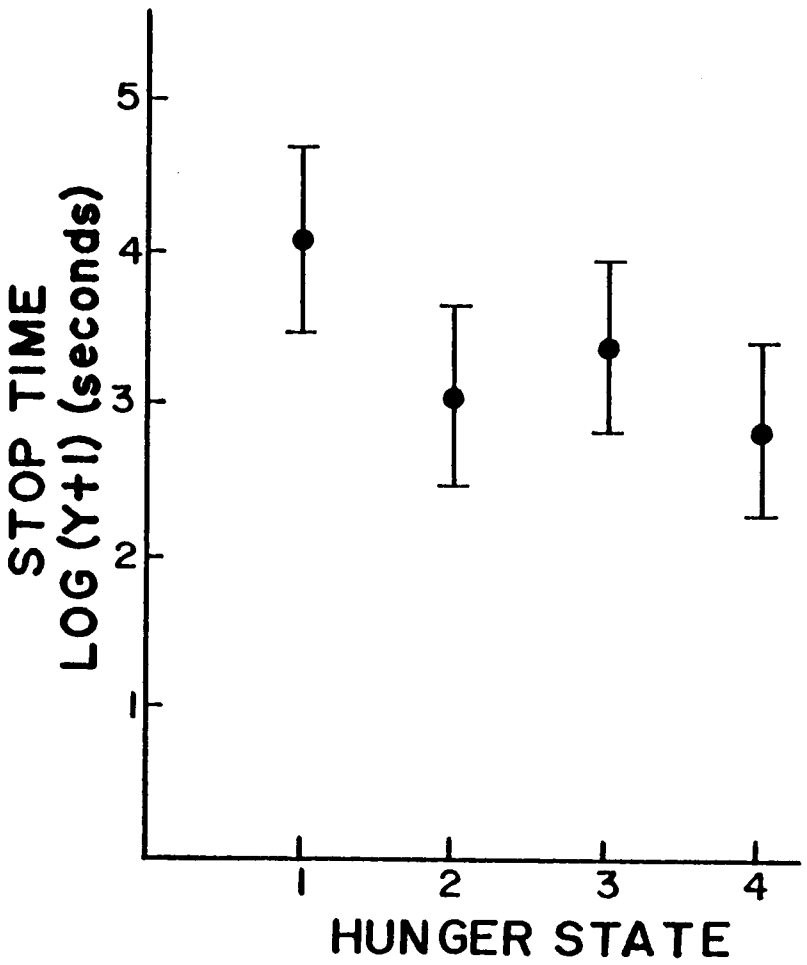


Figure 22. Least squares mean ± 2 S.E. for stop time vs. hunger state.

Table 16. Analysis of variance for wait time with interactions in the model.

Source of Variation	df	ss	ms	F Value	PR>F
REPLICATE	9	47.541	5.282	3.62	*
TREATMENTS	15				
DISTANCE	3				
D	1	57.930		39.69	*
D^2	1	3.470		2.38	
D^3	1	0.765		0.52	
HUNGER	3				
H	1	8.662		5.93	*
H^2	1	2.070		1.42	
H^3	1	3.800		2.60	
DISTANCE*HUNGER	9				
D*H	1	0.554		0.38	
$D*H^2$	1	0.883		0.60	
$D*H^3$	1	0.162		0.11	
D^2*H	1	0.167		0.11	
D^2*H^2	1	1.472		1.01	
D^2*H^3	1	0.283		0.19	
D^3*H	1	0.628		0.43	
D^3*H^2	1	0.713		0.49	
D^3*H^3	1	0.074		0.05	
Corrected total	102				
Error	78	113.845	1.460		

*=significance at alpha 0.05 level.

Table 17. Analysis of variance for wait time with interactions in the error term.

Source of Variation	df	ss	ms	F Value	PR>F
REPLICATE	9	47.541	5.282	3.87	*
TREATMENT	15				
DISTANCE	3				
D	1	57.930		42.43	*
D^2	1	3.470		2.54	
D^3	1	0.765		0.56	
HUNGER	3				
H	1	8.662		6.34	*
H^2	1	2.070		1.52	
H^3	1	3.800		2.78	
Corrected total	102				
Error	87	118.780	1.365		

*=significance at the alpha 0.05 level.

tables. Sources showing significant effects are replicate, linear distance, and linear hunger.

The response surface in Figure 23 was linearly modeled using beta values of 1.90739 + 0.6679D - 0.25223H derived from an equation using the parameters replicate, distance, and hunger.

Least squares means, standard errors, and appropriate comparisons are shown in Table 18. The mean comparisons are the same as those used in stop time, as are the alpha levels. A significant difference was shown to exist between distance 1 and distances 2, 3, and 4. There are also significant differences between distances 2 and 3, and distances 2 and 4. There is no significant difference between distances 3 and 4. The means for wait time vs. distance are plotted in Figure 24. Hunger state 1 is significantly different from states 2 and 4. The probability that hunger state 1 is different from 3 is 0.09. The means are plotted in Figure 25.

Wait time is affected by both distance and hunger.

SURVEY TIME ANALYSIS

Survey time, the second component of stop time, is the time the lizard was stopped and his head was cocked, angled, or in some way deviated from the wait position previously described. Transformed values ranged from 0.0 to 5.18 seconds with 31 values at 0. The histograms shown in Figures 26 and 27 show the effect of distance and hunger state, respectively, on trials with zero survey time. A high frequency of trials with zero survey times occurred at distance 1 with approximately equal measures of linear decline with increasing

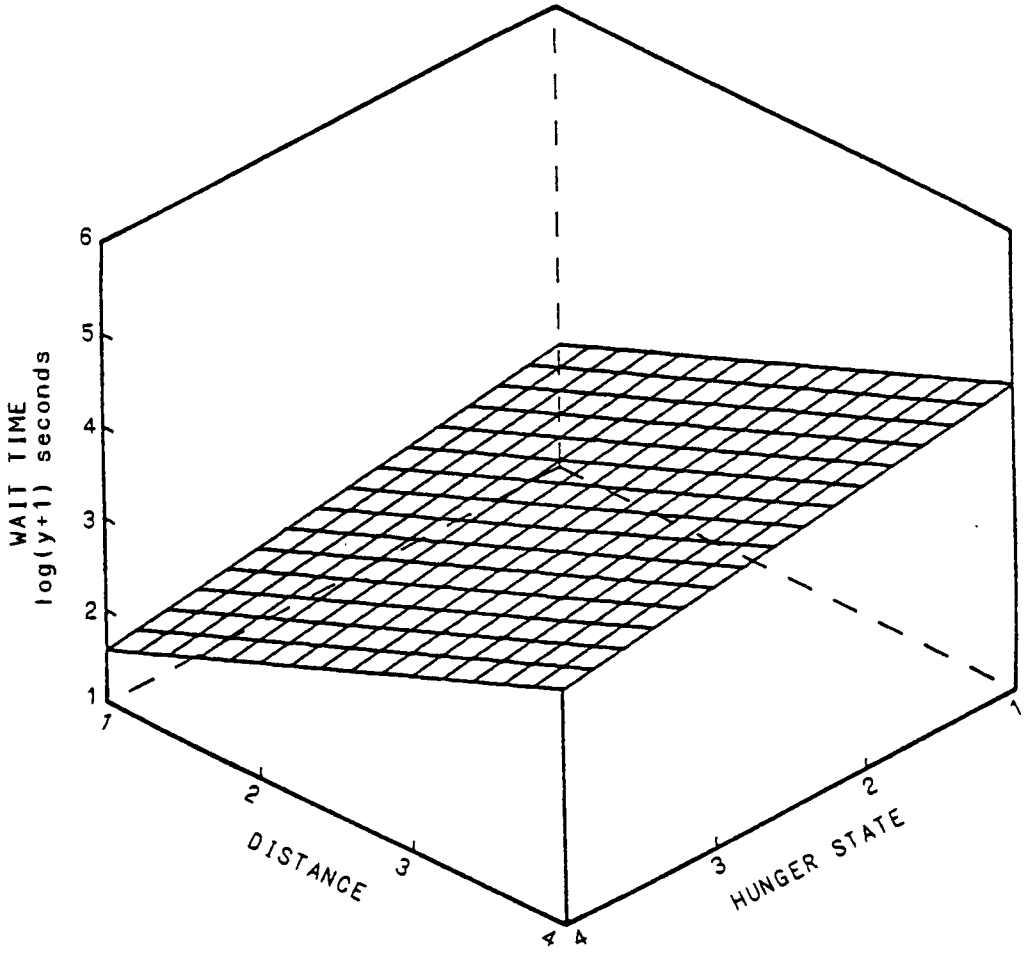


Figure 23. Three dimensional response surface for wait time as affected by distance and hunger state.

Table 18. Least squares means, standard errors, and least squares mean comparisons for wait time.

Variable		LSMEAN	Std. Err.	Ho: LSMEAN (I) = LSMEAN (J) 2	3	4
Distance	1	1.83	0.24	*	*	*
	2	2.66	0.27		*	*
	3	3.52	0.24			
	4	3.67	0.26			
Hunger	1	3.58	0.26	*		*
	2	2.59	0.26			
	3	2.95	0.24			
	4	2.55	0.25			

*=significance at the alpha 0.05 level.

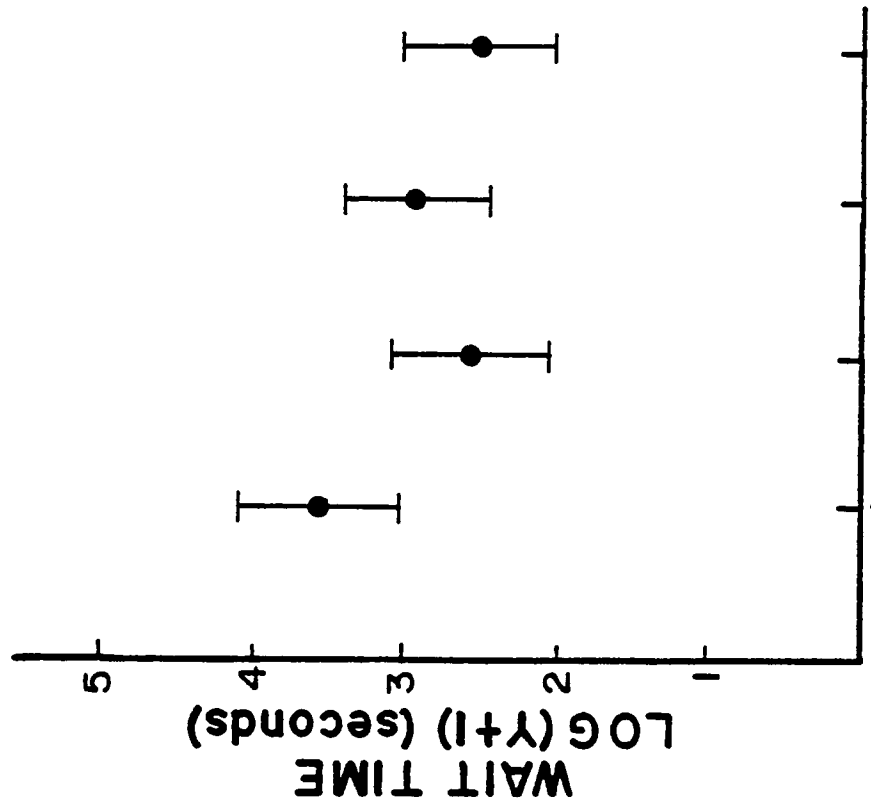


Figure 25. Least squares mean ± 2 S.E. for wait time vs. hunger state.

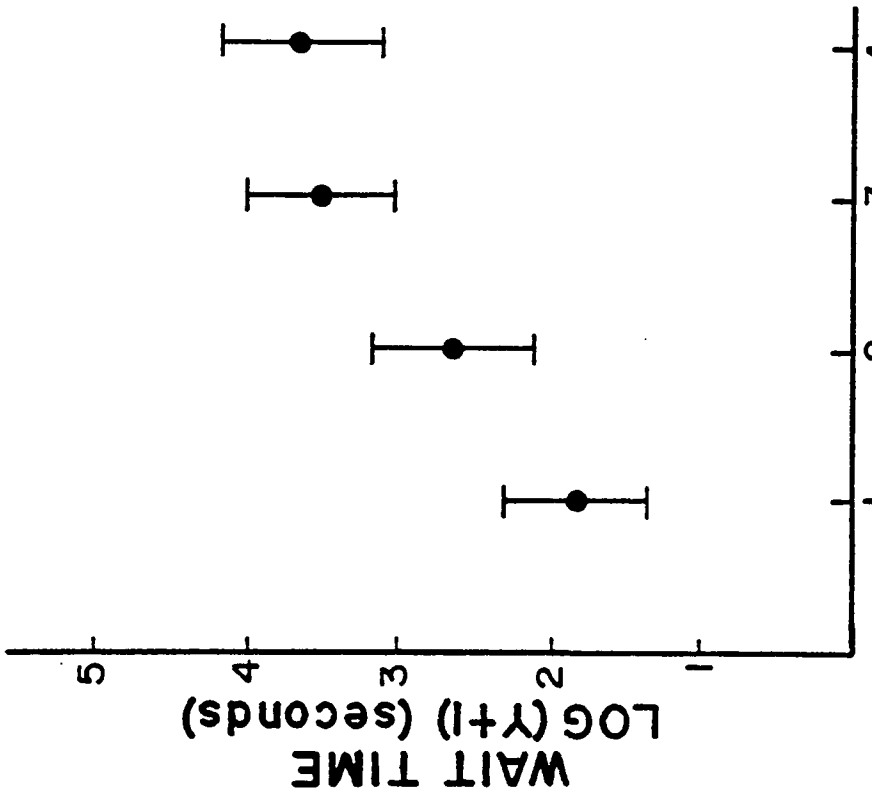


Figure 24. Least squares mean ± 2 S.E. for wait time vs. distance.

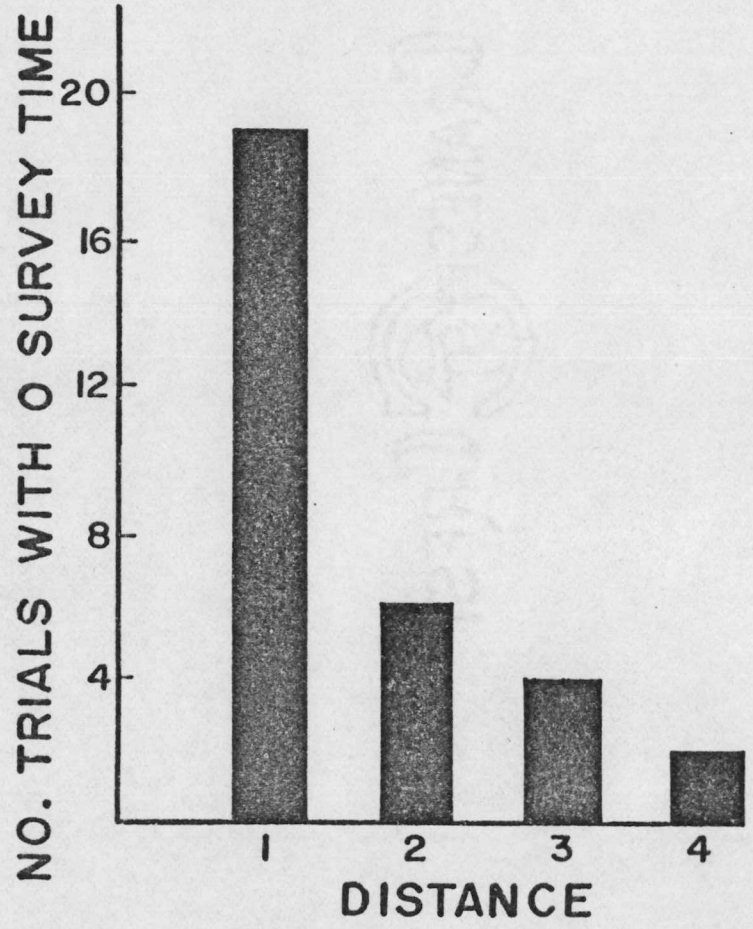


Figure 26. Histogram for trials in which no survey time occurred: frequency vs. distance.

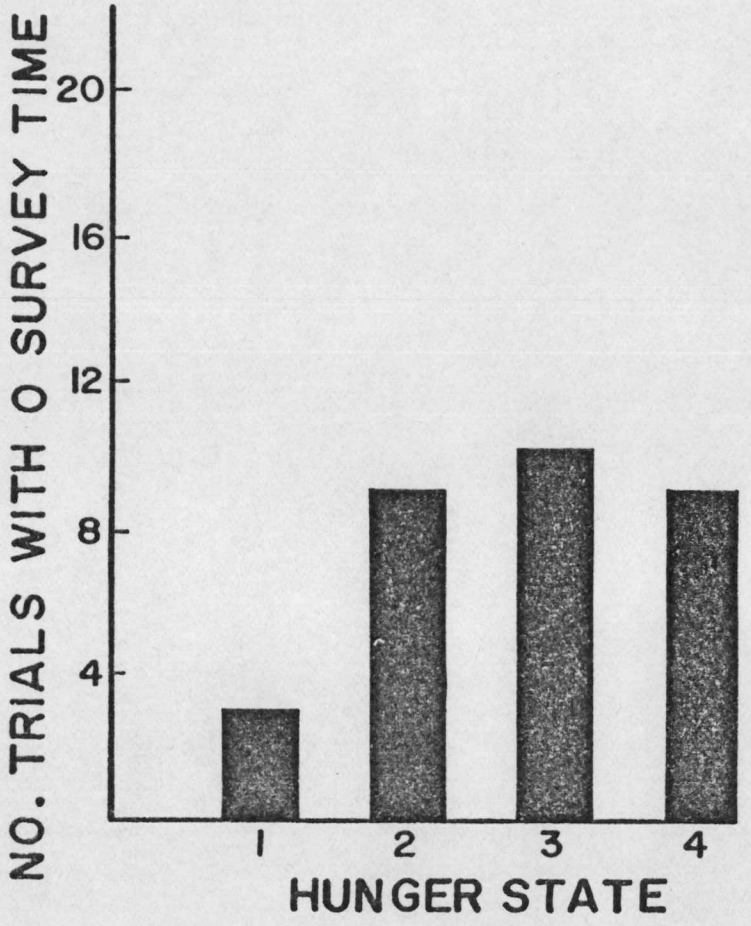


Figure 27. Histogram for trials in which no survey time occurred: frequency vs. hunger state.

distance. It can readily be seen that a significant difference exists between hunger state 1 and the other hunger states.

Analysis of variance results with interactions included in the model are found in Table 19. Analysis of variance results with interactions included in the error term are found in Table 20. Sources of variation showing significant effects are the linear components of both distance and hunger.

The linear model Survey time = REPLICATE DISTANCE HUNGER was used to generate beta values of 1.37059 + 0.66768D - 0.31823H. These values were required to produce the three dimensional presentation in Figure 28.

Least squares means, standard error, and chosen comparisons are shown in Table 21. The mean comparisons and alpha levels are the same as those used in stop time. A significant difference was shown between distance 1 and distances 2, 3, and 4. No other comparison was significantly different. However, distance 2 had a probability of 0.09 of being different from distance 4. The means for survey time vs. distance are plotted in Figure 29. Hunger state 1 is significantly different from 2 and 4; however, the comparison of 1 and 3 yielded a probability of < 0.07. No other significant differences existed. A plot of means is found in Figure 30.

Survey time is affected by both distance and hunger.

Table 19. Analysis of variance for survey time with interactions in the model.

Source of Variation	df	ss	ms	F Value	PR>F
REPLICATE	9	29.695	3.299	1.51	
TREATMENT	15				
DISTANCE	3				
D	1	57.101		26.26	*
D^2	1	3.595		1.65	
D^3	1	0.027		0.01	
HUNGER	3				
H	1	12.265		5.63	*
H^2	1	1.751		0.80	
H^3	1	1.657		0.76	
DISTANCE*HUNGER	9				
D*H	1	0.460		0.21	
$D*H^2$	1	0.003		0.00	
$D*H^3$	1	0.809		0.37	
D^2*H	1	0.311		0.14	
D^2*H^2	1	0.127		0.06	
D^2*H^3	1	2.838		1.30	
D^3*H	1	0.187		0.09	
D^3*H^2	1	4.135		1.90	
D^3*H^3	1	0.001		0.00	
Corrected total	102				
Error	78	169.905	2.178		

*=significance at the alpha 0.05 level.

Table 20. Analysis of variance for survey time with interactions in the error term.

Source of Variation	df	ss	ms	F Value	PR>F
REPLICATE	9	29.695	3.299	1.61	
TREATMENT	15				
DISTANCE	3				
D	1	57.191		27.83	*
D^2	1	3.595		1.75	
D^3	1	0.027		0.01	
HUNGER	3				
H	1	12.265		5.97	*
H^2	1	1.751		0.85	
H^3	1	1.657		0.81	
Corrected total	102				
Error	87	178.774	2.055		

*=significance at the alpha 0.05 level.

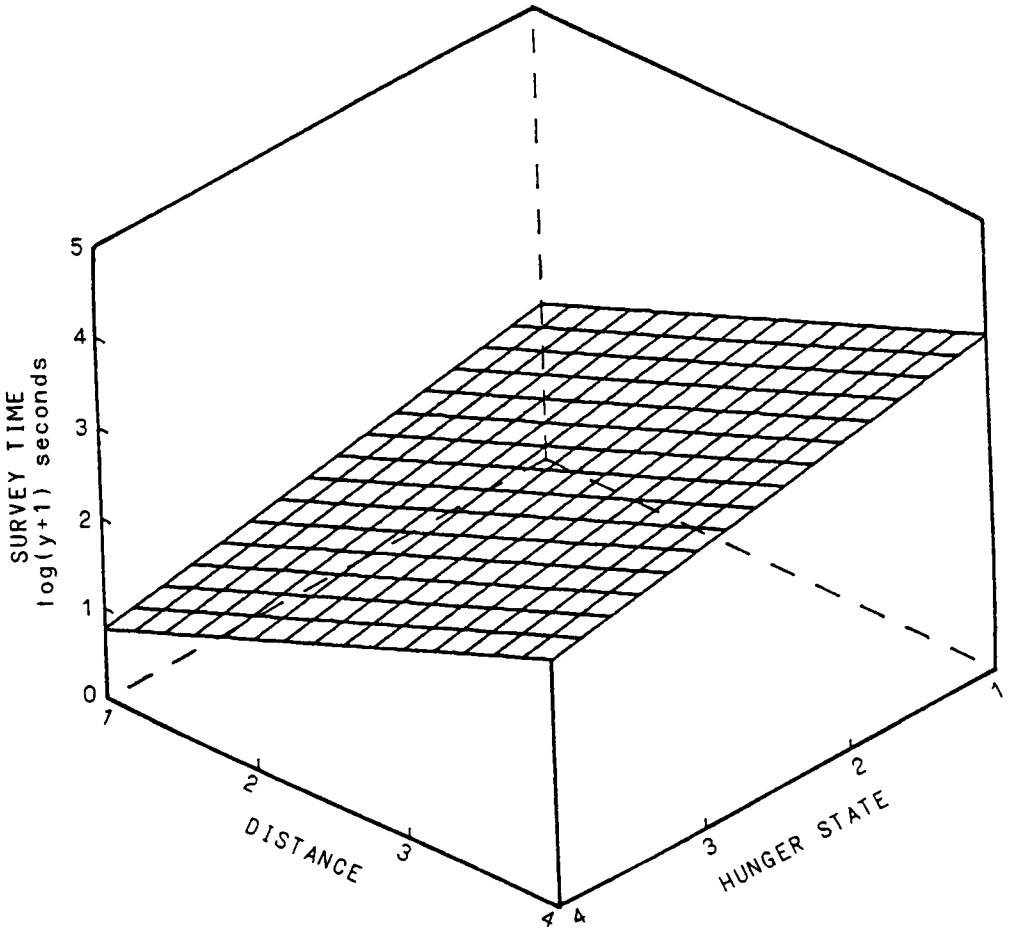


Figure 28. Three dimensional response surface for survey time as affected by distance and hunger state.

Table 21. Least squares means, standard errors, and least squares mean comparisons for survey time.

Variable		LSMEAN	Std. Err.	Ho: LSMEAN (I) = LSMEAN (J) 2	3	4
Distance	1	1.08	0.29	*	*	*
	2	2.16	0.33			
	3	2.72	0.29			
	4	2.96	0.32			
Hunger	1	2.94	0.32	*		*
	2	2.02	0.32			
	3	2.14	0.29			
	4	1.82	0.30			

*=significance at the alpha 0.05 level.

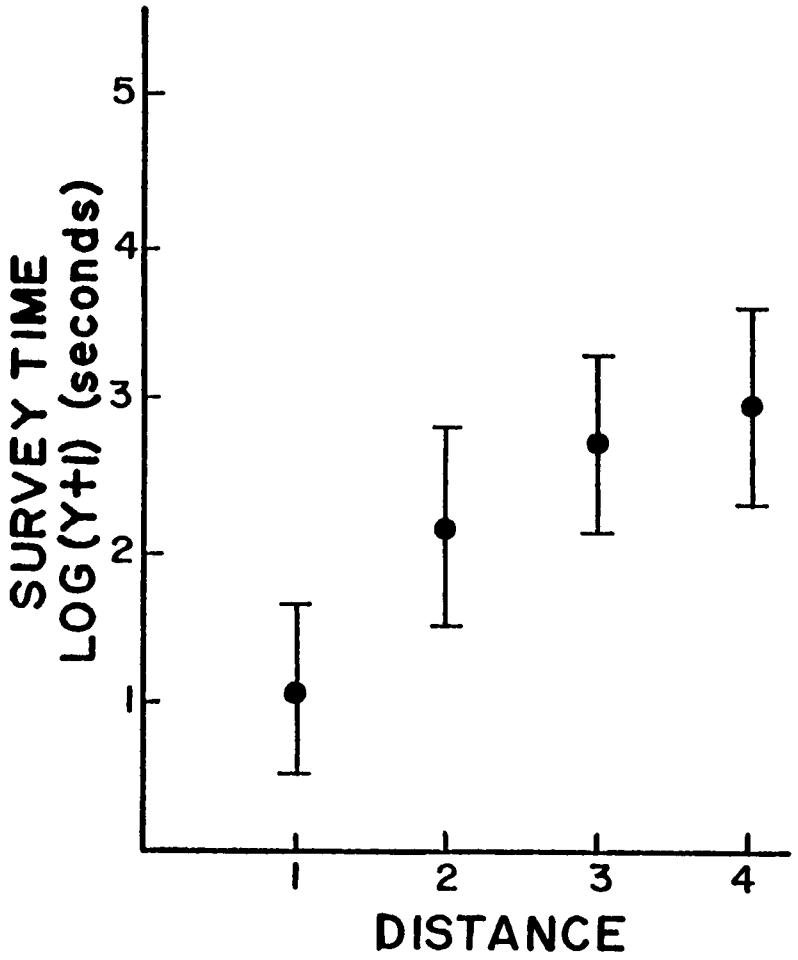


Figure 29. Least squares mean ± 2 S.E. for survey time vs. distance.

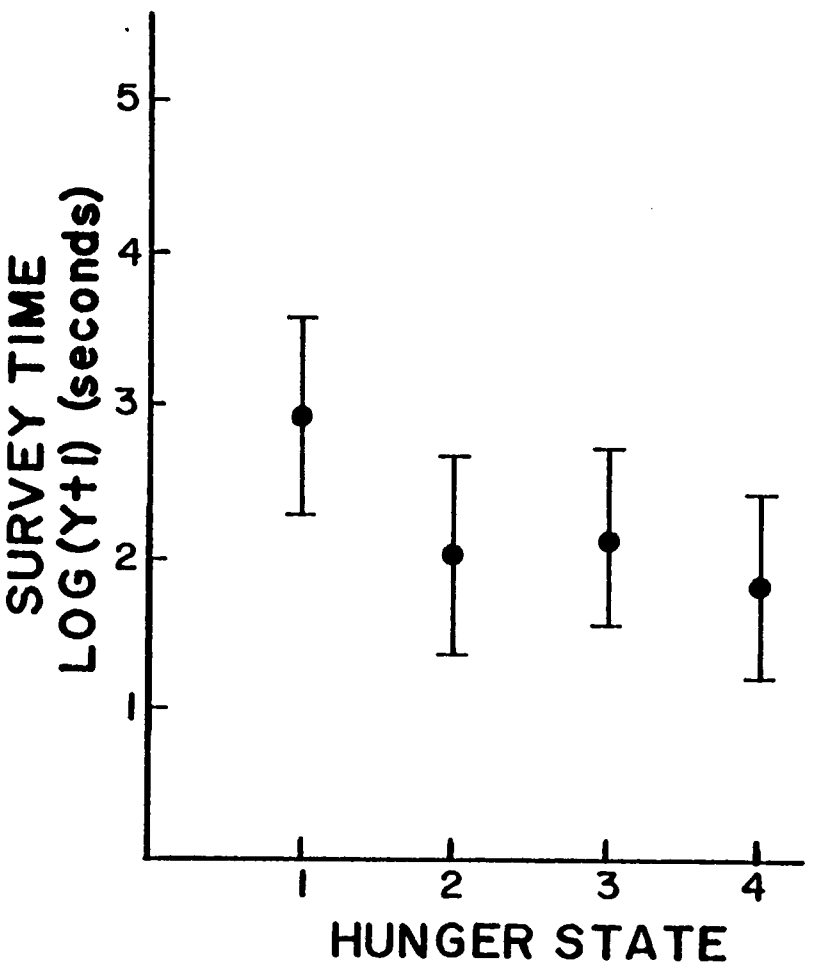


Figure 30. Least squares mean ± 2 S.E. for survey time vs. hunger state.

IV. DISCUSSION AND CONCLUSIONS

The idea of variation in involvement time is not new, but component analysis of this variation is.

It was found that distance had a definite effect on involvement time while hunger had an effect but not a significant one (alpha = 0.06). The subcomponent handling time was not affected by the distance traveled or the hunger state of the individual. This may not hold true for all states of hunger, since this study dealt with states of deprivation instead of satiation. However, further study may find that handling time is affected only by morphological characteristics of the predator (i.e., jaw size, snout-vent length, etc.) and the size and species of the prey item.

Differences found in involvement time can be traced directly to pursuit time. Pursuit time is affected by both distance and hunger. It would appear then that handling time, by nature of its constancy, dampens the effect of hunger on involvement time. Move time is affected by the distance a predator has to travel for a prey item, but not the hunger state of the predator. Although there was a significant difference between hunger state 1 and hunger state 2, this may have been affected by a measure of food in the gut and will be discussed later. Stop time is affected by both distance and hunger. Both sub-variables of stop time (wait and survey time) are affected by these sources of variation.

Therefore, it appears that distance affects all variables in question, with the exception of handling time, and cannot be tied to

any one in particular. This supports Schoener's (1979) statement that pursuit time is a function of distance.

The asymptote at distances 3 and 4 indicate that it required a shorter period of time to travel to distance 4 than would be expected if a strict linear relationship existed. However, due to standard errors, the relationship could be approximated most parsimoniously by a linear expression. This shortening of time could indicate an overcoming of inertia as represented by inhibition caused in a novel situation or it could be due to other risk factors. Charnov (1976) stated there are several risks that hungry mantids take when stalking an item at further distances. These risks include risk of detection by predators, risk of displacement (e.g., knocked from the bush), and the risk of an inappropriate response (with increasing distance it would be more difficult to estimate the qualities of an item). All these risks could be associated with the lizard stalking its prey. Risk minimization does occur in lizards in situations of high predation pressure and exhibits itself behaviorly (Andrews, 1979). In order to reduce the risk over the 80 cm distance, the predator reduced the pursuit time more than expected in a purely linear relationship. There may be a "critical" point somewhere between 60 and 80 cm that elicits a risk reduction response.

Although there are trends in the effect of hunger state to suggest an inverse relationship between hunger state and involvement time, the major difference lies between hunger states 1 and 2. Hunger states 2, 3, and 4 do not appreciably differ. This suggests an important difference between hunger state 1 and the other hunger

states. This could be due to food still in the gut at the end of 24 hours that would have been eliminated prior to 48 hours or hunger state 2. Windell and Sarokon (1976) measured the rate of gastric evacuation in Anolis carolinensis using different prey items (Tenebrio larvae, adults, and crickets) at different temperatures (18°, 25°, and 32° C). Since the lizards (in the present study) were exposed to varying temperatures (at periods other than an actual test), a pinpoint estimate of the mean temperatures would be impossible to obtain. However, since the temperature never got below 23° C, one can concentrate on the gastric evacuation results at 25° and 32° C. Windell and Sarokan (1976) gave results over several time periods and of particular interest are those for 24 and 48 hours. At 32° C after 24 hours there was 33.5% and 29.5% of food, Tenebrio larvae and crickets, respectively, left in the lizards gut, and both food items were at 0% after 48 hours at this temperature. At 25° C there was 44.1% and 49.8%, respectively, after 24 hours and 7.9% and 13.5%, respectively, after 48 hours. The digestability of flies as compared to flour beetle larvae is not known; it seems reasonable to assume it is at least comparable and perhaps more rapid. With that assumption it is possible that there was a definite difference in internal states between hunger state 1 and the other hunger levels. This in turn could have been the cause for the larger effects between 1 and 2 than between other progressive hunger states. Outside of the effects of deprivation on involvement time, its ecological significance could be felt in areas of digestion, food consumption, and overwintering. Although not much is known about short period deprivation, extended

periods (12 days) appear to cause a pronounced decrease in the rate of food passage in Anolis carolinensis (Windell and Sarokon, 1976).

The effect of hunger can be most accurately pinpointed as having the most effect on the amount of time a lizard was stopped, either in wait or survey. Less wait time and survey time with increasing states of hunger may imply a release from the predation risk response or a willingness to accept what is available without trying to find a better quality of prey. The latter concept is derived from the fact that they (the lizards) had been fed a "mixed" diet and may have still been looking for a cricket or mealworm, either of which would have provided more energy per entity than a fly. Although a problem of possible switching existed, it should have been at least partially solved by offering only the one prey item (the fly) for a period of one week prior to any test. The loss of important nutrients from the diet was possible without a mixed diet.

Greenberg (1978) warns that laboratory studies generally rely on a specific behavior performed out of context by animals in an ecologically impoverished environment. He goes on to note that Jenssen (1970) suggested that a behavioral pattern readily demonstrated or easily elicited in the laboratory is a response that an animal is "prepared" to make, and that its causation and function are probably not significantly different from that found in nature. It is recognized that although an introduction period allowed lizards an initial experience with the apparatus, it was still a "novel" environment for them. The novelty invoked some inhibition resulting in longer wait times and more survey behavior. However, in

nature all manner of distraction is possible while an animal is foraging and may affect his behavior in a similar manner. Since each animal in this study was exposed to the same general conditions, the design was randomized, and replicate variation was removed, any differences in the independent variables should be attributed to distance and/or hunger state. The variation removed by the replicate effect was shown to be significant. This variation could have been due to the following:

1. Seasonal variation. (The study was conducted from early summer to early fall.)
2. Laboratory temperatures during hunger state preparation. (This varied within a wide range as previously noted.)
3. Several trials per lizard. (Although within lizard variation was not significantly different from between lizard variation, a difference did exist.)
4. Trial temperature, lizard snout-vent length, and lizard weight. (Although these were not significantly different across hunger states or distances, a difference did exist and may have added variation to the data.)

Results from the present study of involvement time analysis appear to substantiate a general trend found in birds (Smith and Dawkins, 1971), fish (Ware, 1971; Werner, 1974), and spiders (Riechert, ms.). It appears that hunger, no matter whether one is dealing with states of satiation or deprivation, can have an effect on involvement time and even the quality of prey chosen, as shown by Craig (1978) for birds and noted by Riechert and Luczak (in press) for spiders. However, states of deprivation may not have much effect after the gut is completely empty, at least in lizards.

Pyke, et al. (1977) noted three factors in common with most optimal diet models. The results of this study do not support factor 1, which states that each food type has an associated food value measured in calories or units of weight and an associated handling time. Handling time as defined by Pyke then would equal involvement time, which is not constant across several distances or hunger states. Therefore, the same type prey item (species, size, and weight) could be ranked at any point on the continuum depending on the ratio of the food value to involvement time, with involvement time dependent on the distance traveled and/or the hunger state of the animal. This agrees with Charnov's (1976) mantid model in which he found profitability to be a decreasing function of pursuit distance and the hunger level of the mantid. It also appears to agree with Schoener's (1971) theory that a size-distance relationship exists and is important in determining the optimal diet. Future models should take these criteria into consideration when approaching the question of optimal diet.

The distance of a predator from a prey item in nature would appear to be a fairly random thing. However, good perch location and carefully picked territories could narrow the distance a sit-and-wait predator had to travel to capture a prey item. This could be due to habitat structure or to prey density.

Hunger in nature can be attributed to several factors such as season, weather, time of day, and ability to hold a good territory. The first three factors can be seen as having direct effects on the density of prey items available and this in turn having an effect on

the size of individual territories. The initial effects may appear as entry into other territories for food (Greenberg and Noble, 1944). The expansion of territory in Anolis carolinensis due to hunger resulting from low prey density was seen by Gordon (1956), as was the expansion of web size in spiders (Riechert, ms.). Simon (1975) found that natural food abundance was inversely correlated with territory size in Sceloporus jarrovi; this inverse correlation has been demonstrated for a few species of birds also (Homes, 1967; Stenger, 1958).

The distance between predator and prey, hunger state of the predator, and territory size may all be functions of prey density with hunger functioning to monitor the fluctuations in the food supply as suggested by Schoener (1969) and acting as a feedback mechanism to control territory size. If these functional relationships could be worked out, then a better understanding of population dynamics could be achieved.

As previously mentioned, optimal foraging is modeled as a "game" with rules and confines or constraints as well as "rewards." The variable involvement time examined in this study is important in determining the efficiency of any conquest, or how great the initial reward is. However, prior to actual involvement is the decision of whether to get involved or not. Wilson (1976) stated that the major question for the animal to assess in food search is whether to go after an item or not. Would it gain more energy by processing the item, or would it gain more by neglecting it and continuing to search? He also states that a set of items exists on the boundary line of

being accepted or rejected. There are factors other than distance or hunger state. Prey selection is affected by many variables, even such diverse things as habitat location, i.e., island vs. mainland situations and tropic vs. temperate zones (Wilson, 1976). Population and community oriented factors such as predator density and dominance ranking also affect prey selection (Krebs, et al., 1977; Pulliam, 1974). Other factors that might influence this decision in a real world environment are prey crypsis, defense mechanisms, and patchiness of distribution (Krebs, et al., 1977). Goss-Custard (1977) found that the redshank, a wading, probing bird, did not select prey that maximized energy gain. He suggested that the stimuli used by the birds in locating their prey may be important in determining which species is taken in a particular situation. Environmental factors such as temperature possibly affect the mobility of prey items and thus affect the sensitivity of visual searchers. Goss-Custard felt that search images may be formed and one of the stimuli that attracts the avian eye is movement. One reason given for a predator focusing on one type of stimulus rather than another may be that the predator has evolved a particular sensitivity to the stimuli arising from certain prey. This evolution of perceptual mechanisms is indeed important because it allows the predator to detect prey in the first place.

Other behavioral influences may hinder the predator from feeding optimally in a short term situation; one of these is curiosity behavior. During a feeding bout, curiosity may be employed to gain knowledge useful at some future time. This may lower the

present food intake rate below the possible optimum, but it is known that many animals investigate or sample new food objects placed in their environment (Holling, 1965).

A few of the influencing factors and some of the confines of the game for species at the individual and population level that could affect a predator's decision to pursue a food item or not are shown in Table 22. I believe that any attempt to rank these influencing factors in order of importance would be futile. It is important to realize that several factors affect prey choice and act to restrict a predator in ways that may influence the efficiency of his foraging, but at the same time aid in his survival.

One might proclaim that all species are in the same game--that of survival and reproduction. While this may be true, the rules or confines are not the same for all species. Even in the same species the restrictions may not be the same for different populations (i.e., island vs. mainland) or males and females. The emphasis of confines may change seasonally, and/or during the life cycle of the organism. Many aspects must be taken into consideration when judging if an action is optimal or not and what influences have molded (genetically or through experience) the behavior of the individual to forage in the manner it does. No one model or time scale (e.g., short term vs. long term goals) is likely to depict accurately all aspects of feeding behavior of an organism.

The conclusions reached in this study should only be applied to the levels of the variables examined and no broad based generalizations should be made because the effects are fixed. However, this

Table 22. Factors influencing a predator's decision to pursue a prey item or not.

Influencing Factor	Individual Level	Population Level
Hunger level	x	
Distance	x	
Predator size	x	x
Prey size	x	x
Prey movement	x	
Prey caloric content	x	x
Nutrient content	x	x
Predation risk	x	x
Displacement risk (i.e., knocked off branch)	x	
Risk of inappropriate response	x	
Catchability: crypsis, defense mechanisms	x	x
Prey toxicity	x	x
Prey preference	x	x
Density of prey	x	x
Search image	x	
Curiosity behavior	x	
Kinship: parental care	x	
Territory restriction	x	x
Awareness state	x	
Reproductive state	x	
Condition: vigor	x	
Point in life cycle: age, experience	x	
Season	x	x
Temperature	x	x
Climatic zone	x	x
Land mass location (i.e., island vs. mainland)	x	x
Predator social status (dominance hierarchy)	x	x

study has shown that involvement time under certain conditions can be influenced by both the distance a predator must go to obtain food and the hunger state of the animal. This evidence sheds some new light on the old adage (Pyke, et al., 1977) that for each prey type there is a constant involvement time. Equations that ignore the possible effects of hunger and which ignore differential metabolic cost or mortality risk during various components of the foraging process should be re-evaluated. This was initially identified as a drawback of equations similar to Hollings (1959) "disk" equation by Hughes (1979). However, it seems appropriate and fitting in light of the results of this study to recapitulate Hughes' statement concerning the need for re-evaluation of equations lacking the parameters previously mentioned. Equations that do not take these factors into consideration will produce a distorted view of optimal foraging.

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