

TO EAT OR NOT TO EAT?:
THAT IS THE QUESTION OF TREEFROG PREY SELECTION

By

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Frogs have long been considered opportunistic predators. In order to determine if the green treefrog (*Hyla cinerea*) is a non-selective forager, I studied the feeding ecology of this frog on Paynes Prairie State Preserve, Florida, and performed prey selection experiments in the laboratory. The comparison of prey from frog stomachs with prey available in the habitat (determined by tack-trap and sweep netting) indicated that prey selection was not associated with prey availability. Larvae of the families Noctuidae and Cantharidae were the two prey most frequently eaten by *H. cinerea* in the field, but the most common insect families in the habitat were Chloropidae, Cicadellidae, and Entomobryidae. In laboratory preference experiments, the two former prey were ranked highest among the eight natural prey offered to treefrogs. However, the house fly (*Musca domestica*) was consistently selected over all natural prey. The house

fly was included in these experiments for comparative purposes, since it readily elicits feeding behavior from *H. cinerea* in the laboratory.

Three genus-specific variables influenced prey selection by *Hyla cinerea*: (1) prey length, (2) activity patterns exhibited by prey, and (3) the proportion of time devoted by prey to specific behavior patterns. The quality of feeding stimuli (estimated in captures/h) varied within the behavioral repertoire of a genus as well as among genera performing similar activities. Stimulus quality did not influence the degree or speed of the response exhibited by the treefrog, but only the probability of occurrence of that response. Natural prey items that were consistently selected in the laboratory possessed length/width ratios greater than 3:1. The average visual angle subtended by prey used by treefrogs as a cue during selection was 2.3° at an average distance of 22.5 cm. Crawling velocity of prey was not an important selection parameter, but tended to be positively associated with the stimulus value of crawling prey.

OVERVIEW

Hyla cinerea is a common green treefrog found throughout the southeastern United States. In north-central Florida green treefrogs are arboreal and at times semi-aquatic. *Hyla cinerea* is a nocturnal, visually oriented, sit-and-wait pursuer (Schoener 1969) that feeds on a variety of invertebrate prey. Foraging begins in the early evening and continues until dawn. During the day, individuals rest in positions concealed by vegetation, or bask (Freed 1980a) in exposed positions on grasses and shrubs.

Field work was done on Paynes Prairie State Preserve, located 8 km south of Gainesville, Florida. Hardwood meso-xeric hammock surrounds the study site that consists of three temporary sinkhole ponds adjacent to Alachua Sink. In March, ponds begin drying up, and the area is eventually overgrown by annual plants. Pigweed (*Amaranthus australis*), bagpod (*Sesbania vesicaria*), and sicklepod (*Cassia obtusifolia*) are the most plentiful annuals. Interspersed among these weeds grow several common grasses: coast cockspur (*Echinochloa walteri*), vaseygrass (*Paspalum urvillei*), and guineagrass (*Panicum maximum*).

The vegetation of an area is very important to a treefrog population, since it provides cover, and influences the potential prey available. All invertebrate prey are directly or indirectly associated with these plants. Most of these invertebrates utilize one or more of these plants as food. Stinkbugs (*Euschistus* and *Oebalus*) suck plant juices whereas caterpillars, flea beetles, and snails (*Spodoptera*,

Disonycha, and *Polygyra* respectively) chew or rasp leaves or stems. Those invertebrates that do not rely on plants for food utilize vegetation as foraging areas, and eat herbivorous insects associated with these plants (e.g. *Chauliognathus* and *Clubiona*). Treefrogs are associated with the vegetation in a fashion similar to these predatory invertebrates.

This dissertation addresses the question of prey selection by the green treefrog. The natural diet of the treefrogs found on Paynes Prairie is presented in section one. The food items and their degree of utilization pertain only to this particular population. Other populations occupying nearby habitats may utilize different prey (see Kilby 1945) mainly due to the differences in floral composition of that area. Section one also includes data from laboratory preference experiments designed to determine the degree of prey selectivity exhibited by *H. cinerea*. These laboratory results are compared to data gathered on prey selection under natural conditions.

In section two I examine the potential cues that are used by the green treefrog in selecting prey. Consistent selection of particular invertebrates from a variety of potential prey indicates that treefrogs utilize certain visual cues. In this section I present those cues that are most probably used by *H. cinerea* during prey selection.

SECTION I

A TREEFROG'S MENU: SELECTION FOR AN EVENING'S MEAL

Introduction

Pulliam (1974) defined feeding strategy as the choices a predator makes upon encountering different food items, *i.e.*, whether to eat or to ignore a prey. MacArthur and Pianka (1966) presented a model that predicts the optimal diet of a predator based upon the availability of prey species. Later models considered prey availability and also the relative value of the prey to the predator. Emlen (1966), Rapport (1971), Schoener (1971), Cody (1974), Pulliam (1974), Ellis *et al.*, (1976), Estabrook and Dunham (1976), Pyke *et al.*, (1977), Hughes (1979), Sih (1979), and Stenseth and Hansson (1979) defined an optimal diet as one that maximizes energy per unit time. The importance of prey nutrient value to the predator is also recognized (Marten 1973; Pulliam 1975; Rapport 1980). None of these models explains mechanisms allowing for predator discrimination among prey items.

Amphibians in general, and ranids, bufonids, and hylids in particular, are described as indiscriminate predators (Korschgen and Baskett 1963; Johnson and Bury 1965; Klimstra and Myers 1965; Linzey 1967; Heatwole and Heatwole 1968; Hedeon 1972; Kramek 1972; Bury and Martin 1973; Blackith and Speight 1974; Clark 1974; Tyler and Hoestenbach 1979). Oplinger (1967), Johnson and Christiansen (1976), and Labanick (1976), all working on hylids, concluded that availability and abundance of prey rather than preference determine the type of

food consumed by these frogs. Conversely, Cott (1940), Sweetman (1944), Bragg (1957), Turner (1959), Brower and Brower (1962), and Toft (1980) suggested anurans are capable of discrimination among prey. Ingle and McKinley (1978) and Ewert *et al.* (1979) showed that anurans respond differentially to various artificial prey stimuli. I showed that activity patterns of insect prey are differentially utilized as cues in prey selection experiments with *Hyla cinerea* (Freed 1980b).

In behavioral studies, both Ewert (1968) and Ingle (1968) reported frogs and toads show consistent size-selectivity in choice of artificial prey. The configuration of a moving stimulus is an important selection parameter (Ewert 1968; Borchers *et al.*, 1978; Ingle and McKinley 1978). Worm-like forms are better feeding stimuli for toads than similarly moving square objects. However, small square stimuli moving in a stepwise fashion elicit stronger feeding responses from toads than squares moving at constant velocity (Borchers *et al.*, 1978). These experimental stimulus movements represent crude simplifications when compared with the diversity and complexity of activity patterns of natural prey (Borchers *et al.*, 1978).

I combined a field study on treefrog feeding ecology with laboratory preference experiments utilizing natural prey. Emphasis was placed on the quality of the behavior patterns exhibited within and among nine prey types. These activity patterns may be used as cues for selection of prey by a foraging predator. The purposes of this study were (1) to identify the prey most frequently eaten by *Hyla cinerea* in the field, (2) to determine the degree to which prey discrimination is developed in the green treefrog, and (3) to estimate the strength of the behavioral cues utilized by the frog during prey selection.

Methods

Field work on hylid feeding ecology was conducted between May 1977 and May 1978 on Paynes Prairie. Stomach contents of 163 *Hyla cinerea* were obtained via pumping (Legler and Sullivan 1979). Prey abundance was estimated by using Tack Trap[®] placed on the ground and 0.6, 1.2, and 1.8 m above the ground. Each 315 cm² plastic sheet of Tack Trap was left overnight or for a 24 h period. Though a significantly greater total number of prey were sampled on ground than aerial traps ($\chi^2 = 518$, $df = 18$, $P < 0.001$), samples were combined for analysis since family representation at all levels was similar (Spearman Rank Correlation, $r_s = 1$, $P = 0$, $N = 8$). Sweep net samples were taken between 2100 and 2400 h.

Arthropods were identified to family, and where possible, to genus and species. The rank of prey in the diet of *Hyla cinerea* was determined by calculating the percent biomass-occurrence (%BO) for each item:

$$\%BO = \sqrt{\left(\frac{M_i}{M_t} \times 100\right) \left(\frac{N_i}{N_t} \times 100\right)}, \quad (1)$$

where M_i is the estimated mass of prey i , M_t is the estimated mass of all prey items eaten by the sample population, N_i is the number of stomachs containing prey i , N_t is the total number of stomachs containing food. The index %BO is the geometric mean of two common indices, % biomass and frequency of occurrence. This compound index determines prey rank based on evenly weighting the potential value of the prey and its frequency of utilization by the predator. It minimizes the effect of extremes in the ranking process, such as abundant tiny prey or

rare large prey, either of which may be insufficient to meet the long term energy requirements of the predator. The length of all whole prey items was measured, and mass estimated by using length-mass regression equations prepared by myself (Appendix 1) or taken from Zug and Zug (1979). The %BO was calculated for the most frequently utilized prey genera, and then divided by the summed %BO to adjust these values to 100 percent (Table 1).

Thirty-five (18 male, 17 female) *Hyla cinerea* (Snout-Vent-Length: $\bar{X} \pm SE = 4.74 \pm 0.06$ cm, Range = 3.8 - 5.2 cm) were collected during the summer of 1980. They were maintained at room temperature (24°C, light uncontrolled) in the laboratory 1 wk prior to experimentation. The eight top ranked genera of prey as determined by %BO, and the house fly (*Musca domestica*), were used as prey for the preference experiments. *Palthus* was omitted from the top eight (Table 2) due to its similarity to *Spodoptera*. The house fly was included for comparative purposes since treefrogs preferred this insect over four mosquito species in laboratory experiments (Freed 1980b). The eight prey were divided into two subgroups, each including the house fly. The subgroups were made up of all odd or all even ranked prey as determined by %BO. *Clubiona* was switched with *Oeobalus* to avoid having two pentatomids in subgroup 2. Subgroup 1 consisted of *Musca*, *Spodoptera* (noctuid caterpillar), *Gryllus* (cricket), *Oeobalus* (stinkbug), and *Polygyra* (land snail). Subgroup 2 included *Musca*, *Chauliognathus* (soldier beetle larva), *Euschistus* (stinkbug), *Clubiona* (spider), and *Disonycha* (leaf beetle). These two subgroups were used in 40 initial trials. Ten trials involving each subgroup were run in daylight (20 trials), and the remaining 20 trials were run at night under red light. The latter

Table 1. Percentage biomass-occurrence of the most frequently utilized prey genera in the diet of *Hyla cinerea*.

Genus	Family	Number	Stomachs	Est.	Adj.
			with item	biomass (g)	
<i>Spodoptera</i> (larva)	Noctuidae	23	21	2.03	20.39
<i>Chauliognathus</i> (larva)	Cantharidae	46	32	0.79	15.73
<i>Gryllus</i>	Gryllidae	6	6	0.77	8.66
<i>Euschistus</i>	Pentatomidae	12	11	0.43	6.76
<i>Polygyra</i>	Polygyridae	8	8	0.53	6.41
<i>Disonycha</i>	Chrysomelidae	22	11	0.31	5.75
<i>Palthus</i>	Noctuidae	12	9	0.32	5.31
<i>Clubiona</i>	Clubionidae	22	18	0.13	4.81
<i>Oebalus</i>	Pentatomidae	9	8	0.28	4.69
<i>Languria</i>	Languriidae	8	6	0.31	4.24
<i>Cariblatta</i>	Blattidae	7	6	0.20	3.40
<i>Mormidea</i>	Pentatomidae	6	5	0.10	2.18
<i>Ishnoptera</i>	Blattidae	2	2	0.22	2.07
<i>Eudigogus</i>	Curculionidae	6	5	0.08	1.99
<i>Lycosa</i>	Lycosidae	4	3	0.13	1.96
<i>Centrinaspis</i>	Curculionidae	11	8	0.05	1.89
<i>Limonethe</i>	Ichneumonidae	3	3	0.09	1.60
<i>Crematogaster</i>	Formicidae	17	12	0.01	1.17
<i>Pardosa</i>	Lycosidae	3	2	0.03	0.99

Table 2. Comparison of the percent abundance of prey families represented by at least two individuals in the diet of *Hyla cinerea* with relative abundance estimates derived from tack trap and sweep net sampling. N equals the total number of individuals obtained for each type of sample.

Family	Stomach	Tack trap	Sweep net	Tack + Sweep
Noctuidae	15.21	2.88	2.51	2.72
Cantharidae	10.74	0.24	0.68	0.44
Pentatomidae	8.29	0.24	5.03	2.35
Formicidae	6.49	1.38	7.01	3.86
Chrysomelidae	6.04	1.56	1.37	1.48
Curculionidae	5.82	0.60	2.44	1.41
Clubionidae	5.15	0.78	2.06	1.34
Alleculidae	4.70	0.06	0.08	0.07
Sminthuridae	3.58	17.66	0.23	9.97
Gryllidae	3.13	1.32	0.76	1.07
Phalangidae	2.68	0.30	0.00	0.17
Blattidae	2.24	0.00	0.23	0.10
Cicadellidae	2.01	13.27	12.18	12.79
Lycosidae	2.01	0.30	2.51	1.28
Polygyridae	1.79	0.00	0.76	0.34
Languriidae	1.79	0.00	0.00	0.00
Reduviidae	1.79	0.00	0.91	0.40
Chloropidae	1.57	25.05	45.70	34.15
Araneidae	1.57	1.62	4.64	2.96

Table 2. Continued.

Family	Stomach	Tack trap	Sweep net	Tack + Sweep
Forficulidae	1.34	0.00	0.76	0.34
Carabidae	1.34	0.54	0.23	0.40
Scarabaeidae	1.34	0.00	0.15	0.07
Tetrigidae	1.34	0.36	0.30	0.34
Entomobryidae	0.89	28.65	0.00	16.02
Flatidae	0.89	0.00	0.00	0.00
Porcellionidae	0.89	0.00	0.00	0.00
Salticidae	0.89	0.30	1.29	0.74
Tetragnathidae	0.67	0.06	0.61	0.30
Dictynidae	0.67	0.00	0.00	0.00
Ichneumonidae	0.67	0.24	0.00	0.13
Cerambycidae	0.67	0.00	0.00	0.00
Staphylinidae	0.45	1.80	0.15	1.07
Lygaeidae	0.45	0.06	0.91	0.44
Tettigionidae	0.45	0.12	6.32	2.85
Phloeothripidae	0.45	0.60	0.15	0.40
N	447	1665	1313	2978

experiments were an attempt to determine if prey selection was affected by time of day. A total of ten prey in equal ratios (2 prey/genus) were available during each run. Twenty frogs were each used in two experimental trials, once with subgroup 1, the other with subgroup 2. The three most preferred prey from each subgroup were used in the final 15 trials; a different frog was used each time. *Musca* and *Spodoptera* were obtained from the United States Department of Agriculture Insect Research Laboratory, Gainesville, Florida. All other prey were collected on Paynes Prairie.

The frogs were tested in a gridded plexiglass chamber (28 × 28 × 28 cm) with white paper covering three walls of the cube; the front and top were left uncovered to permit observation. The white wooden floor of the chamber had a sliding panel containing two small chambers recessed on opposite sides outside of the cube (see Figure 1, Gardner 1964). This allowed introduction of the frog into the feeding chamber. Ten prey (2/genus) were placed into the chamber 5 min prior to the release of the predator. During the 30 min experiment the following were recorded: order of prey capture, estimated distance of prey from frog at recognition, and behavior of prey just prior to capture.

The following electivity equation (e_i) was developed to estimate predator preferences. This equation produces an index that varies from 0, indicating that the prey item is completely ignored by the predator, to 1, indicating that the predator specializes only on that prey:

$$e_i = \frac{\sum_{j(i)} \left(\frac{1}{n_i(j)/N} \right) \left(\frac{1}{R_j} \right)}{\sum_{j(i)} \frac{1}{n_i(j)/N}}, \quad (2)$$

where $n_i(j)$ is the number of individuals of prey species i present just prior to capture of individual j of the species i , N is the total number of all individuals of all prey types present just prior to the capture of individual j , and R_j is the ordinal rank of individual j captured by the predator.

None of the measures of preference presented in the literature (Ivlev 1961; Rapport and Turner 1970; Chesson 1978; Cock 1978) considers the order of prey capture. These equations were designed for application to open systems in which the predator encounters only one or few prey types at any given time. In such a system, choice is limited either to pursuing or not pursuing prey coming within reach. In my experiments the predator was simultaneously presented with ten prey items of several prey species. Discretion here included the ability to focus on one prey species in the presence of other, potentially distracting, prey species. Ranking allows assignment of higher values to each successive member of a prey type captured within a rank, thus emphasizing the predator's capacity for type-selection as the absolute abundance of the preferred prey type decreases. Therefore, if a series of one prey type was captured in sequence, the same rank (R_j) was assigned to all individuals in that set. In other words, if the first three prey items consumed out of ten possible items (3 different species) were the same kind, each of the three would carry a rank of 1, since any of them could have been captured first. In addition to prey rank, the relative abundance of prey types was calculated at each predation. With the closed system utilized, prey replacement is eliminated and rank order of prey capture becomes extremely important. If prey selection were random, a single predation could almost halve the

chance of a second successive predation on the same species, an obvious departure from natural conditions. The value e_i is relative, and like all measures of preference its value for a particular item will be greatly influenced by alternative choices available at the time of selection. Consequently, mean values of e_i were used for comparing the electivity of the various prey species.

An activity index was developed by recording the behavior of each prey several seconds prior to capture. The following activities were ranked 0 through 5 on the basis of increasing levels of activity: 0--motionless, 1--antennae waving, 2--grooming, 3--searching, 4--crawling, and 5--flying. Searching behavior of prey was defined as vertical and/or lateral waving of the anterior third of the body. If a prey was observed performing several behaviors simultaneously, it was given the highest appropriate ranking. This index is the mean rank of all recorded pre-capture and first attempted capture activity for a particular prey genus. Uneaten prey were assigned a 0 in order to avoid bias that results in an increase in index values for genera that characteristically spend long periods of time motionless and thereby escape predation.

An activity budget was developed for each prey genus by recording the time spent on each characteristic behavior during a 2 min time period. Depending upon the number of behavior patterns commonly displayed by a genus, a total of 6 to 12 min were spent on each individual to record all activity. The behavior of ten individuals from each genus was recorded during daylight and an equal number for each genus was recorded at night under red light. This time budget was for isolated prey and differs from the activity index in that the latter involved interacting individuals and included predator disturbance.

The time budget in conjunction with the level of predation recorded for each activity pattern of each genus allowed the determination of the strength of feeding stimulation (s) associated with prey behavior. The following index provides an estimation of the stimulus strength (in predations/h) for each behavior pattern exhibited by prey:

$$s = \frac{P_i(x)}{t_i(x) T_i} , \quad (3)$$

where $P_i(x)$ is the number of predations and/or attempted captures on prey genus i performing behavior x , $t_i(x)$ is the proportion of time normally spent performing behavior x by prey genus i in the absence of the predator, and T_i is the total number of hours prey i was exposed to the predator.

Lastly, the difficulty of capture (I) for each prey was calculated by dividing the number of misses of prey i by the number of capture attempts recorded for that prey genus.

Results

Families of prey represented in the sample population by at least two individuals in the stomach contents of *Hyla cinerea* are presented in Table 2. A list of all identified prey is included in Appendix 2. Spearman's rank correlation was used to compare the proportions of prey from stomachs with those of potential prey available in the habitat. Tests performed using prey families with a minimum of five items in stomachs ($N = 7$) showed that no significant correlation exists between prey eaten by treefrogs and prey available for consumption. However, a

significant correlation was found when all 35 prey families from Table 2 were compared to the proportions of prey obtained from sweep net ($r_s = 0.41, P = 0.02$) and combined ($r_s = 0.34, P = 0.05$) samples. Depending on the number of prey families included in the statistical analysis, it is possible to conclude that either the frog was a non-selective feeder or a discriminating forager. Naturally rare prey families were rarely included in the frogs' diet. Therefore, by adding many infrequently utilized prey families to the Spearman rank analysis, the coefficient increasingly approaches significance.

Since no significant difference (ANOVA, $F = 0.01, P = 0.91$) was found between the e_i 's generated by frogs under the two different light regimes, data from light and dark experiments were combined. *Musca* was the most preferred prey item in laboratory experiments (Table 3). *Spodoptera* and *Chauliognathus* larvae ranked respectively second and third in the initial trials, but were reversed in the standings of the final preference experiments. This is not unexpected since both the latter two prey were highly favored in the field by treefrogs. A comparison of initial e_i 's with field ranks determined by %BO of the eight natural prey genera revealed a significant correlation between these independent indicators of prey preference (Table 4A).

Prey selection significantly correlates with prey activity (Tables 4B and 5) and length (Tables 4C and 6) but not mass (Table 4D). A parametric test for partial correlation between predator selectivity, prey length, and prey activity indicated that 42% ($r = 0.65, P < 0.1$) and 55% ($r = 0.74, P < 0.05$) of the variability observed in e_i are accounted for by prey activity, and prey length, respectively. Substituting mass for the estimate of size, the variation in e_i

Table 3. Mean electivity coefficients (e_i) for nine prey genera.
 N equals the number of preference experiments performed.
 The number of each genus used equals 2N.

Prey Genus	Initial			Final			Combined		
	\bar{X}	SE	N	\bar{X}	SE	N	\bar{X}	SE	N
<i>Musca</i>	0.416	0.04	40	0.408	0.06	15	0.414	0.05	55
<i>Spodoptera</i>	0.340	0.05	20	0.137	0.03	15	0.253	0.05	35
<i>Chauliognathus</i>	0.269	0.03	20	0.209	0.06	15	0.243	0.05	35
<i>Gryllus</i>	0.136	0.03	20	0.131	0.03	15	0.134	0.03	35
<i>Euschistus</i>	0.075	0.04	20	0.003	0.01	15	0.045	0.03	35
<i>Oebalus</i>	0.074	0.02	20						
<i>Disonycha</i>	0.071	0.02	20						
<i>Clubiona</i>	0.049	0.01	20						
<i>Polygyra</i>	0.000	0.00	20						

Table 4. Spearman's coefficient of rank correlation, r_s , for predator-prey variables (two-tailed test). N equals the number of prey genera.

Correlation	N	r_s	P
A. Prey rank (%BO) vs electivity	8	0.79	0.021
B. Prey rank (%BO) vs prey activity	8	0.75	0.031
C. Prey rank (%BO) vs prey length (stomach)	8	0.76	0.028
D. Prey rank (%BO) vs prey mass (stomach)	8	0.57	0.139 (NS)
E. Electivity vs prey activity	9	0.83	0.006
F. Electivity vs prey length	9	0.42	0.265 (NS)
G. Electivity vs prey mass	9	0.00	1.000 (NS)
H. Electivity vs capture difficulty	9	-0.37	0.332 (NS)
I. Electivity vs medium cm from frog	9	-0.45	0.223 (NS)
J. Electivity vs % prey within 10 cm	9	0.29	0.452 (NS)
K. Electivity vs % prey within 5 cm	9	0.67	0.047
L. Prey activity vs % prey within 5 cm	9	0.90	0.001

Table 5. Indicators of relative activity for nine prey genera. The activity index is calculated as the mean rank of all recorded precapture activity as well as activity prior to the first unsuccessful capture attempt. The activity scale runs from 0 to 5, 5 representing the greatest activity level. *I* equals misses/attempts.

Prey Genus	Index of Prey Activity			Capture Difficulty
	\bar{X}	SE	N	<i>I</i>
<i>Musca</i>	3.3	0.2	110	0.47 (68/145)
<i>Spodoptera</i>	2.1	0.2	70	0.02 (1/ 43)
<i>Chauliognathus</i>	2.2	0.2	70	0.23 (10/ 44)
<i>Gryllus</i>	2.0	0.2	70	0.49 (28/ 57)
<i>Euschistus</i>	1.4	0.2	70	0.85 (23/ 27)
<i>Oebalus</i>	1.0	0.3	40	0.20 (2/ 10)
<i>Disonycha</i>	0.6	0.2	40	0.00 (0/ 8)
<i>Clubiona</i>	1.7	0.3	40	0.52 (11/ 21)
<i>Polygyra</i>	1.0	0.3	40	1.00 (13/ 13)

accounted for by activity and mass is 51% ($r = 0.71$, $P < 0.05$) and 0.01% ($r = 0.009$, $P > 0.05$) respectively. When considering all nine prey items including *Musca*, prey selection is significantly associated with prey activity (Table 4E) but not with size (Tables 4F and G). Partial correlations indicated that activity accounts for 77% ($r = 0.88$, $P < 0.05$) of the variation observed in e_i , whereas length accounts for only 21% ($r = 0.46$, $P > 0.05$) of the observed variation. Using mass as an estimator of size, mass accounts for 0.25% ($r = -0.05$, $P > 0.05$) of the observed variation of e_i , whereas activity accounts for 74% ($r = 0.86$, $P < 0.05$) of the observed variability of the electivity coefficients.

The activity time budget for each genus is presented in Table 7. There was no significant difference (t tests, $P > 0.05$) in prey behavior between day and night observations, and therefore the data were combined. The activity index may be considered circular, since it relies on predator response as a signal for recording prey behavior. Nevertheless, this index best represents the observed activity of prey during an experiment. The prey-specific activity indices are significantly correlated ($r_g = 0.59$, $P = 0.048$, one-tailed test) with activity ranks obtained from time budget data. These ranks were derived by multiplying the numerical value (0-5) of each type of behavior by the proportion of time devoted to that behavior (Table 7). Therefore, the activity index does correlate with the activity time budget, an independent estimator of the mean level of prey activity.

The activity patterns displayed by the prey and the proportion of time devoted by the prey to each behavior influence prey selection. The strength of the feeding stimulus associated with each prey genus

Table 7. Activity time budget and summary of predations associated with each activity pattern of nine prey.
 Note: α = value for palp drumming. b = value for spinning silken retreat.

Genus	Variable	N	Motion- less	Antennae wave	Behavior Pattern				
					Groom	Search	Crawl	Fly	
<i>Musca</i>	1. % activity time ($\bar{X} \pm SE$)	20	8 \pm 3	-	40 \pm 4	-	50 \pm 4	3 \pm 0	
	2. # eaten	77	-	-	5	-	64	8	
	3. # missed behavior noted	15	-	-	2	-	12	1	
	4. # not eaten	18	-	-	-	-	-	-	
<i>Spodoptera</i>	1. % activity time ($\bar{X} \pm SE$)	20	47 \pm 6	-	6 \pm 2	22 \pm 3	26 \pm 5	-	
	2. # eaten	42	1	-	-	21	20	-	
	3. # missed behavior noted	1	-	-	-	-	1	-	
	4. # not eaten	27	-	-	-	-	-	-	
<i>Chauliognathus</i>	1. % activity time ($\bar{X} \pm SE$)	20	3 \pm 3	-	5 \pm 1	12 \pm 8	79 \pm 3	0 \pm 0	
	2. # eaten	34	1	-	-	2	31	-	
	3. # missed behavior noted	6	-	-	-	1	5	-	
	4. # not eaten	30	-	-	-	-	-	-	

Table 7. Continued.

Genus	Variable	N	Motion- less	Behavior Pattern				
				Antennae wave	Groom	Search	Crawl	Fly
<i>Gryllus</i>	1. % activity time ($\bar{X} \pm SE$)	20	41 \pm 6	7 \pm 2	19 \pm 3	-	33 \pm 5	-
	2. # eaten	29	1	3	1	-	24	-
	3. # missed behavior noted	12	-	3	-	-	9	-
	4. # not eaten	29	-	-	-	-	-	-
<i>Euschistus</i>	1. % activity time ($\bar{X} \pm SE$)	20	31 \pm 6	4 \pm 2	23 \pm 2	-	41 \pm 6	0 \pm 0
	2. # eaten	4	-	1	-	-	3	-
	3. # missed behavior noted	21	-	1	1	-	17	2
	4. # not eaten	45	-	-	-	-	-	-
<i>Oebalus</i>	1. % activity time ($\bar{X} \pm SE$)	20	54 \pm 6	0 \pm 0	18 \pm 3	-	27 \pm 6	0 \pm 0
	2. # eaten	8	-	-	-	-	8	-
	3. # missed behavior noted	2	-	-	-	-	2	-
	4. # not eaten	30	-	-	-	-	-	-

Table 7. Continued.

Genus	Variable	N	Motion- less	Behavior Pattern					
				Antennae wave	Groom	Search	Crawl	Fly	
<i>Disomycha</i>	1. % activity time ($\bar{X} \pm SE$)	20	31 \pm 4	6 \pm 1	40 \pm 3	-	22 \pm 5	0 \pm 0	
	2. # eaten	8	-	2	1	-	5	-	
	3. # missed behavior noted	0	-	-	-	-	-	-	
	4. # not eaten	32	-	-	-	-	-	-	
<i>Clubiona</i>	1. % activity time ($\bar{X} \pm SE$)	20	55 \pm 8	0 \pm 0 ^a	5 \pm 2	19 \pm 7 ^b	21 \pm 4	-	
	2. # eaten	10	-	-	-	1	9	-	
	3. # missed behavior noted	7	-	-	-	-	7	-	
	4. # not eaten	23	-	-	-	-	-	-	
<i>Polygyra</i>	1. % activity time ($\bar{X} \pm SE$)	20	36 \pm 8	-	-	24 \pm 3	40 \pm 7	-	
	2. # eaten	0	-	-	-	-	-	-	
	3. # missed behavior noted	13	2	-	-	3	8	-	
	4. # not eaten	27	-	-	-	-	-	-	

while performing a specific behavior is presented in Table 8. Behavior patterns exhibited within a prey genus vary tremendously in their ability to elicit feeding behavior in *Hyla cinerea*. For example, grooming behavior in the cricket (*Gryllus*) is associated with a level of predation of 0.2 captures/h whereas crawling elicits 2.9 predations/h. In addition, similar behavior patterns of different genera vary in their stimulus strength. To the treefrog, crawling flea beetles (*Disonycha*) represent a feeding stimulus 61% less effective than crawling crickets, which in turn represent a feeding stimulus 27% less effective than crawling spiders (*Clubiona*). Since 3.9 predations/h are associated with spider crawling, it is surprising that *Clubiona* was ranked only eighth in overall preference. This low rank is due to the proportion of time the spider remained motionless (54%), greater than any of the other prey included in this experiment. *Musca*'s high rank is due to the combination of two powerful frog orienting stimuli, flight and crawling. The flight-crawl behavioral sequence accounts for 53% of the fly's activity time budget and resulted in 8.1 predations/h. Linkage between searching and crawling behavior patterns, associated with 2.7 and 2.3 predations/h respectively, probably accounts for the high ranking received by *Spodoptera*. Conversely, *Chauliognathus* crawling at 1.3 captures/h is a mildly effective stimulus for a highly ranked prey type, but the soldier beetle larvae spent 80% of their observed time performing this behavior. The combination of crawling and searching behavior (0.7 captures/h) accounts for 92% of the beetle larvae's activity time budget.

Finally, prey selection is not affected by the difficulty involved in capturing a prey (Tables 4H and 5), or the distance of prey

Table 8. Strength of feeding stimulus (s) associated with prey behavior. Values in the table are for s = captures/h (see text). a = values for palp drumming. b = value for spinning silken retreat.

Prey Genus	Behavior					
	Motionless	Antennae wave	Groom	Search	Crawl	Fly
<i>Musca</i>	0.0	-	0.3	-	2.8	5.3
<i>Spodoptera</i>	0.1	-	0.0	2.7	2.3	-
<i>Chauliognathus</i>	0.9	-	0.0	0.7	1.3	-
<i>Gryllus</i>	0.1	2.6	0.2	-	2.9	-
<i>Euschistus</i>	0.0	1.4	0.1	-	1.4	2/0
<i>Oebalus</i>	0.0	0.0	0.0	-	1.9	0.0
<i>Disonycha</i>	0.0	1.6	0.1	-	1.1	-
<i>Clubiona</i>	0.0	0.0 ^a	0.0	0.3 ^b	3.9	-
<i>Polygyra</i>	0.3	-	-	0.6	1.0	-

Table 9. Percentage of predation experienced by each genus within a specified distance from the treefrog. Included are estimated median distances of frogs from prey just prior to pursuit and capture.

Prey Genus	Distance from Predator			
	N	0-5 cm	0-10 cm	Median (cm)
<i>Musca</i>	84	71	92	4.0
<i>Spodoptera</i>	39	46	72	7.5
<i>Chauliognathus</i>	37	62	76	5.0
<i>Gryllus</i>	36	44	50	10.3
<i>Euschistus</i>	22	41	46	11.5
<i>Oebalus</i>	16	38	50	10.3
<i>Disonycha</i>	8	38	63	8.0
<i>Clubiona</i>	8	44	50	10.3
<i>Polygyra</i>	9	44	78	7.5

from the predator prior to attack (Tables 4I, J and 9). However, there is a significant association between e_i and the percentage of predations occurring within a 0 to 5 cm distance from the frog (Table 4K). In turn, the percentage of predations between 0 and 5 cm is highly correlated with prey activity, emphasizing the greater probability of predator encounter associated with more active prey (Table 4L).

Discussion

Spodoptera and *Chauliognathus* were the two prey items most frequently consumed by *Hyla cinerea* in the field. Both are worm-like, a configuration shown to be a strong stimulus in eliciting feeding (Ewert 1974; Ingle 1976). However, *Musca* was the most consistently preferred food item offered in laboratory experiments in which prey were equally available at the beginning of each trial. Previous work (Freed 1980b) showed that *Musca* was most preferred, although the mean e_i generated from that study was 0.745 versus the present e_i of 0.416. Electivity is relative, and can be greatly influenced by the alternative choices available at the time of selection. The lower e_i for *Musca* in this study reflects the greater stimulus value of alternative prey. Mosquitoes were the only alternate prey available in the previous study; they are almost completely ignored by treefrogs in their natural habitat.

Hyla cinerea is capable of consistently selecting specific prey. This high degree of discrimination is emphasized by similar ranks generated in laboratory preference experiments and ranks based on stomach content analysis of the sample population. Three prey-specific variables influence selection under laboratory conditions: prey size,

prey activity, and the frequency of occurrence of various attack-inducing behaviors. Prey mass, unlike length, may not be easily discernible at a distance, and is not an important parameter. Prey length does influence prey selection in the field. However, this association does not exist in laboratory experiments that include house flies. This indicates that even though prey length is an important cue utilized by the frog, it could be overshadowed by the cues provided by prey activity. *Hyla cinerea* differentially selects prey in relation to the proportion of time a prey species remains active, as well as the types of activity most often displayed. An increase in the proportion of a specific prey activity results in a subsequent increase in the functional density of that prey (Werner and Hall 1974), thus resulting in greater predation. Since the various behavior patterns within a prey genus are not equally stimulating to frogs, the stimulus value of prey is not fixed, but (in accordance with its activity time budget) will fluctuate over time. Similar behaviors shared among different prey also vary in their ability to elicit feeding in *H. cinerea*. This variation is most likely related to genus-specific differences in configuration, and in the case of crawling and flight, differences in velocity (Luthardt and Roth 1979a). *Hyla cinerea* select prey that most frequently display the behaviors of greatest stimulus value. Thus if *Clubiona* partitioned their activity time in a manner similar to *Musca* or *Chauliognathus*, these spiders would probably rank equal to or higher than house flies or soldier beetles in the diet of the treefrog.

The difficulty involved in capturing each prey does not influence prey choice; however, several interesting observations were noted. First, the humeral spines located on the prothorax of *Euschistus* are an

effective predator deterrent. Treefrogs repeatedly rejected stinkbugs after lodging these spines between their jaws. Second is the unexpected difficulty encountered by frogs attempting to capture the pulmonate land snail *Polygyra*. The adhesion of the snail to the substratum by mucus secretion interrupted the timing of the frog. This resulted in the jaws closing slightly before the snail was completely in the mouth, forcing the snail off the frog's tongue. Finally, *Chauliognathus* larvae, assumed to be distasteful due to the presence of cantharidin (Carrel and Eisner 1974), were consistently eaten by some individuals and completely ignored by others. The propensity of some individuals to select *Chauliognathus* could be attributed to learning (Luthardt and Roth 1979b) or possibly to polymorphism (Arnold 1977) in the hylid population.

In conclusion, the great variety of behavior patterns exhibited by the different prey form a complex of cues that differentially influence feeding behavior in *Hyla cinerea*. Behavioral patterns vary within and among prey genera in quality, *i.e.*, in the ability to elicit orientation and prey capture by the frog. Selection is closely related to the time devoted by each prey to specific behaviors. Size, as measured by length, is also a cue used in the selection of prey but can be overshadowed by prey behavior. Behavior modification is probably a major evolutionary process affecting the interactions between visually-oriented predators and their prey. Predators that utilize only cues that represent large proportions of the prey's activity time budget should have a selective advantage. Conversely, a reallocation of the prey's available activity time away from high risk behavior patterns or changes in the level of activity thus altering its stimulus value are

mechanisms that may function over ontogenetic as well as evolutionary time.

SECTION II

VISUAL CUES: YOU LOOK GOOD ENOUGH TO EAT

Introduction

Discrimination is a prerequisite for prey selection. Upon encountering potential prey, predators evaluate the suitability of that item. This evaluation results in the decision to pursue or ignore the prey. Behavioral studies of different species of anurans demonstrated that size (Ewert 1968, 1970; Ingle 1968, 1971; Ingle and Cook 1977), configuration (Borchers *et al.*, 1978; Ewert and Kehl 1978; Ewert *et al.*, 1979; Ingle and McKinley 1978), velocity (Ewert 1968, 1970; Ewert *et al.*, 1979) and movement pattern (Borchers *et al.*, 1978; Ingle 1975) of artificial prey stimuli are important parameters in eliciting feeding behavior. Since no biological relationship exists between the natural food items and the dummy prey stimuli used, data that are the product of predator encounters with artificial prey lack ecological significance.

In Section I, I showed that green treefrogs (*Hyla cinerea*) select natural prey according to the behavior patterns displayed by the prey, and the proportion of time devoted to each prey-specific behavior (also see Freed 1980*b*). Prey length was also an important selection parameter, but its value as a cue may be overshadowed by prey activity. The following hypotheses were formed based on experimental observations: (a) preferred prey items elicit larger turns during orientation by *H. cinerea* than prey items of lower preference, (b) the time involved

for the predator to recognize and attack prey, as well as the latency period separating these two events, varies inversely with prey rank in the frog's diet, and (c) highly preferred prey elicit predator recognition at greater distances than lower ranked prey. The purposes of this study were (1) to test these hypotheses and determine if these variables are suitable indicators of predator preference, and (2) to quantify the natural cues utilized by the green treefrog during the process of prey selection.

Methods

Ten adult (6 males, 4 females) *Hyla cinerea* (SVL: $\bar{X} \pm SE = 4.6 \pm 0.1$ cm, Range: 3.8 - 4.9 cm) were collected in Gainesville, Florida. Treefrogs were maintained in 1 L containers, each housing three or four frogs. Upon capture, individuals were fed once with house flies. Frogs were then starved four days prior to and between experimental trials to minimize any effect of satiation. The frogs were fed only during the experimental trials. The experimental chamber was the plexiglass cube described previously. The top and the front plexiglass walls were left uncovered to allow lighting and filming of the predator-prey encounter. A digital stopwatch was positioned in the lower left corner of the chamber allowing timing of sequences.

Previous experiments in Section I allowed treefrogs to choose from a variety of prey; the present study focused on one-on-one predator-prey encounters. The same nine invertebrates (Table 3) described in Section I were used in these trials. Frogs were placed in the experimental chamber a minimum of 15 min prior to the beginning of the experimental trial. After a frog assumed a resting position, a prey item was placed

in the chamber at the farthest point away from and directly behind the frog. An aspirator was used to position the prey item. At the time the prey was placed in the chamber, the stopwatch and the movie camera were started simultaneously. Since the fly was known to be a highly preferred food item, it was always used to start a session, testing the readiness of the frog. After capturing the prey, the next trial did not begin until the frog reassumed a resting position. If a prey was ignored by the treefrog, the trial was terminated at the end of 5 min.

Predator-prey interactions were recorded on 16 mm Kodak black and white Tri-X reversal film using a motorized Bolex H-16 Rex movie camera with a 10 mm wide angle lens. A remote controlled Viewlex M-16 TA 16 mm stop-frame projector allowed single frame analysis of predator and prey. The following data were recorded directly from the film: time to recognition of prey, time to attack, prey behavior at the time of recognition, prey behavior just prior to prey capture, prey length, prey velocity, and coordinate location of frog and prey at the time of prey recognition by the predator. Recognition was defined as the first visible movement of the frog in response to the prey. This movement varied from a head twitch to the initiation of orientation towards the prey item. Since prey width could not always be measured accurately from the film, it was estimated from measurements of prey length using various length-width regression equations developed for each prey (Appendix 3). The period of latency separating recognition and attack was calculated as the difference between these variables.

Location data were used to recreate the positions of predator and prey at the time of prey recognition by the frog. This was done by using a gridded cardboard box that was identical in size to the feeding

chamber. Two walls were removeable to facilitate measurements: a model frog and prey were attached to the walls in their respective positions, and a string was tightly strung from the prey to a point between the model frog's eyes. Three dimensional orientation (Mardia 1972) by the treefrog was determined by measuring the angle of rotation about the horizontal axis of the frog and the frog's angle of vertical elevation towards the prey. The distance between the predator and the prey item was also measured. The angle of the frog's visual field subtended by prey (θ) was calculated by incorporating the size of the prey (length and width) and the distance at the time of recognition:

$$\theta = \text{TANGENT}^{-1} \left(\frac{\text{SIZE}}{\text{DISTANCE}} \right). \quad (4)$$

Since Ingle and Cook (1977) showed that within 15 cm, *Rana pipiens* feeding behavior is dependent on real object size and visual angles are only utilized at farther distances, visual angles are presented only for prey that were recognized by the frog at distances greater than 15 cm.

Results

The mean spherical direction in which *Hyla cinerea* oriented toward each prey is presented in Figure 1 and Table 10. A Watson and Williams multi-sample test (Mardia 1972) indicated that a significant difference exists ($F = 2.18$; $df = 8, 100$; $P < 0.05$) among the mean angles rotated by treefrogs toward the various prey types. However, Spearman's test for rank correlation showed that no significant correlation exists between prey ranks (e_i) generated in laboratory preference experiments (Table 3) and the frog's mean directional rotation towards a prey genus (Table 11A).

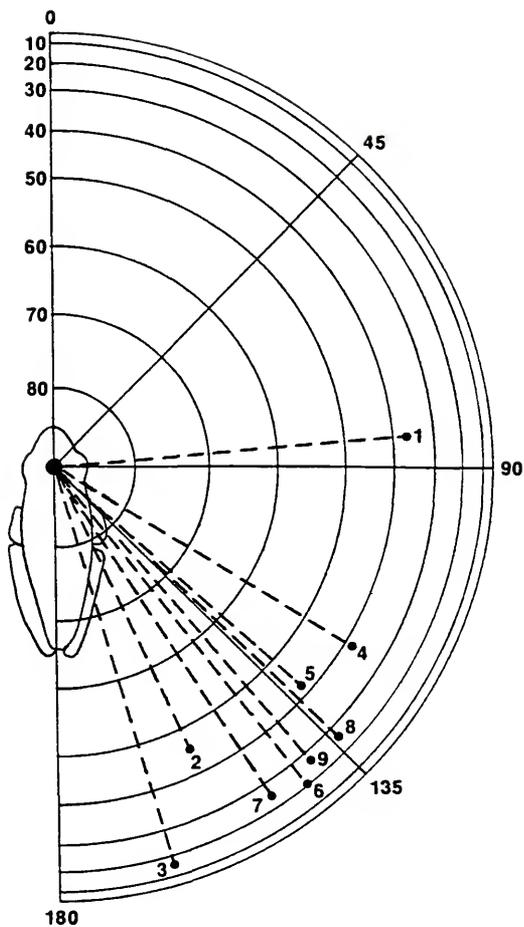


Figure 1. Schematic illustration showing mean rotational orientation towards each of nine prey. The frog is located at the center of the sphere and the prey, represented by dots, are located on the surface of the sphere. Numbers 1 through 9 refer to prey listed in Table 10. Concentric circles represent degrees latitude that define vertical location of prey.

Table 10. Mean spherical direction (Mardia 1972) of the orientation of *Hyla cinerea* towards various prey genera. S = the spherical variance. N = the number of predator-prey encounters analyzed.

Prey Genus	Horizontal Angle (degrees)	Vertical Angle (degrees)	S	N
1. <i>Musca</i>	86	37	0.3	18
2. <i>Spodoptera</i>	155	45	0.2	16
3. <i>Chauliognathus</i>	164	16	0.1	9
4. <i>Gryllus</i>	122	39	0.2	14
5. <i>Euschistus</i>	132	42	0.3	13
6. <i>Oebalus</i>	142	20	0.1	10
7. <i>Disonycha</i>	147	25	0.1	8
8. <i>Clubiona</i>	134	26	0.2	9
9. <i>Polygyra</i>	140	26	0.1	12

The average time used to identify and subsequently attack each prey, the latency period separating these two events, and the mean distance of the prey from the predator at the time of recognition are presented in Table 12. A Kruskal-Wallis one-way analysis of variance (Siegel 1956) indicated that time between prey introduction and recognition by the frog does not significantly differ among the nine prey ($\chi^2 = 13.6$, $df = 8$, $P = 0.09$). No significant correlation exists between predator electivity (e_i) and the frog's time to recognition of prey (Table 11B). However, when considering only the eight natural prey, a significant negative correlation was found between the time to predator recognition and the average crawling velocity of the prey (Table 11C). The correlation for all prey, including the house fly, is also negative but not significant (Table 11C). A significant difference did exist among the treefrog's latency periods separating the times for recognition and attack ($\chi^2 = 31.5$, $df = 8$, $P = 0.0001$). However, no association was found between predator electivity and these latency periods (Table 11D). Similarly, there are significant differences in the amount of time preceding predator attack ($\chi^2 = 25.7$, $df = 8$, $P = 0.001$), but there is no significant correlation between e_i and the time to attack for each prey genus (Table 11E). In addition, the average distance at the time of recognition for each prey does not significantly differ ($\chi^2 = 9.9$, $df = 8$, $P = 0.27$), and no significant correlation is observed when rank order of prey selection is compared to these distances (Table 11F).

Significant differences exist for both length ($\chi^2 = 81.6$, $df = 8$, $P = 0.0001$) and width ($\chi^2 = 80.6$, $df = 8$, $P = 0.0001$) among the nine prey genera (Table 13). A significant correlation with prey selection

Table 11. Spearman's coefficient of rank correlation, r_s , for predator-prey variables from one-on-one encounters of *Hyla cinerea* with prey (two-tailed test).

Correlation	Natural Prey (N = 8)		Prey (N = 9)	
	r_s	P	r_s	P
A. Electivity <i>vs</i> horizontal angle of orientation	0.33	0.420(NS)	-0.07	0.865(NS)
B. Electivity <i>vs</i> time to predator recognition	-0.14	0.736(NS)	0.05	0.898(NS)
C. Time to predator recognition <i>vs</i> prey velocity	-0.74	0.037	-0.55	0.125(NS)
D. Electivity <i>vs</i> predator latency to attack	-0.14	0.736(NS)	-0.20	0.606(NS)
E. Electivity <i>vs</i> time to attack	0.02	0.955(NS)	0.17	0.668(NS)
F. Electivity <i>vs</i> prey distance at recognition	0.40	0.320(NS)	-0.02	0.966(NS)
G. Electivity <i>vs</i> prey length	0.83	0.010	0.33	0.379(NS)
H. Electivity <i>vs</i> prey width	-0.33	0.420(NS)	-0.50	0.171(NS)
I. Electivity <i>vs</i> length/width ratio of prey	0.67	0.071(NS)	0.55	0.125(NS)
J. Electivity <i>vs</i> visual angle of prey length at distances \geq 15 cm	0.76	0.028	0.23	0.546(NS)

Table 11. Continued.

Correlation	Natural Prey (N = 8)		Prey (N = 9)	
	r_s	P	r_s	P
K. Electivity <i>vs</i> visual angle of prey width at distances \geq 15 cm	-0.41	0.320(NS)	-0.43	0.244(NS)
L. Electivity <i>vs</i> prey velocity (crawling)	0.17	0.693(NS)	0.37	0.332(NS)
M. Stimulus of crawling prey <i>vs</i> predator latency	-0.69	0.058(NS)	-0.70	0.036
N. Stimulus of crawling prey <i>vs</i> prey velocity	0.67	0.071(NS)	0.73	0.025
O. Electivity <i>vs</i> stimulus of crawling prey	0.29	0.493(NS)	0.33	0.381(NS)

Table 12. Response times of *Hyla cinerea* for nine prey genera.
Distance was recorded at the time of prey recognition.

Prey Genus		Time to	Latency	Time to	Distance	N
		Recognition	(sec)	Attack		
		(sec)	(sec)	(sec)		
<i>Musca</i>	\bar{X}	70.8	12.5	86.4	18.0	16
	SE	23.8	4.8	25.7	3.3	
<i>Spodoptera</i>	\bar{X}	71.1	20.5	91.6	27.4	15
	SE	22.3	4.2	23.0	1.4	
<i>Chauliognathus</i>	\bar{X}	46.5	14.6	61.1	22.1	9
	SE	22.5	7.9	29.6	3.1	
<i>Gryllus</i>	\bar{X}	25.8	19.8	52.2	28.2	12
	SE	10.3	5.4	16.3	3.5	
<i>Euschistus</i>	\bar{X}	40.9	45.1	70.9	19.6	13
	SE	22.4	37.3	42.2	2.8	
<i>Oebalus</i>	\bar{X}	17.1	8.9	22.7	21.1	10
	SE	4.0	2.2	3.3	2.6	
<i>Disonycha</i>	\bar{X}	47.6	23.2	70.8	21.0	8
	SE	29.9	17.2	46.4	5.6	
<i>Clubiona</i>	\bar{X}	41.3	4.6	45.8	20.9	9
	SE	23.0	1.2	23.0	3.0	
<i>Polygyra</i>	\bar{X}	104.3	67.4	210.3	24.7	12
	SE	29.4	20.3	39.6	2.0	

exists for length of natural prey but not when *Musca* is included in the analysis (Table 11G). This indicates that other cues (e.g., activity level and behavior) may be more important during selection than prey size. When prey width was substituted as the variable describing prey size, no significant correlation with e_z was found (Table 11H). However, length/width ratios approach a significant correlation with selection of natural prey (Table 11I).

The mean visual angles subtended by each prey at distances greater than 15 cm from the frog's eye (Table 13) are significantly different for both prey length ($\chi^2 = 45.4$, $df = 8$, $P = 0.0001$) and prey width ($\chi^2 = 54.3$, $df = 8$, $P = 0.0001$). The mean angles subtended in the visual field of the frog by the lengths of the eight natural prey are significantly correlated with prey selection (Table 11J). Including the house fly in this comparison eliminates this association (Table 11J). Again, the activity level and behavior that characterize *Musca* may have compensated for the fly's small visual angle and induced the frog to select it over prey subtending larger angles. Likewise, no correlation was found relating prey selection to the visual angles subtended by the width of prey as perceived by the frog (Table 11K).

Even though significant differences exist among the crawling velocities of the nine prey types ($\chi^2 = 58.8$, $df = 8$, $P = 0.0001$), no significant association was found that relates these velocities to the selection of invertebrate food items by *Hyla cinerea* (Table 11L). The stimulus value of crawling in the eight natural prey approaches a significant negative correlation with the latency period separating predator recognition and attack (Table 11M). This negative association is significant when all nine prey items are considered (Table 11M).

Table 13. Prey cues possibly utilized by *Hyla cinerea* during the process of prey selection.

Prey Genus	Size Length (mm)	Size Width (mm)	Visual Angle	Visual Angle	Crawling Velocity (cm/sec)
			Length ≥ 15 cm (degrees)	Length ≥ 15 cm (degrees)	
<i>Musca</i>	\bar{X} 6.3	2.1	1.5	0.5	4.9
	SE 0.1	0.1	0.2	0.1	0.6
	N 16	16	11	11	14
<i>Spodoptera</i>	\bar{X} 20.9	2.8	4.6	0.6	0.3
	SE 1.0	0.2	0.3	0.0	0.1
	N 14	14	14	14	7
<i>Chauliognathus</i>	\bar{X} 9.6	1.9	2.2	0.4	1.4
	SE 0.7	0.1	0.2	0.1	0.1
	N 9	9	7	7	10
<i>Gryllus</i>	\bar{X} 12.9	3.7	2.4	0.7	5.9
	SE 1.0	0.3	0.3	0.1	1.1
	N 12	12	10	10	10
<i>Euschistus</i>	\bar{X} 11.9	8.3	2.6	1.8	1.6
	SE 0.5	0.4	0.3	0.2	0.2
	N 10	10	7	7	12
<i>Oebalus</i>	\bar{X} 9.3	4.5	2.3	1.1	1.3
	SE 0.3	0.1	0.3	0.1	0.2
	N 10	10	7	7	6

Table 13. Continued.

Prey Genus	Size Length (mm)	Size Width (mm)	Visual Angle	Visual Angle	Crawling Velocity (cm/sec)	
			Length ≥ 15 cm (degrees)	Length ≥ 15 cm (degrees)		
<i>Disonycha</i>	\bar{X}	6.3	3.0	1.6	0.8	0.9
	SE	0.2	0.1	0.3	0.2	0.2
	N	7	7	5	5	6
<i>Clubiona</i>	\bar{X}	6.9	2.2	1.5	0.5	4.9
	SE	0.6	0.2	0.2	0.0	0.5
	N	9	9	6	6	9
<i>Polygyra</i>	\bar{X}	7.9	5.2	1.9	1.3	0.1
	SE	0.6	0.4	0.2	0.1	0.0
	N	12	12	12	12	4

The stimulus value of crawling prey is positively correlated with the characteristic crawling velocity of that prey (Table 11N). However, the stimulus value of crawling prey is not significantly associated with prey selection (Table 11O).

Discussion

Prey/non-prey discrimination at the level of the retina and the optic tectum of the brain in anurans precedes the behavioral motor response (Schürg-Pfeiffer and Ewert 1981). Toads and frogs express initial interest for a prey item by orienting towards the location of a stimulus (Ewert and Burghagen 1979). My results showed that orienting movements directed towards the stimulus location are not useful indicators of the stimulus value of natural prey in *Hyla cinerea*. *Spodoptera* and *Chauliognathus* larvae are highly preferred by *H. cinerea* both in the laboratory and the field (Table 4). The time utilized in the recognition-attack sequences for these insects does not distinguish these prey from less preferred items. However, prey with high crawling stimulus values do tend to shorten the period of latency separating recognition from attack. Since the configurational meaning of an artificial stimulus is independent of distance in *Alytes obstetricans* and *Bufo bufo*, and the discrimination ability has common components in *A. obstetricans*, *B. bufo*, *Bombina variegata*, *Hyla arborea*, and *H. cinerea* (Ewert and Burghagen 1979), it is surprising to find that *H. cinerea* does not recognize and pursue preferred prey at greater distances than for prey of lower rank. The desirability of the prey item apparently does not influence the degree or alacrity of the response exhibited by the treefrog, but only the probability of the occurrence of that

response. Similarly, Heatwole and Heatwole (1968) found that the motivational state of *Bufo fowleri* (i.e., degree of satiation) does not affect the speed with which responses are given when they occur, but rather whether they occur at all.

Ingle (1968) showed that *Rana pipiens* respond to stimuli on the basis of real object size. Ewert and Burghagen (1979) found that worm-like objects 6 to 12 mm long were particularly attractive to *Hyla cinerea*. Optimal prey catching response occurred when 8 mm long black rectangles were moved at a constant velocity of $20^\circ/\text{s}$ (1 cm/s). This size range approximates the data generated in this study using invertebrate prey whose mean was 10.2 mm (SE = 1.5, N = 9). However, the average length of the most preferred natural prey item (*Spodoptera*) was approximately 21 mm, which is 2.6 times larger than the optimal artificial stimulus cited above.

Prey width alone is not an important selection parameter. However, there is an indication that wild treefrogs select prey that possess length/width ratios greater than 3:1. *Bufo bufo* discriminates between prey and non-prey when dummy stimuli with length/width ratios greater than 3:1 are presented (Ewert 1968; Ewert *et al.*, 1979). Ewert (1976) stated that square objects represent neutral or indifferent stimuli and fall between horizontally (i.e., prey) and vertically (i.e., enemy) oriented rectangles in ability to elicit prey catching behavior in toads. Even so, prey items that are almost "square" (e.g., *Euschistus*) are frequently eaten by treefrogs.

Actual prey size is utilized by frogs within predator-prey distances of 15 cm. Beyond this distance the visual angle cue is involved in prey choice (Ingle 1968, Ingle and Cook 1977). Preferred

stimulus angles at various distances have been reported for a variety of amphibians (Ewert 1968, 1970; Ewert *et al.*, 1979; Himstedt 1967; Ingle 1968, 1971; Ingle and Cook 1977; Roth 1976). Mean visual angles utilized by *Hyla cinerea* varied from 1.5° to 4.6°. The average for all prey genera utilized was 2.3° (SE = 0.3, N = 9) at an average distance of 22.5 cm (SE = 1.2, N = 9). This value is identical to that recorded by Ingle and Cook (1977) for *Rana pipiens*. The functional stimulus angles utilized by *H. cinerea* varied from a minimum of 0.8° for *Disonycha* at 42.5 cm, to a maximum of 6.1° recorded for *Spodoptera* at 20 cm. If frogs did cue on visual angles of prey less than 15 cm distant, the maximum angle utilized was 54.5° for *Musca* at 0.5 cm.

Although *Hyla cinerea* does not always select prey items that characteristically display high crawling velocities, the time to recognition of natural prey is shorter for fast moving invertebrates. Fast crawling prey also possess high stimulus values for treefrogs. Increasing stimulus angular velocity in a range from 5°/s to 40°/s (0.7 cm/s to 4.9 cm/s at 7 cm) increased the overall prey-catching activity of toads towards artificial prey objects (Ewert *et al.*, 1979). Roth (1978) found that the efficacy of a stimulus in eliciting feeding activity in salamanders increases with greater velocity from 0.5 cm/s to 3.1 cm/s. Roth (1976) noted that anurans, unlike the salamander *Hydromantes italicus*, do not show sensitivity to fast movement. *Hydromantes italicus* optimally responds to angular velocities of 4.8°/s to 72°/s and a maximum velocity of 172°/s (6 cm/s) at a distance of 2 cm. The response of *Bufo bufo* decreases significantly at 90°/s (11 cm/s at 7 cm) when compared to its optimal response for stimuli moving at 20°/s (2.4 cm/s) (Ewert *et al.*, 1979). In addition, neurophysiological

studies on *Rana esculenta* showed that responses of class-2-ganglion cells ("bug detectors") decrease sharply when stimulus velocity exceeds $100^\circ/\text{s}$ and almost cease at $140^\circ/\text{s}$ (Finkelstein and Grüsser 1965). However, treefrogs do orient toward flying *Musca*. Flies have an average flight velocity of 93.8 cm/s ($\text{SE} = 6.18$, $N = 3$). The estimated angular velocity for a fly in flight 18 cm (Table 12) away from the frog exceeds $300^\circ/\text{s}$. *Musca* commonly walks within 2 cm of resting treefrogs. Average crawling speed at this distance approximately equals an angular velocity of $140^\circ/\text{s}$; this corresponds to the point at which class-2-ganglion cease responding in *Rana esculenta*.

In addition to prey size and velocity, activity patterns displayed by prey are also important parameters in eliciting feeding response in amphibians. Small squares, known to be poor stimuli for eliciting prey capture in *Bufo bufo*, are more attractive if moved in a step-wise manner rather than in a continuous fashion (Borchers *et al.*, 1978). Ingle (1975) noted that discontinuous motion facilitates prey capture in *Rana*. In *Hydromantes*, step-wise movement is more effective than continuous moving stimuli for eliciting fixation and approach (Roth 1976, 1978). Luthardt and Roth (1979a) stated that stimuli of certain orientation must move in a specific manner and at specific velocities in order to elicit optimal prey catching behavior in *Salamandra salamandra*. Prey selection by *Hyla cinerea* is influenced by the activity patterns exhibited by the prey and the proportion of the time each prey genus devotes to each behavior pattern (Section 1, p. 19). Analysis indicated that 62% of all prey were crawling at the time of recognition and 67% were performing the same behavior just prior to predation. Even so, treefrog preference is not associated with the stimulus value of crawling prey, since these

values are time-specific for each prey genus. If each prey spent equal time crawling, the stimulus value for each prey genus would reflect the rank of that prey in the diet of the green treefrog.

The effect of activity patterns on prey selection is best illustrated by *Musca domestica*. Though its configuration provides a poorer stimulus than many of the more elongate natural prey, it was the most often eaten in laboratory experiments. This is due to the fly's characteristic crawling pattern and the linkage of this behavior with flight (Section 1, p. 19). The combination of these two behaviors produces a very discontinuous or jerky activity pattern (see Ingle 1975 and Roth 1978) and accounts for a large proportion of the fly's activity time budget (Table 7).

In conclusion, preference is expressed as the greater probability that orientation and attempted prey capture will occur, not the degree or speed at which these processes take place. The cues utilized by *Hyla cinerea* during the selection of natural prey are prey size, configuration, and activity pattern (which includes the variable prey velocity). This is in close agreement with the findings of experiments using artificial prey stimuli, though *H. cinerea* uses a broader range of some of these parameters with natural prey items. Although the experiments with artificial stimuli are useful in defining cues utilized by frogs during the prey selection process, natural prey elicit responses not predicted from the analysis of anuran encounters with prey dummies.

CRITIQUE: IF I COULD ONLY DO IT OVER AGAIN

This work possesses certain methodological flaws that are inherent in behavioral studies. A major departure from reality exists since prey activity time budgets lack time periods for foraging behavior. The difficulty of providing food for the various prey and the subsequent decrease in prey visibility (*e.g.*, prey hidden by food) precluded the placing of food in the experimental chamber during time budget analysis. Ideally, time budgets should be developed in the field; however, locating and observing invertebrates in dense vegetation at night is a formidable task. The omission of foraging time from prey activity budgets may be of insignificant consequence since these time budgets were complete for the artificial environment in which the preference testing took place. Conversely, the time prey spend feeding may affect the probability of capture in the field; however, the agreement found between field and laboratory determinations of prey diet rank indicated that this is not the case. A possible explanation for this is that feeding behavior time may already be included in one of the recorded time budget periods. For example, prey may characteristically remain motionless while eating (*e.g.*, *Euschistus* and *Oebalus*) making periods of rest and feeding indistinguishable. The time spent foraging by predatory prey (*e.g.*, *Chauliognathus* and *Clubiona*) is included in the search period; however, the time spent motionless may be underestimated since actual feeding time could add to this period.

Another bias is found in the closed system in which treefrogs were forced to forage. One could argue that prey should be replaced after being eaten, thus maintaining a constant relative prey abundance for predators to choose from. However, natural habitats presumably are not characterized by a constant relative abundance of prey. In addition the electivity equation was specifically designed to analyze prey capture in a closed system. By differentially weighting the order of prey captured in the ranking process, the electivity equation assigns the highest electivity values to prey types that are captured both early and consecutively. Prey that are captured late in the experiment and/or non-consecutively will have low ranks due to the increasing probability of being eaten as total prey abundance decreases.

Finally, the identification of prey taxa may not be important in the foraging ecology of treefrogs. Prey items could be classified as to the presence of important physical and behavioral components utilized by predators during the selection process. Prey with similar morphology, behavior patterns, and size may be classified by the predator as one prey type. Many insects that look and move similarly belong, not only to different genera, but to different orders (*e.g.*, *Spodoptera* and *Chauliognathus* larvae) and, depending on the predator's discriminative ability, may be regarded as one prey (ranked 2,3 in the initial trials and 3,2 in the finals, respectively). In addition, the fifth and sixth ranked prey in this experiment may also be considered a single prey type; though belonging to different genera (*Euschistus* and *Oebalus*) they belong to the same family and exhibit many similar morphological and behavioral features. I assumed that I was offering treefrogs a choice among nine different prey genera, but in reality, frogs may have

recognized only seven distinct types of prey. I consider this and the above criticisms valid, but of minor consequences; they do not alter the conclusions concerning the discriminative ability of *Hyla cinerea* or the visual cues used during the selection process.

APPENDIX 1
PARAMETER ESTIMATES FOR LENGTH-MASS EQUATIONS

Power function model: $y = bx^m$. Length is in mm, mass in mg. *Polygyra* size range is for shell diameter, not extended length.

Genus	Size Range (mm)	b ($b \times 10^{-2}$)	m	r	N
<i>Spodoptera</i> (larva)	5.5-33.5	2.1	2.8289	0.99	35
<i>Chauliognathus</i> (larva)	6.9-14.0	0.6	3.2725	0.97	20
<i>Gryllus</i>	7.0-23.0	14.5	2.6319	0.88	24
<i>Euschistus</i>	8.9-14.0	6.6	2.8041	0.90	20
<i>Oebalus</i>	7.5-11.6	76.9	1.6334	0.83	20
<i>Disonycha</i>	6.0- 7.9	8.8	2.7496	0.95	20
<i>Clubiona</i>	4.3- 7.9	3.8	3.1804	0.96	20
<i>Polygyra</i>	5.2-10.8	28.9	3.0294	0.99	20

APPENDIX 2
DIET OF GREEN TREEFROG

Prey identified from the stomachs of 163 *Hyla cinerea*. L = larva

Prey Item	Total No. of items	Est. Biomass (g)	No. of Frogs	Adjusted %BO
Insecta				
Coleoptera	158	2.766	105	21.56
Alleculidae	21	0.356	5	1.91
Cantharidae (L)	46	0.793	32	7.21
Cantharidae	2	0.048	2	0.45
Carabidae	6	0.124	5	1.13
Cerambycidae	3	0.130	3	0.90
Chrysomelidae	27	0.387	15	3.45
Curculionidae	26	0.239	21	3.21
Elateridae	1	0.016	1	0.19
Hydrophilidae	1	0.002	1	0.06
Languriidae	8	0.307	6	1.94
Scarabaeidae	6	0.235	3	1.20
Staphylinidae	2	0.035	2	0.38
Tenbrionidae	1	0.094	1	0.44
Unknown	8	-	8	-
Collembola	21	-	13	-
Dermaptera	6	0.059	6	0.75

APPENDIX 2. Continued.

Prey Item	Total No. of items	Est. Biomass (g)	No. of Frogs	Adjusted %BO
Insecta				
Diptera	16	0.009	13	0.45
Hemiptera	49	1.161	41	8.73
Alydidae	1	0.050	1	0.32
Coreidae	1	0.095	1	0.44
Lygaeidae	2	0.015	1	0.17
Pentatomidae	37	0.806	30	7.04
Reduviidae	8	0.195	8	1.79
Homoptera	14	0.194	13	2.01
Cicadellidae	9	0.114	8	1.37
Cercopidae	1	0.055	1	0.33
Flatidae	1	0.025	1	0.22
Unknown	3	-	3	-
Hymenoptera	41	0.150	35	2.90
Formicidae	29	0.053	23	1.57
Ichneumonidae	3	0.088	3	0.73
Platygasteridae	1	0.0001	1	0.02
Unknown	8	-	8	-
Lepidoptera	128	8.223	104	36.99
Gelechiidae	3	0.007	1	0.12
Geometridae	6	0.269	5	1.63
Noctuidae (L)	66	6.402	54	26.61

APPENDIX 2. Continued.

Prey Item	Total No. of items	Est. Biomass (g)	No. of Frogs	Adjusted %BO
Insecta				
Lepidoptera				
Noctuidae	2	0.433	2	1.34
Nolidae (L)	2	0.006	1	0.12
Psychidae (L)	1	0.003	1	0.08
Zygaenidae (L)	4	0.029	2	0.34
Unknown (L)	31	0.569	25	5.30
Unknown	13	0.505	13	3.60
Odonata	1	0.109	1	0.41
Orthoptera	41	2.044	40	11.43
Acrididae	1	0.220	1	0.67
Blattidae	10	0.418	9	2.77
Gryllidae	14	1.041	14	5.46
Tetrigidae	6	0.352	6	2.08
Tettigoniidae	2	0.013	2	0.23
Unknown	8	-	8	-
Thysanoptera	3	-	3	-
Unknown	67	-	49	-
Arachnida				
Acarina	55	-	5	-
Araneae	72	0.712	62	8.40
Araneidae	7	0.083	5	0.92

APPENDIX 2. Continued.

Prey Item	Total No. of items	Est. Biomass (g)	No. of Frogs	Adjusted %BO
Arachnida				
Araneae				
Clubionidae	23	0.168	19	2.56
Dictynidae	3	0.003	3	0.14
Linphiidae	2	0.006	2	0.16
Lycosidae	9	0.275	7	1.99
Mimetidae	1	0.001	1	0.05
Pisauridae	2	0.019	2	0.28
Salticidae	4	0.041	3	0.50
Tetragnathidae	3	0.025	3	0.39
Unknown	18	0.092	17	1.80
Opiliones	12	0.285	12	2.34
Chilopoda				
Lithobiomorpha	1	-	1	-
Crustacea				
Isopoda	4	0.035	4	0.47
Gastropoda				
Stylommatophora	9	0.592	9	2.92
Polygyridae	8	0.526	8	2.94
Unknown	1	0.066	1	0.36
Reptilia				
Squamata	1	0.252	1	0.64

APPENDIX 2. Continued.

Prey Item	Total No. of items	Est. Biomass (g)	No. of Frogs	Adjusted %BO
Reptilia				
Squamata				
Iguanidae	1	0.252	1	0.72
Total (Order)	699	16.592		100.00
Total (Family)	513	16.095		99.63

APPENDIX 3
PARAMETER ESTIMATES FOR LENGTH-WIDTH EQUATIONS

Logarithmic function model: $y = b + mlnx$. Power function model: $y = bx^m$. Length and width are in mm. *Polygyra* width estimate = $0.652 \times \text{length}$ (see Table 6).

Genus	Model	b	m	r	N
<i>Musca</i>	Log	-5.31470	4.04408	0.92	10
<i>Spodoptera</i> (larva)	Power	0.06713	1.22141	0.99	14
<i>Chauliognathus</i> (larva)	Power	0.20221	0.98155	0.99	9
<i>Gryllus</i>	Power	0.25731	1.04462	0.99	17
<i>Euschistus</i>	Log	-16.64649	10.10852	0.80	10
<i>Oebalus</i>	Power	0.68178	0.84693	0.97	10
<i>Disonycha</i>	Log	-3.88884	3.76397	0.85	10
<i>Clubiona</i>	Power	0.33842	0.96167	0.96	10
<i>Polygyra</i>	-	-	-	-	-

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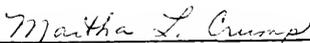
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BIOGRAPHICAL SKETCH

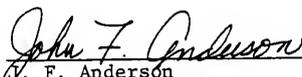
On 14 March 1952, Arthur Nelson Freed was born in the city of brotherly love. His formative years were spent on the streets of Philadelphia and in the woods of Fairmont Park (the largest city park in the world). He graduated from Northeast High School but decided not to enter Temple University (considered by many to be Northeast's 13th grade). Instead, he headed west to study biology at Indiana University of Pennsylvania (Pennsylvania's largest state owned university). After four glorious years in the mountains of west-central Pennsylvania, Arthur returned to Philadelphia with one blue Alfa Romeo 1750 Spider Veloce and a B.S. in biology. He entered the Intern Teaching Program for College Graduates at Temple University (it was his destiny) and after two years earned an M.Ed. During those two years, he experienced the tragic loss of a Porsche 911E Targa, but bravely continued teaching seventh grade life science at Upper Moreland Junior High School, Upper Moreland, PA. He then decided not to devote his life to educating children, bought a Lotus Elan Sprint, and headed with élan south to the University of Florida in pursuit of the elusive Ph.D. He was half-heartedly accepted into the zoology graduate program, not being offered support until his second year. After two frustrating and three invigorating years he finally reached the top of the graduate student pecking order and tried vainly to apply for tenure. Seeing no hope of attaining *Nirvana*, he threw up his hands in disgust, and graduated.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



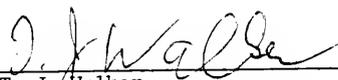
M. L. Crump, Chairperson
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



J. F. Anderson
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



T. J. Walker
Professor of Entomology and
Nematology

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

May 1982

Dean for Graduate Studies
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