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PREFACE

This dissertation is prepared as two chapters. Each chapter will be submitted to Ecology, a refereed journal.

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Foraging and Habitat Distribution Patterns of Juvenile Turtles (Chrysemys): Phylogenetic and Ontogenetic Variation

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ABSTRACT

Diet and habitat distributions of hatchling and yearling painted (Chrysemys picta) and red-eared (C. scripta) turtles are examined to detect phylogenetic and ontogenetic variations. Young turtles, hatched from eggs incubated in the laboratory, were released into a large pond-enclosure, recaptured at a later date, and stomach contents analyzed. Diet breadth, overlap, and selectivity indices were calculated.

Overlap values in this study reflect the general similarity in diets across an extensive array of food categories. A consequence is that interspecific overlap values are statistically indistinquishable from complete overlap despite notable differences in consumption of some major food categories (e.g., C. scripta ate plant matter while C. picta did not feed upon vegetation). Intraspecific (hatchling vs. yearling) overlap values were also indistinguishable from complete overlap. However, prey size appears correlated with juvenile turtle size, and negates the likelihood of a complete diet overlap between hatchlings and yearlings. Measures of diet breadth suggested diverse and non-random feeding.

The enclosure contained two distinct habitats: an open area dominated by the submergent plant Najas and an area dominated by cattails (Typha). C. scripta were hand caught more often in the Typha stand than in the open Najas habitat. C. picta captures were distributed throughout the enclosure.

INTRODUCTION

Chrysemys picta and C. scripta overlap extensively in their geographic ranges and are often the predominant turtles in lakes and ponds (Ernst and Barbour 1972). Although their taxonomic status as congeners is controversial (c.f., Vogt and McCoy 1980), behavioral and ecological similarities between the two species abound. However, few specific comparative ecological studies have been undertaken (Hart 1979, Snow 1984a). Such studies can distinguish adaptive patterns of these freshwater turtles, and enhance our understanding of the functional roles turtles have in aquatic environments.

The early life history stages of turtles are potentially fruitful areas for comparative studies (Mahmoud and Klicka 1979, Bury 1979). Characteristic of young turtles in both species is the importance of rapid growth in alleviating hazards imposed by their small size and in allowing early attainment of sexual maturity. Growth-related strategies may include delayed emergence from nests until resource availability is most suitable for rapid growth (Carr and Ogren 1959, Wilbur 1975a,b, Gibbons and Nelson 1978), delayed maturity so that resource allocation favors a continued high growth rate (Wilbur 1975b), egg lipid storage destined for hatchling growth rather than embryonic development (Congdon and Tinkle 1982), and increased egg size (and consequently hatchling size) as a function of increased female body size (Congdon and Tinkle 1982). While these processes may have a selective advantage, their importance is secondary compared to

efficient foraging and its potential contribution to rapid growth and attainment of sexual maturity.

Identification of foraging attributes that may promote rapid growth and survivorship are restricted to considerations of a dietary shift whereby young turtles increase the proportion of plant material consumed relative to animal matter as they increase in size. The explanation for the change is that it is energetically expensive for large turtles to search and pursue small prey. A shift to plant matter allows for a higher rate of energy intake relative that associated with consumption of the small prey (Parmenter 1980, Wilbur 1975b, Clark and Gibbons 1969). The ontogenetic shift appears common among chelonians (see review Hart 1983), but a lack of information on juvenile diets limits discussion based on interspecific variation to qualitative statements. Part of the reason for the paucity of data on juvenile feeding is the difficulty of locating sufficient numbers of young turtles to make valid comparisons. This problem has also plagued turtle demographic studies (c.f., Ernst and Ernst 1972, Ernst 1971). Furthermore, traditional trapping methods are ineffective in collecting small turtles (Ream and Ream 1966).

In this study, foraging habits and habitat utilization patterns of juvenile Chrysemys picta and Chrysemys scripta are compared. Additionally, intraspecific comparisons are made between hatchling and yearling age (size) classes. I circumvent the problem of locating and capturing small turtles by incubating eggs and subsequently releasing

hatchlings into a large pond-enclosure where they can be more readily sampled. The comparative experimental design allows the factoring out of phylogenetic and ontogenetic trends in diets and habitat distribtion.

METHODS AND MATERIALS

Source of Juvenile Turtles.--Field experiments were conducted with juveniles hatched from eggs of females induced to ovulate by injecting them with oxytocin using Ewert and Legler's (1978) procedures. Chrysemys scripta females were caught in ponds near Sulfur, Oklahoma. Chrysemys picta females were obtained from ponds located in the upper pennisula of Michigan (Snow 1982). Eggs were placed in 3.8 l jars (1 to 10 eggs/jar) containing vermiculite (500 ml) and water (250 ml). Lids were occasionally removed and eggs were lightly sprinkled with water. Upon hatching, weight and plastron length measurements were recorded. Hatchlings were marked for individual recognition using marginal notching and a numbering system similar to that suggested by Ernst et al. (1974). All marks persisted through the study.

Pond and Enclosure Description Used Field Experiments.--A hardware cloth fence (1 cm mesh size) was used to enclose a portion of a man-made pond (Fig. 1) located at the University of Oklahoma Aquatic Sciences Laboratory in Noble, Oklahoma. The enclosure (approximately 75 cm in height) was divided into six 3 X 20 m sections. Cattails (Typha sp. L.) and Najas quadilupensis (Spreng.) dominated 67% and 33%, respectively, of the enclosure area. These two areas are

referred to as the Typha and Najas habitats.

Depth within the enclosure varied along a gently sloping pond bottom. The difference between maximal and minimal depth at any one time was approximately 50 cm. Ground water was pumped into the pond occasionally to maintain an average enclosure depth at about 40 cm.

Design of Field Experiments.--Hatchlings were released into the enclosure during August in two sucessive years. The first year, 240 individuals of each species were released followed by 90 individuals of each species the second year. Each enclosure section received an equal portion of hatchlings. However, sections 1 and 4 contained only C. picta, sections 3 and 6 contained only C. scripta, and sections 2 and 5 had an equal density of both species (Fig. 1).

Between the first and second releases, some individuals were hand collected to gather information on growth, habitat distribution, and preliminary information of feeding habits. On September 23, (28 days after the second group of newly hatched turtles was released) 100 individuals were recaptured (50 individuals/species, 25 individuals/age class). These 4 groups are referred to as "size classes".

Stomach contents were sorted into species groups and individuals counted. Counts of ingested Ceriodaphnia were estimated using the same procedure as that used to estimate zooplankton numbers in plankton tow samples (see below).

Dry weights were determined for all stomach items. Plant matter and rare stomach items were dried for 24 hrs at 35°C to avoid loss of volatile constituents (Southwood 1978). These items were subsequently weighed on a Cahn Electrobalance. Dry weights (35°C for 24 hrs) for all other items are estimates based upon regression equations using body dimensions (usually head width or body length).

Estimating Prey Abundances.--Immediately after the 100 turtles were captured, plankton and bottom samples were collected along transects within the enclosure. A Wilding stovepipe sampler (Merritt and Cummins 1978) was used to collect bottom samples. The cylinder was thrust down through the vegetation to the pond bottom. The contents within the cylinder were scooped out and poured into a seining bucket. Samples were returned to the lab, gently washed using a 250 μm seive to retain fauna and vegetation and then preserved in 70% alcohol. Later, fauna were separated from the vegetation, sorted to species, counted, and body dimensions recorded.

Zooplankton were collected in horizontal plankton tows (mesh size=153 μm, volume=0.1 m^3) in each habitat. Because large numbers of plankton were collected, counts of individuals by species are based upon estimates. Each tow sample was diluted to 80 ml and gently stirred. A Hensen-Stemple pipet was used to obtain 1 ml subsample from the dilution. The 1 ml subsample was placed in a Sedgewick-Rafter cell and individuals of each zooplankton species were counted. A total of six subsamples was used to estimate the number of

individuals collected in each plankton sample.

Several rules were followed in estimating the abundance of each potential prey species in each habitat. Plankton tow samples in this study presumably represent a subset of those items found in stovepipe samples. Consequently, data from the latter are generally used to estimate abundances. Exceptions to this rule:

1. Counts of cladocerans, copepods, and ostracods are based solely on plankton tow samples, since no attempt was made to count these items in stovepipe samples.

2. Counts of individuals found only in plankton samples and not stovepipe samples were used when necessary.

Over 70% of the prey species were found in both habitats (Snow 1984b, Appendix A). The abundance estimates for each species were compared (i.e., Najas vs. Typha) using t-tests to determine if they were statistically different. If no significant difference was found, data from samples taken in both habitats were pooled and abundance estimates subsequently based on the pooled data. Approximately 40% of the species had significantly different abundance estimates (Snow 1984a, Appendix A).

Diet selectivity, breadth, and overlap indices.--Most food items were consumed intact and used to determine "counts" of individuals ingested. Vegetation was not enumerated to provide counts of individuals. Therefore, diet analyses utilize average dry weight

biomass (Wallace 1981) of each food group consumed rather than individual counts.

Pearre's (1982) prey selection index (V) is used to measure selectivities of prey items. Pearre recognized that his selectivity index (V) does not satisfy all of the criteria considered important by Lechowicz (1982). However, Pearre's index does appear to meet the criteria more nearly other indices reviewed by Lechowicz. According to Pearre, negative V values suggest avoidance and positive values indicate preference for the prey by the predator. V is calculated as follows:

$$V = \frac{a_d b_e - a_e b_d}{(a\ b\ d\ e)^{1/2}}$$

Symbols are defined in Table 1.

Petraitis's (1979) measures of diet breadth and overlap are used. The breadth measure (W) is calculated as follows:

$$W = (\lambda)^{1/N}$$

where $$\ln\lambda = \sum_{j=1}^{r} n_{ij}(\ln q_j - \ln p_{ij})$$

and n_{ij} is the average biomass of prey type j consumed by predator i ($p_{ij}=n_{ij}/N$, where $N = \sum_{j=1}^{r} n_{ij}$ and r = the number of prey types). Furthermore, m_j is the average biomass (mg/m^3) of prey type j in the environment ($q_j=m_j/M$, where $M=\sum_{j=1}^{r} m_j$). Plant material is not considered

in breadth measures since no attempt was made to quantify vegetation biomass in the pond. W is a relative measure.

The overlap index (O_{12}) measures diet similarity between size classes of turtles. O_{12} is calculated as follows:

$$O_{12} = (\gamma)^{1/T}$$

where $$\ln\gamma = \sum_{i=1}^{2}\sum_{j=1}^{r} n_{ij}(\ln u_j - \ln p_{ij})$$

where $u_j = a_j/T$, $a_j = n_{1j} + n_{2j}$, and $T = \sum_{j=1}^{r} a_j$. The measure O_{12} ranges from zero for no similarity in diet to one for complete similarity. Since $-2\ln\gamma$ is a chi-square variate with r-1 degrees of freedom (Petraitis 1979), a goodness of fit test can be used to evaluate the null hypothesis of complete overlap ($p_{1j}=p_{2j}$). Plant matter is not included in calculations of W, but is included in calculations of O_{12}.

Habitat distributions.--Hatchlings were hand caught. Searching for hatchlings involved both tactile and visual detection. I waded through the enclosure, raking my fingers along the pond bottom to feel for hatchlings. Masses of submerged vegetation were gently squeezed when encountered to detect turtles. Simultaneously, I surveyed the surface for basking or swimming turtles.

Upon capturing a turtle, the species and identification number were recorded along with the location of the turtle within the enclosure with reference to an X,Y-coordinate system. Turtles not caught while swimming or basking were recorded as being found either in unvegetated

patches, Najas plant masses, or Typha root masses.

RESULTS

Habitat prey abundance estimates.--Copepods, Ceriodaphnia, ostracods, and Physa were the dominant organisms in terms of abundance (individuals/m^3) in both habitats (Table 2). Libellulids were also relatively common. The estimate for this group reflects pooled data from four species (Erythemis, Pachydiplax, Plathemis, and Tramea). The 4 species were grouped because of the difficulty in identifying very early instars into appropriate taxon. Chironomid species were among the least abundant groups, but had the greatest diversity within any one family.

Physa is the dominant species in terms of biomass (mg/m^3) in both areas (Table 2). Odonates and ephemeropterans are also important contributers to the total faunal biomass in each habitat. Ostracods and Ceriodaphnia are important relative to some other groups, but less so than their importance based on abundance.

Gut Analyses.--Sixty-four percent of the C. picta hatchlings used in diet analyses were captured in the Typha. Ninety-two percent of the yearling C. picta captures were made in the Typha. Additionally, 92% and 88%, respectively, of the hatchling and yearling C. scripta were caught in the Typha section of the pond.

A list of prey items found in turtle stomachs is provided in Table 3 along with identification numbers used in identifying prey in

subsequent tables. Plant material (Najas) was consumed only by Chrysemys scripta (Table 4). The species found most frequently (70%) in all stomachs was the mayfly, Callibaetis (Table 4). Callibaetis were ingested by 95% of the yearling C. picta. The cladoceran, Ceriodaphnia, appeared frequently in gut contents of hatchling C. scripta (74%) and to a lesser extent in C. scripta yearlings (36%). Ceriodaphnia were not found in stomachs of C. picta hatchlings caught in the Typha habitat, but one hatchling caught in the Najas habitat had Ceriodaphnia in its stomach. Ceriodaphnia appeared relatively infrequently in yearling C. picta (17%) caught in the Typha habitat. Snails (Physa) are dominant species in terms of biomass and numbers in both habitats. Despite their abundance, snails were rarely ingested by turtles. Only 5 of 84 turtles captured in the Typha habitat ingested snails (Table 4) as determined by the presence of snail shells in turtle stomachs.

Forty-three percent of the prey species were ingested by all size classes, while 26% were unique to a single size class. In the latter case, items were rare and occurred in an average of less than 6% of the stomachs. Food items common to all four size classes occurred in an average of 24% of the stomachs analyzed.

C. picta yearlings had the broadest diet breadth in terms of prey species richness and evenness; C. picta hatchlings had the narrowest diet breadth (Table 5). The chi-square variate, $-2\ln\lambda$, is used as a goodness-of-fit test of each turtle size class's use of prey resources

to habitat availability (Petraitis 1979). The null hypothesis ($p_{ij}=q_j$) is rejected in all cases (Table 5) except for hatchling C. picta. Note also that Najas is not included in breadth calculations. Najas was found in C. scripta stomachs but not C. picta (Table 6).

Prey selectivities were measured using Pearre's (1982) prey selection index (V). Within each turtle size class, prey were ranked by their associated V values (Table 7). The same five prey groups have the lowest ranks within each turtle size class. Concordance of prey selectivities between sizes classes breaks down at higher rankings. Overall, the correlation (Spearman's rho, Snedecor and Cochran 1982) of prey rankings between turtle size classes ranges from r=0.53 to 0.81 (Table 8). Prey rankings correlate least between C. scripta yearlings and C. picta hatchlings and most between yearling C. picta and C. scripta.

All overlap values (O_{12}) are statistically indistinguishable from complete overlap (Table 9) despite a considerable range in their values. Hatchling C. scripta and hatchling C. picta had the lowest overlap value ($O_{12}=0.66$). Hatchling and yearling C. scripta have the highest index value ($O_{12}=0.96$) relative to other pairs considered. Considering that Najas was not found in C. picta stomachs yet was found relatively frequently in C. scripta stomachs, acceptance of the null hypothesis of complete overlap is quite tenuous for interspecific comparisons.

Gut Analyses: Typha vs Najas Habitat.--Only diets of C. picta hatchlings caught in the Najas habitat and in the Typha habitat are compared. C. scripta and C. picta yearlings and C. scripta hatchlings were caught almost exclusively in the Typha habitat making between-habitat comparisons impractical.

Many of the same prey species were preyed upon by hatchling C. picta in both habitats (Table 10). The calculated breadth measure for C. picta hatchlings in the Najas habitat is W=0.10. The null hypothesis ($p_{ij}=q_j$) of resource use by hatchlings in proportion to resource abundance is not rejected ($X^2=15.37$, df=13, ns). Recall that the same test of the null hypothesis ($p_{ij}=q_j$) for C. picta hatchlings collected in the Typha habitat was also not rejected.

The calculated overlap in diets of hatchling C. picta from the Typha versus Najas habitat is $O_{12}=0.88$. The null hypothesis ($p_{1j}=p_{2j}$) of complete overlap is not rejected ($X^2=1.82$, df=19, ns).

Gut Analyses: Interspecific Comparisons.--Hatchling and yearling gut data were pooled in interspecific comparisons. C. picta and C. scripta caught in the Typha habitat had breadths of W=0.15 and 0.12, respectively. The null hypothesis ($p_{ij}=q_j$) was rejected for C. scripta ($X^2=107.65$, $p<.05$), but not for C. picta ($X^2=25.6$, ns). But diet overlap is relatively high ($O_{12}=.96$). The null hypothesis of complete overlap ($p_{1j}=p_{2j}$) is not rejected ($X^2=2.72$, ns) despite the fact that Najas is included in the calculation of overlap.

Growth and survival.--Individual growth was monitored between the release of first and second cohorts. In general, growth ceased from approximately mid-October to late March (Fig. 2). Stomachs of individuals captured after 20 October 1981 and before 16 March 1982 were found empty when examined. Pond temperatures on sampling dates during this interval ranged from 9°C to 18°C.

Of six enclosure sections, two contained only C. picta, two had only C. scripta, and the remaining two contained a mixture of both species. This arrangement allows an analysis of variance (ANOVA) of growth to detect interspecific effects. Growth of individuals recaptured during the last census (Fig. 2) in each of the two single-species treatments is compared to conspecifics in mixed-species treatments. ANOVA results suggest that growth is not influenced by the presence of congeners (Table 11).

Growth rates of hatchlings released the second year are available only for the first 28 days they were in the enclosure, since no attempt was made to monitor growth after the first year of the study. However, initial growth rates differ significantly between years for C. picta (One-way ANOVA: $F=124.0$, $df=1,108$ $p>F=0.0001$) and for C. scripta ($F=50.1$, $df=1,97$ $p>F=.0001$). C. picta hatchlings released on August 22 of the first year increased in plastron length an average of 3.9 mm (SE=.132, n=85) during their first 32 days in the pond and C. picta hatchlings released the second year increased 0.9 mm (SE=.194, n=25) during their first 28 days. C. scripta released the

first year grew an average of 3.74 mm (SE=.158, n=74) during their initial 32 days in the pond and C. scripta released the second year grew an average of 1.66 mm (SE=.184, n=25) during their initial 28 days.

Hatchling mortality was low during the study. A total of 240 individuals of each species was released initially. Of those turtles, 100 C. picta and 101 C. scripta were terminally removed from the pond for preliminary analyses of feeding habitats during the first year of the study. As a result, a maximum of 140 C. picta and 139 C. scripta should have been in the enclosure at the end of the first year, assuming no mortality nor emigration. These maximal population sizes are within two $SE_{\hat{N}}$'s of the mark-recapture population estimate (Table 12) for the number of turtles remaining in the pond at the end of the first year. The numbers of turtles within each enclosure section were also estimated. However, the extremely high variances associated with the estimates (Table 12) make any further considerations (e.g., mortality in mixed-species vs. single-species sections) impractical.

Habitat distribution.--Two trends are apparent in the data. First, C. scripta appears to favor Typha over the Najas habitat while C. picta demonstrates no clear habitat preference. C. scripta were caught 30 times in the Najas habitat (33% of the enclosure area) and 318 times in Typha (67% of the enclosure area). The distribution of the captures is significantly different from that expected if C. scripta were randomly distributed between the two habitats

(G=119.2, df=1). Analyses of distributions in individual sections containing C. scripta produced similar results (Table 13).

C. picta were caught 142 times in the Najas habitat and 312 times in the Typha habitat. In contrast to C. scripta, C. picta appear to be distributed randomly between the two habitats (G=.84, df=1, ns). Analyses of distributions in individual sections containing C. picta produced similar results (Table 13).

The second general trend is that C. scripta and C. picta differ in microdistribution within each habitat. C. picta were seldom found within in plant masses as contrasted with C. scripta where over 50% of those individuals not swimming or basking when captured were found imbeded in plant masses (Table 14). In the Najas habitat the plant masses consisted of dense strands of the Najas plant. In the Typha habitat, the dense masses consisted of cattail roots partially extruding from the substrate.

DISCUSSION

Breadth measures, in conjunction with evaluations based on the chi-squared variate $-2\ln\lambda$, suggest that hatchling and yearling C. scripta and C. picta feed on a relatively diverse prey set and that prey selection is non-random. Prey selectivity values (V) indicate that the non-random feeding patterns are a result of some abundant prey species being fed upon infrequently (e.g., Physa) and other less common species being eaten relatively often (e.g., C. picta feeding on Callibaetis, or C. scripta feeding on Ceriodaphnia).

While breadth measures, overlap indices, and prey selectivity indices are useful in making generalizations about diets of the four turtle groups, some obvious as well as subtle trends escape detection. For example, analyses of the chi-square variate $-2\ln Y$ indicated complete overlap in diets of turtles caught in the Typha habitat. The null hypothesis ($p_{1j}=p_{2j}$) was not rejected in any comparison at the .05 level of significance. The non-significant results do not prove the hypothesis correct, only that the data do not justify rejecting it.

As noted, the plant Najas was not found in C. picta stomachs, but was found in C. scripta stomachs. Preliminary observations of hatchling feeding provide additional evidence to support this conclusion. Of 51 C. picta hatchlings removed from the pond for preliminary feeding analyses none had Najas in their stomachs, but 19 of 44 C. scripta hatchling stomachs did contain Najas (pers. obs.). Plant utilization appears to be a major interspecific difference in the feeding habits of young Chrysemys and negates the potential for complete overlap in the diets of the two species. Overlap indices were also used in measuring intraspecific similarities. Null hypotheses of complete overlap in intraspecific comparisons were not rejected. In these comparisons, the null hypothesis is explicit: $p_{1j}=p_{2j}$, where j identifies each taxonomic group. Since the null hypotheses of complete overlap were not rejected, it might be concluded that hatchling and yearling diets are similar within species. However, these comparisons assume all individuals of prey j

are equally vulnerable to turtle predation. Prey such as odonates, that have substantial size differences between smallest and largest instars may strain this assumption. Yearling turtles may be able to swallow an entire range of instar sizes while smaller hatchlings are probably restricted to smaller instars. Furthermore, juveniles turtles selecting prey that maximize their intake of energy may ingest only a narrow range of instar sizes (Snow 1984a).

Overlap indices were calculated solely for Callibaetis to demonstrate the importance that prey size can have in influencing overlap calculations. Data used in overlap calculations are offered in Snow (1984a). Briefly, Callibaetis were sorted into 14 size classes and overlaps calculated where $p_{ij}=n_{ij}/N$ with n_{ij}= number of Callibaetis (size j) ingested and $N=\sum n_{ij}$. Overlap is greatest between similar sized turtle groups and the null hypothesis of complete overlap is rejected in all comparisons (Table 15). These comparisons suggests that an accurate interpretation of overlap values may require more than just considerations of taxonomic grouping (i.e., order, family, genus) of prey items. It also indicates that intraspecific differences in diets may be as important as interspecific differences in distinguishing trophic units (Livingston 1982).

Anaylses of how young turtles respond to fluctuating resources should consider not only the abundance of each prey species, but also the abundance of individuals within each size class of instar. For

example, an acute drop in the abundance of relatively large nymphs (such as during emergence in the case of Callibaetis) may have a negative impact on growth of yearling turtles, but have little influence on the growth of smaller turtles utilizing smaller nymph classes.

Prey selectivity indices may also produce misleading results if prey size is not taken into consideration. For example, two odonate groups (Anax and Libellulidae) are ranked among the 5 most "avoided" prey species in all turtle size groups (Table 5). But they are also among the most frequently occurring prey items in stomachs (Table 3). Part of the reason for this apparent contradiction is that the selectivity index does not incorporate information on selection of specific sizes within each prey group. Larger individuals represent a large proportion of the total biomass within these prey groups. Young turtles are probably incapable of swallowing large odonate nymphs resulting in only a small proportion of the total biomass being consumed. The consequence would be that selectivity indices indicate avoidance of odonates because biomass is dominated by large instars. By combining information on frequency of occurrence of prey items with prey selectivity coefficients, a more accurate appraisal of prey selectivity is possible. For example, Physa snails have the lowest prey selection coefficient among all prey items (Table 5) and suggests Physa is avoided more often than any other prey item. Also, Physa occurs infrequently in diets despite being abundant in enclosures. Large Physa are probably too large for the smaller hatchlings to

swallow, although smaller Physa may be easily ingested. In this example, the prey selectivity index appears to portray accurately the negative turtle selection for Physa (relative to other prey items).

Prey size appears to be an important component in the prey selection process by young Chrysemys. A general trend is apparent whereby prey size and turtle size are correlated, at least within the range of turtles examined in this study and Snow (1984a). An exception to this general rule is that Ceriodaphnia were heavily preyed upon by the turtles, particularly by C. scripta. One C. scripta stomach contained an estimated 24800 Ceriodaphnia (pers. obs., this study). This enormous number suggests Ceriodaphnia are not preyed upon individually, but rather engulfed many at a time.

Belkin and Gans (1968) describe the mechanics of neustophagia whereby turtles (including C. picta) expand their pharynx allowing water containing fine particles of food to flow into their mouths. As the inward flow begins to slow, the mouth is closed and water is forced out between the edges of the jaws. In the process, food is filtered and retained in the mouth. This mechanism may also be applied by turtles in capturing large numbers of Ceriodaphnia. Also, copepods were not found in turtle stomachs despite their being extremely abundant in the enclosure (Table 2). Assuming turtles filter zooplankton prey indiscrimantly, this suggests that copepods are very adept at avoiding capture by this process.

While the two species are predicted to differ their capacities to utilize plant and animal matter, both are expected to select prey that tend to maximize energy intake. A possible consequence is that prey size tends to increase with juvenile size. However, increasing turtle size does not necessarily mean small items are not eaten. Turtles exploit small items (e.g., Ceriodaphnia) when abundant. Overall, these trends suggest juveniles of both species are selecting resources in a manner that enables them to take advantage of favorable fluctuations in prey levels while reducing the impact of unfavorable resource levels when they occur.

Habitat distributions.--C. scripta and C. picta differed in their use of the two pond habitats. C. scripta were generally found in the Typha stand while C. picta were found throughout the enclosure. Aggressive interactions between captive juvenile C. picta and C. scripta (Ernst 1971) appear to be a negligable factor influencing distributions since individuals in single-species enclosures had distributions similar to individuals in mixed-species enclosures. Interspecific interference has not been observed in other studies where mixed-species aggregations of turtles existed (Hart 1979, Boyer 1965).

The primary benefits to turtles in inhabiting structurally complex vicinities within ponds are concealment, enhanced protection, and food availability (Froese 1978). These benefits are likely to be more important for young turtles than adults. Small juveniles are more

vulnerable than adults to predators and fauna that serve as prey items for juveniles are generally more abundant in complex environments. Both species are notably associated with aquatic vegetation (Marchand 1942, Cagle 1950, Cagle and Chaney 1950, Carr 1952, Sexton 1958, Webb 1961, Gibbons 1968, Ernst and Ernst 1972, Ernst and Barbour 1972, McAuliffe 1978, Petokas 1981). However, detailed habitat selection studies are uncommon. Webb (1961) suggested that fluctuating water levels within an Oklahoma reservoir inhibited Pseudemys (=Chrysemys) scripta from prolonged associations with any particular habitat and that turtle movements were nomadic as a result. Sexton (1958) noted shifting population centers of C. picta in a pond in southeastern Michigan. Centers coincided with vegetated areas rather than being distributed randomly in relation to the pond surface. Typha communities were highly populated with turtles. But, Sexton suggested that the attraction of Typha habitats might not be the presence of Typha, per se, but rather a filamentous algae mat extending out from the Typha plants.

Both Webb and Sexton's studies are based primarily on pooled observations of various life history stages. Hart (1979, 1983) reported ontogenetic shifts in habitat selection and indicated the possibility that these shifts were functionally related to dietary shifts. At times turtles may benefit from relying on plant communities for both food and shelter. At other times, reliance on plant communities for protective cover may be costly in terms of food intake (and vice-versa). Typha may offer an obstruction against

surface or aerial predators and selection for behaviors that enhance predator avoidance may result in greater use of Typha relative to the more open Najas habitat.

Microhabitat variation in captures of submerged turtles may reflect interspecific differences in the intensity of behaviors related to predator avoidance. C. scripta, but not C. picta, were often found imbeded in plant masses. Turtle burrowing, utilization of crevices, and close contact with plant masses is frequently considered as a means for avoiding predation (Moll and Legler 1971, Cagle 1944, Ernst 1972, Hart 1983, Sexton 1958, Burger 1976, Bennett et. al. 1970). Marchand (1942) noted that C. scripta generally do not swim away to avoid capture, but hide in vegetation or beneath basking structures.

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Table 1. Symbol definitions for Pearre's (1982) prey selection index. Symbol a_d is the biomass (mg) of the target species in stomachs while b_d is the total biomass of all other species in stomachs. Symbol a_e is the biomass of the target species (mg/m^3) in the Typha habitat while b_e is the total biomass of all other species.

	Prey Species		
	Target Species	All Others	Total
Diet	a_d	b_d	$a_d+b_d=d$
Environment	a_e	b_e	$a_e+b_e=e$
Total	$a_d+a_e=a$	$b_d+b_e=b$	$a_d+a_e+b_d+b_e=n$

Table 2. Estimated number of individuals/m^3. in each habitat. Means are divided by 0.0284 (sample volume) to obtain estimates/m^3. Asterick in "Diet Item" column indicates species was preyed upon by turtles.

Species	Diet Item	Habitat	N	Mean (SE)	Estimated Number/m^3	Dry Wgt (mg/m^3)
DIPTERA						
Ceratopogonidae	*	Typha	18	4.56 (1.513)	160.5	2.37
		Najas	18	4.56 (1.513)	160.5	2.37
Chironomidae						
Ablabesmyia	*	Typha	18	2.78 (0.743)	97.8	14.45
		Najas	18	2.78 (0.743)	97.8	14.45
Anatopynia		Typha	18	0.06 (0.056)	2.1	0.23
		Najas	18	0.06 (0.056)	2.1	0.23
Chaoborus	*	Typha	18	0.44 (0.232)	15.5	0.87
		Najas	18	0.44 (0.232)	15.5	0.87
Clinotanypus	*	Typha		---	---	
		Najas	6	2.33 (0.494)	82.0	8.38
Cryptochironomus	*	Typha	18	0.39 (0.389)	13.7	1.16
		Najas	18	0.39 (0.389)	13.7	1.16
Labrundinia	*	Typha	12	0.17 (0.112)	6.0	0.14
		Najas	6	1.17 (0.307)	41.2	1.00
Microtendipes	*	Typha	18	0.11 (0.076)	3.9	0.06
		Najas	18	0.11 (0.076)	3.9	0.06
Polypedilum	*	Typha	12	0.75 (0.411)	26.4	0.87
		Najas		---	---	
Procladius		Typha	12	0.33 (0.256)	11.6	0.87
		Najas	6	4.17 (1.740)	146.8	11.50
Rheotanytarsus		Typha	12	0.33 (0.256)	11.6	0.29
		Najas	6	8.50 (2.446)	299.2	32.36

(Table 2 cont.)

Culicidae						
Culex	*	Typha	6	4.04 (1.503)	142.2	6.36
		Najas		---	---	
Anopheles	*	Typha	6	1.15 (0.330)	40.5	2.31
		Najas	6	0.06 (0.056)	2.1	0.12
Stratomyidae	*	Typha	12	0.09 (0.045)	3.2	0.87
		Najas	12	0.09 (0.045)	3.2	0.87
Tabanidae						
Chrysops		Typha	18	2.24 (0.590)	78.8	68.53
		Najas	18	2.24 (0.590)	78.8	68.53
ODONATA						
Aeshnidae						
Anax	*	Typha	12	3.00 (0.640)	105.6	190.68
		Najas	6	---	---	
Coenogrionidae						
Ischnura	*	Typha	18	5.11 (1.464)	179.9	48.54
		Najas	18	5.11 (1.464)	179.9	48.54
Libellulidae*	*	Typha	12	23.75 (4.732)	835.9	1071.27
		Najas	6	9.17 (1.939)	322.7	413.72
EPHEMEROPTERA						
Baetidae						
Caenis	*	Typha	12	1.00 (0.348)	35.2	5.78
		Najas	6	17.50 (3.519)	615.9	99.38
Callibaetis	*	Typha	18	15.06 (2.990)	530.0	200.50
		Najas	18	15.06 (2.990)	530.0	200.50

(Table 2 - continued)

HEMIPTERA						
Belostomatidae						
Belostoma	*	Typha	18	0.06 (0.056)	2.1	8.87
		Najas	18	0.06 (0.056)	2.1	8.87
Notonectidae						
Buenoa	*	Typha	18	1.50 (0.390)	52.8	206.86
		Najas	18	1.50 (0.390)	52.8	206.86
Hebridae	*	Typha	6	0.06 (0.039)	2.1	0.17
		Najas	6	0.06 (0.039)	2.1	0.17
Mesovelidae						
Mesovelia		Typha	18	0.17 (0.121)	6.0	2.64
		Najas	18	0.17 (0.121)	6.0	2.64
CRUSTACEA						
Astacidae		Typha	18	0.06 (0.056)	2.1	N/A
		Najas	18	0.06 (0.056)	2.1	
COLEOPTERA						
Dytiscidae						
Acilius		Typha	18	0.11 (0.076)	3.9	0.06
		Najas	18	0.11 (0.076)	3.9	0.06
Halipidae		Typha	18	0.06 (0.056)	2.1	N/A
		Najas	18	0.06 (0.056)	2.1	
Hydroptilidae						
Tropisternus	*	Typha	18	0.22 (0.173)	7.7	N/A
		Najas	18	0.22 (0.173)	7.7	
Berosus	*	Typha	18	0.89 (0.241)	31.3	27.20
		Najas	18	0.89 (0.241)	31.3	27.20
Hydrotilinae	*	Typha	12	0.32 (0.124)	11.3	0.84
		Najas	12	0.32 (0.124)	11.3	0.84

(Table 2 - continued)

HYMENOPTERA		Typha	12	0.03 (0.029)	1.1	N/A
		Najas	12	0.03 (0.029)	1.1	
ARACHNIDA		Typha	12	0.03 (0.029)	1.1	N/A
		Najas	12	0.03 (0.029)	1.1	
HYDRACARINA	*	Typha	12	0.29 (0.141)	10.2	0.98
		Najas	12	0.29 (0.141)	10.2	0.98
GASTROPODA						
Physidae						
Physa	*	Typha	12	86.50 (16.912)	3044.3	1557.50
		Najas	6	174.17 (27.293)	6130.0	3135.80
CLADOCERA						
Daphnidae						
Simocephalus	*	Typha	12	1.13 (0.353)	39.8	1.30
		Najas	12	1.13 (0.353)	39.8	1.30
Ceriodaphnidae						
Ceriodaphnia	*	Typha	6	1257.83 (283.26)	15323.1	163.34
		Najas	6	121.50 (47.63)	1480.1	15.78
COPEPODA		Typha	6	3822.50 (544.30)	46566.4	N/A
		Najas	6	344.67 (156.23)	4198.8	
OSTRACODA	*	Typha	6	737.67 (248.12)	8986.4	284.87
		Najas	6	53.33 (13.76)	649.7	20.59

* Libellulidae = Erythemis, Pachydiplax, Plathemis, and Tramea.

Table 3. Prey taxon and corresponding identification numbers used to reference prey in some tables.

Prey Taxon	ID Number	Prey Taxon	ID Number
Ceratopogonidae	1	Callibaetis	16
Ablabesmyia	2	Belostoma	17
Chaoborus	3	Buenoa	18
Clinotanypus	4	Hebridae	19
Crytochironomus	5	Tropisternus	20
Labrundinia	6	Berosus	21
Microtendipes	7	Hydroptilinae	22
Polypedilum	8	Hydracarina	23
Culex	9	Physa	24
Anopheles	10	Simocephalus	25
Stratomyidae	11	Ceriodaphnia	26
Anax	12	Ostracoda	27
Ischnura	13	Noteridae	28
Libellulidae	14	Najas	29
Caenis	15		

Table 4. Frequency of occurrence food items were found in stomachs of each set of turtles captured in Typha habitat. Number in parentheses refers to number of turtles in sample.

ID Number	C. picta		C. scripta	
	Hatchlings(16)	Yearlings(23)	Hatchlings(23)	Yearlings(22)
1	0.06	0.17	0.04	0.04
2	0.44	0.26	0.13	0.09
3				0.04
4		0.14		
5		0.14		
6	0.06		0.04	
7	0.12	0.09		
8		0.04	0.04	
9	0.25	0.26	0.39	
10	0.12	0.13	0.17	0.09
11			0.04	
12	0.06	0.26	0.30	0.14
13	0.25	0.43	0.26	0.23
14	0.25	0.43	0.43	0.36
15	0.38	0.35	0.07	0.23
16	0.81	0.96	0.56	0.50
17				0.04
18	0.06	0.04	0.04	0.04
19			0.04	
21		0.04		0.04
22	0.47	0.17	0.17	0.09
23	0.06			
24	0.06	0.13	0.04	0.04
25	0.06	0.43	0.48	0.04
26		0.17	0.74	0.36
27	0.50	0.17	0.35	
28	0.06	0.17	0.09	
29			0.13	0.23

Table 5. Diet breadths of each size class in the Typha habitat. Petraitis's (1979) W is used as an index of dietary breadth.

Parameter Estimate	C. picta		C. scripta	
	Hatchling	Yearling	Hatchling	Yearling
W	.053	.216	.089	.124
$-2\ln\hat{\lambda}$	23.74	40.26	46.71	174.50
N	4.0	13.1	9.67	41.8
df	18	22	20	16

Table 6. Dry weights (mg) of each prey category in stomachs of individuals caught in the Typha habitat. Counts corresponding to prey biomass are offered in Appendix B. C. picta hatchlings and yearlings are denoted by CP1 and CP2, respectively. CS1 and CS2 refer to C. scripta hatchling and yearling, respectively. Habitat dry weights are in mg/m^3 (n/a = not available).

Taxon	ID #	Stomach Dry Weight				Habitat Dry Wgt
		CP1	CP2	CS1	CS2	
Ceratopogonidae	1	0.299	0.342	0.043	0.043	2.37
Ablabesmyia	2	3.359	1.429	0.759	0.233	14.45
Chaoborus	3				0.234	9.05
Clinotanypus	4		0.477			0.00
Crytochironomus	5		0.134			1.16
Labrundinia	6	0.014	0.040	0.015		0.14
Microtendipes	7	0.049	0.075			0.06
Polypedilum	8		0.022	0.022		0.87
Culex	9	4.974	3.500	7.169		6.36
Anopheles	10	0.271	0.247	0.815	0.03	2.31
Stratomyidae	11			4.191		0.87
Anax	12	0.135	8.058	2.960	18.76	190.68
Ischnura	13	6.389	18.405	2.719	19.647	48.54
Libellulidae	14	3.326	29.529	8.931	95.036	1071.27
Caenis	15	16.583	15.938	0.404	16.052	5.78
Callibaetis	16	21.170	109.723	9.407	71.075	200.50
Belostoma	17				4.380	8.87
Buenoa	18	0.388	2.268	0.280	0.388	206.86
Hebridae	19			0.093		0.17
Tropisternus	20				0.074	0.06
Berosus	21		0.869		0.869	27.20
Hydroptilinae	22	6.134	0.369	0.591	0.148	0.84
Hydracarina	23	0.098				0.98
Physa	24	0.300	2.453	0.005	3.250	1557.50
Simocephalus	25	0.131	2.483	1.928	0.033	1.30
Ceriodaphnia	26		103.072	179.450	690.704	163.34
Ostracoda	27	0.693	0.567	1.102		284.87
Noteridae	28	0.644	1.404	1.616		0.00
Najas	29			6.204	29.210	n/a

Table 7. Prey selectivities based on Pearre's (1982) prey selection index (V). Prey items are ranked from according to their corresponding V value. Negative and positive V values suggest avoidance and preference, respectively.

	Chrysemys picta				Chrysemys Scripta			
	Hatchlings		Yearlings		Hatchlings		Yearlings	
Rank	ID #	V	ID #	V	ID #	V	ID #	V
1	24	-.0278	24	-.0484	24	-.0418	24	-.0860
2	14	-.0167	14	-.0246	14	-.0269	14	-.0414
3	27	-.0079	20	-.0164	27	-.0134	27	-.0297
4	12	-.0072	18	-.0123	18	-.0118	18	-.0248
5	18	-.0069	12	-.0066	12	-.0085	12	-.0142
6	26	-.0069	21	-.0030	21	-.0043	21	-.0077
7	21	-.0028	23	-.0010	17	-.0024	2	-.0060
8	17	-.0016	11	-.0009	16	-.0022	9	-.0043
9	5	-.0006	8	-.0006	5	-.0009	10	-.0024
10	8	-.0005	20	-.0002	1	-.0009	1	-.0024
11	11	-.0005	5	.0004	23	-.0008	5	-.0018
12	20	-.0001	10	.0005	8	-.0004	25	-.0017
13	21	.0010	2	.0008	2	-.0003	23	-.0017
14	23	.0026	6	.0009	13	-.0002	8	-.0016
15	25	.0030	1	.0011	7	-.0002	11	-.0016
16	10	.0047	19	.0022	20	-.0002	19	-.0007
17	12	.0052	7	.0033	6	.0002	6	-.0006
18	13	.0059	22	.0038	15	.0004	22	-.0004
19	14	.0066	9	.0138	19	.0027	7	-.0004
20	13	.0249	25	.0237	10	.0062	20	.0016
21	2	.0254	13	.0245	22	.0081	17	.0052
22	16	.0400	17	.0338	25	.0220	13	.0079
23	9	.0587	15	.0720	9	.0369	16	.0113
24	22	.1723	16	.0793	11	.0566	15	.0402
25	15	.1968	26	.0839	26	.1863	26	.3346

Table 8. Spearman's rank correlation coefficient (r) values for concordance between rankings of prey items according to their corresponding prey selection index values (V). Actual ranks are listed in Table 7. CP1 and CP2 refer to hatchling and yearling C. picta, respectively. CS1 and CS2 refer to hatchling and yearling C. scripta, respectively. Correlation coefficients are provided in the upper right portion of the table. Approximate probabilities that r=0 are given in lower left.

	CP1	CP2	CS1	CS2
CP1	-	.689	.594	.527
CP2	<.001	-	.609	.815
CS1	.002	.001	-	.559
CS2	.006	<.001	.004	-

Table 9. Diet overlap values for groups in the Typha habitat. Petraitis's (1979) O_{12} is used as an index of dietary overlap and is presented along with the value of $-2\ln Y$. CP1 and CP2 refer to hatchling and yearling C. picta, respectively. CS1 and CS2 refer to hatchling and yearling C. scripta, respectively. O_{12} coefficients are reported in the upper right portion of the table and the Chi-square variate $-2\ln Y$ are in the lower left.

	CP1	CP2	CS1	CS2
CP1	-	.848	.658	.814
CP2	5.64	-	.850	.912
CS1	11.51	7.39	-	.965
CS2	15.87	10.14	3.62	-

Table 10.--Dry weight (mg) biomass of prey items found in stomachs of individuals caught in the Najas habitat. Habitat dry weights are in mg/m^3 (dashes indicate item was not found in Najas habitat samples).

Taxon	ID #	Stomach Dry Weight CP1	CP2	CS1	CS2	Habitat Dry Wgt
Ceratopogonidae	1		1.801			2.37
Ablabesmyia	2	1.690	1.379	0.629		14.45
Clinotanypus	4		2.632		1.376	8.38
Crytochironomus	5					1.16
Labrundinia	6	0.172				1.00
Microtendipes	7			0.360		0.06
Polypedilum	8	0.147				—
Culex	9	0.232	4.221	1.064		—
Anopheles	10	0.025	0.131			0.12
Anax	12	0.134	0.436	0.058	0.473	--
Ischnura	13	1.486	7.366		1.288	48.54
Libellulidae	14	2.281	5.252	0.017	25.986	413.72
Caenis	15	16.160	0.860		3.434	99.38
Callibaetis	16	5.291	4.289	0.667	14.313	200.50
Buenoa	18		1.271			206.86
Hydroptilinae	22	0.148	0.148			0.84
Hydracarina	23	0.098	0.197			0.98
Simocephalus	25		0.635	0.327		1.30
Ceriodaphnia	26	2.356		0.309	59.398	15.78
Ostracoda	27	0.220		0.189		20.59

Table 11. ANOVA statistics for consideration in the examination of interspecific influences on hatchling growth. Plastron lengths (mm) of individuals recaptured during the last census are used to calculate growth. Two replications of single-species treatments against mixed-species treatments are analysed.

Species	Source of Variation	df	SS	MS	F	p>F
C. scripta	Treatment	1	0.92	0.92	0.09	0.76
	Replication	1	1.04	1.04	0.10	0.75
	Error	35	354.06	10.12		
	Total	37	356.02			
C. picta	Treatment	1	0.12	0.12	0.01	0.92
	Replication	1	0.32	0.32	0.03	0.87
	Error	57	643.80	11.70		
	Total	57	644.24			

Table 12.--The following information is used in evaluating hatchling survivorship. The estimate ($\hat{N}$) refers to the number of individuals, belonging to the first cohort of hatchlings released, that were in the pond at the end of the first year and just prior to the release of the second cohort. The estimates and associated standard errors of the estimate ($SE_{\hat{N}}$) are based on mark-recapture data using the Lincoln Index (Southwood 1978). Also presented are numbers of hatchlings terminally removed from the pond and the expected number of hatchlings in the pond during the census (see text). Estimates are provided for individual enclosure sections and for the entire enclosure (referred to as "pooled").

Species	Enclosure Section	$\hat{N}$	$SE_{\hat{N}}$	Number Removed	Expected
C. picta	1	38	39	33	47
	2	45	281	16	24
	4	47	51	33	47
	5	23	0	18	22
	pooled	116	54	100	140
C. scripta	2	132	14520	15	25
	3	67	349	35	45
	5	21	0	17	23
	6	43	17	34	46
	pooled	130	68	101	139

Table 13. G-test statistics used in evaluating the spatial distributions of turtle captures relative to the areas covered by Najas and Typha (33% and 67%, respectively). C. scripta appear to be distributed non-randomly in the enclosure with most captures occurring in the Typha habitat. C. picta appear randomly distributed (α=.05, **=p<.01) between the two habitats.

Species	Enclosure	Number of Captures: Najas Habitat	Number of Captures: Typha Habitat	G-statistic
C. scripta	2	2	41	21.4 **
	3	7	108	50.1 **
	5	2	56	32.3 **
	6	19	113	24.6 **
	pooled	30	318	119.2 **
C. picta	1	47	97	0.88 ns
	2	25	68	1.79 ns
	4	53	96	0.34 ns
	5	17	51	1.83 ns
	pooled	142	312	0.84 ns

Table 14. G-test for Independence (Sokal and Rohlf, 1981). The null hypothesis under consideration is that whether or not a turtle is captured while imbeded in a plant mass is independent of its species affinity. Plant masses in the Najas habitat consist of dense Najas strands. Cattail roots, protruding from the substrate, compose plant masses in the Typha habitat. The null hypothesis is rejected for both habitats (*=p<.05, **=p<.01).

Microhabitat	Number of Captures		G-test for Independence
	C. picta	C. scripta	
Najas mass	8	10	4.2 *
Unvegetated patch	44	15	
Typha roots	5	141	62.9 **
Unvegetated patch	78	133	

Figure 1. Map of experimental pond and enclosure. Dashed lines indicate the location of a hardware cloth fence. Each of the six enclosures is 3 X 20 m. Shaded area within the enclosure represents the Najas habitat and the open area is the Typha section of the pond.

Figure 2. Average plastron growth (mm) of recaptured individuals during first year in the enclosure. The last census date preceded the introduction of the second cohort of turtles. The dashed line represents C. scripta juveniles while the solid line denotes C. picta juveniles.

Figure 1.

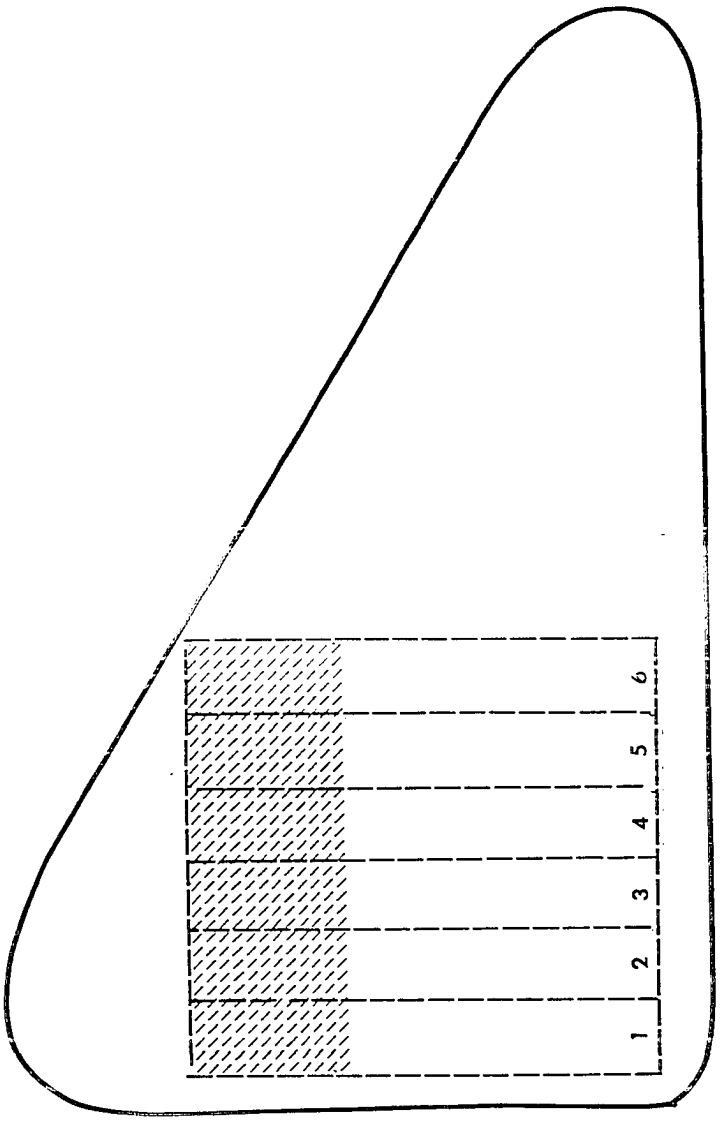
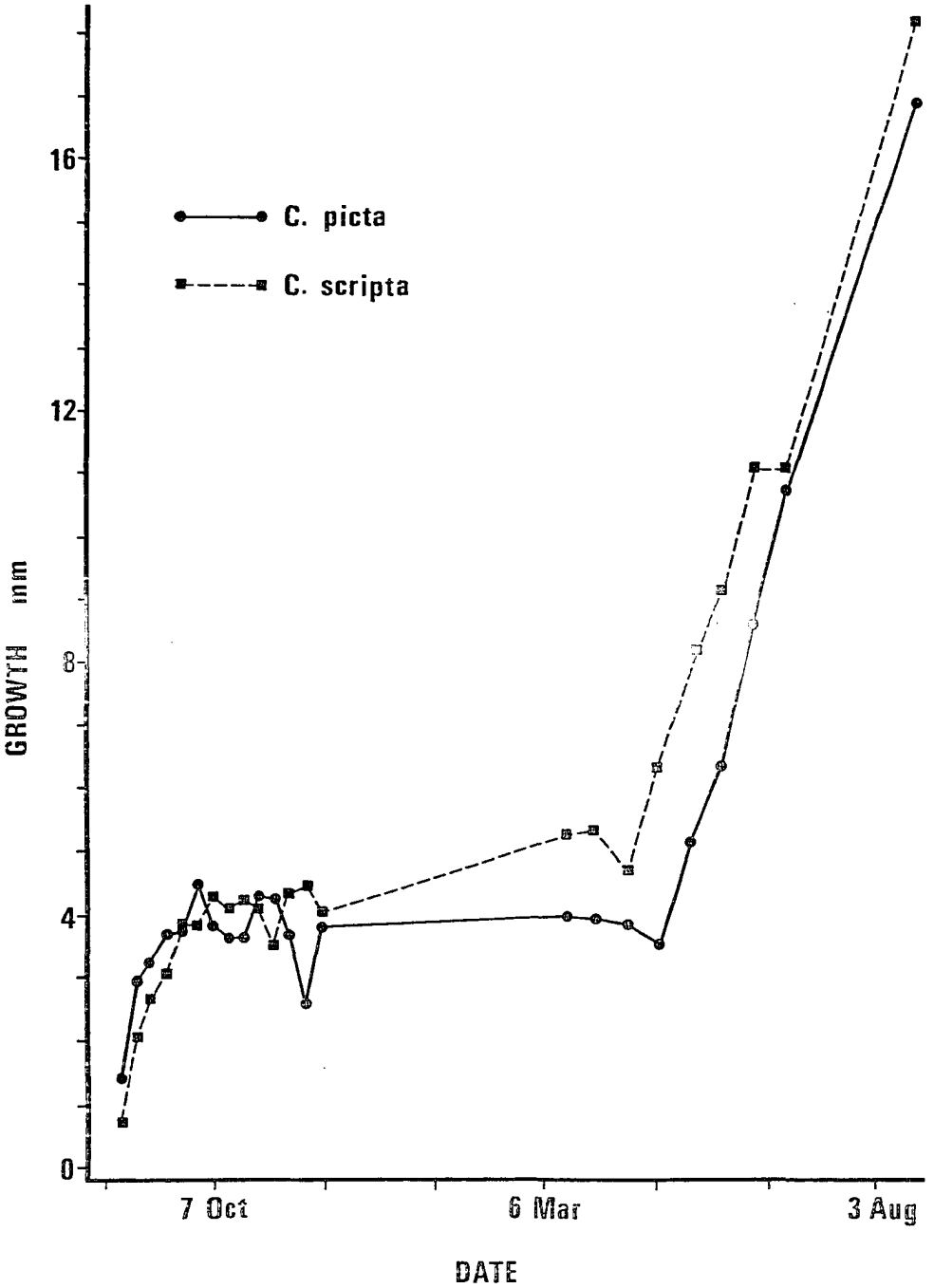


Figure 2.



Energy Acquistion by Juvenile Turtles (Chrysemys): Test of a Prey Selection Model

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ABSTRACT

Growth of Chrysemys picta and C. scripta juveniles appears very sensitive to changes in prey abundance and quality. As a result of differences in food availability, substantially different-aged cohorts have been observed reaching maturity simultaneously. These turtles may be under intense selective pressure to maximize the intake of resources necessary to sustain high growth rates. A foraging model that predicts the net energy intake for juvenile turtles feeding on a range of Callibaetis nymph sizes is examined. Those nymph sizes that maximize the net energy intake in the model are considered against nymph sizes in actual diets of four turtle size classes (C. picta and C. scripta hatchlings and yearlings).

Search, pursuit, and handling times, and capture probabilities of different-sized Callibaetis nymphs were measured in laboratory experiments. Regression equations, based on these measurements, were used to derive estimates of the model parameters. C. picta and C. scripta were not statistically different in search, pursuit, and handlings, nor in capture probabilities. Consequently, data from both species were pooled.

The model predicts that diets that maximize net energy intake will overlap considerably among the turtle size-classes considered. But, small turtles should select slightly smaller nymph sizes than larger turtles. The breadth of prey sizes eaten should be narrower than the breadth of available prey sizes for each turtle size considered. Diets of turtles feeding under the same resource regime considered in the model are qualitatively similar to predictions.

INTRODUCTION

Freshwater turtles are characterized as having potentially long intervals between hatching and sexual maturity (2 to 18 yrs, Bury 1979). Most mature upon attaining a critical size (Bury 1979, Moll, 1979) rather than age, per se, and there is a direct relationship between growth rate and span of the juvenile stage. Furthermore, turtles demonstrating rapid growth relative to other individuals gain the reproductive advantage associated with earlier maturity (Cole 1954, Stearns 1976).

Considerable variation in turtle growth rates, within and between populations, has been observed. Cagle (1948) found that age estimates based on size alone were rarely reliable in an Illinois population of Chrysemys scripta because first year growth was so variable. Size overlap in one to three year old turtles was evident with the result that some juveniles of different ages likely attain maturity simultaneously.

Between populations, cohorts of similar ages have been observed growing at substantially different rates. Cagle (1946) suggested that first season growth of three separate Chrysemys scripta populations was related to the quality of the aquatic system inhabited by each respective population. He found that juveniles from a drainage system with an apparently bountiful supply of invertebrates demonstrated an average growth rate of nearly three times that of young turtles inhabiting a pond subject to occasional drying. Juveniles inhabiting

a lake Cagle considered less beneficial for growth (due to limited vegetation and associated invertebrate fauna) had growth rates intermediate to the above two systems. He suggested that growth is sensitive to and limited by ecological factors (particularly available resources).

Gibbons (1967) examined growth rates of individuals from three Chrysemys picta populations in southwest Michigan inhabiting a marsh, lake, and river, respectively. The marsh population had the slowest growth rate, the river population had the highest, and the lake population's growth rate was intermediate. He suggested that diet quality was responsible for the variation in growth rate. The slow-growing (marsh) population fed almost entirely on vegetation, the river population having rapid growth relied heavily on invertebrates, and the lake population fed upon invertebrates but included more plant material in its diet.

Extraordinary high juvenile growth rates were recorded for Chrysemys scripta inhabiting a pond receiving heated effluent from a nuclear reactor as compared to other populations in the vicinity living in unaltered ponds (Gibbons 1970, Christy et al. 1974). Enhanced growth was only secondarily due to the higher pond temperature. Parmenter (1980) analyzed stomach contents of turtles from different populations within the area in relation to food availability. Turtles from the heated pond included a greater portion of high protein food in their diets relative to individuals from other

the ponds. Available protein was also found to be higher in the heated pond. As a result of rapid growth females in the heated pond matured in four years while females in nearby unaltered ponds reached maturity in approximately 8 years.

Jackson (1970), Bury (1979), and Hart (1982) have reviewed chelonian growth studies in varying detail. A consistent trend is apparent whereby juvenile growth responds sharply to changing food levels. The breadth of ages of turtles in their first year of maturity probably reflects growth variation as influenced by environmental factors (particularly the abundance and quality of available resources).

The relationship between turtle size and diet should be explored if the impact of fluctuating resources is to be related to turtle growth, attainment of sexual maturity and ultimately to the role that turtles have in shaping aquatic communities. This study examines the foraging behavior of Chrysemys picta and Chrysemys scripta juveniles. Laboratory experiments are conducted to estimate parameters of a foraging model used to predict net energy intake (E_T) of first year (hatchlings) and second year individuals provided with identical resource regimes. The model is based on the notion that animals feeding selectively on appropriate prey items can maximize net energy intake. As a result, they are able to allocate larger energetic quantities to growth and reproduction relative to animals feeding less selectively. Predictions of the foraging model are compared to field observations.

METHODS AND MATERIALS

Foraging Model.--The model considered in this study was proposed by Pearson (1976). The critical value in the model is E_T, the net energy intake during the foraging interval. E_T varies with changes in the array of prey available to the predator (at any particular instant of time), as well as with characteristics hypothesized to be important in the interaction between predator and prey (e.g., size changes reflective of turtle growth). Specifically:

$$E_T = \frac{\Sigma \lambda_i C_h - E_s}{1 + \Sigma \lambda_i t_{h_i}}$$

where $t_h = t_{p_i} + P_i t_{c_i}$

$C_h = P_i(aV_i - E_c t_{c_i}) - E_p t_{p_i}$

and λ_i = number of prey(i) encountered/sec searching

P_i = probability of capturing prey(i)

V_i = energetic content of prey(i)

a = portion of V_i assimilated

E_s, E_p, E_c = energy costs of searching, pursuing, and consuming prey(i).

t_{p_i} and t_{c_i} = time spent pursuing and consuming prey(i).

Subsequent use of the terms "profit" or "profitability" refer specifically to C_H. Prey(i) refers to an array of mayfly (Callibaetis) size classes. These nymphs were selected as experimental prey because they were frequently found in stomachs of juvenile C. picta and C. scripta in related studies (Snow 1984a) and can provide a good base on which model predictions can be compared.

Parameter estimates for the model were determined by laboratory experiments for λ_i, P_i, t_{c_i}, and t_{p_i}. The basic experimental design involved placing a turtle in a 60 l aquarium containing a preselected density of nymphs. Search, pursuit, and handling events were then timed and recorded with the aid of an ISAAC/Apple computer system (Model 91A, Cyborg Corp., Newton, Mass). Computer programs were written in LABSOFT language and are provided in Snow (1984b, Appendix D).

Pursuit intervals (t_p) were those periods from sighting of prey to grasping the prey within the turtle's jaws or until prey escaped. Handling intervals (t_c) encompassed the period from prey grasping to the end of prey swallowing. The remainder of time was apportioned to searching activity with the exception of instances when turtles surfaced (presumably to replenish oxygen supplies). The aquarium was housed within a laboratory fume hood. The hood's sliding sash was transformed into a one-way window using Scotch Tint (3M Corporation).

C. scripta individuals used in the experiments ranged in size from 9.8 to 149.0 gms while C. picta ranged from 4.8 to 82.6 gms. Prey

were hand sorted into separate size classes prior to the start of the experiments. The mean nymph dry weight in each experiment ranged from 0.17 to 0.87 mg. Prey densities ranged from 3 to 20 individuals/l in each experiment. Turtles were starved during the 24 h preceding the feeding experiment.

An adiabatic bomb calorimeter was used to obtain estimates of the energetic content (V_i) of prey. ASTM (1982) standard methods were followed in the combustion process. Nymphs were freeze-dried for 24 h prior to combustion. A correction for heat of formation of nitric acid was made in calculating the heat of combustion. Caloric estimates are converted to joules in calculating E_T.

Energy costs (J/gm/s) of searching (E_s), pursuing (E_p), and handling (E_c) are considered equivalent in this study. Stockard and Gatten (1983) estimated metabolic rates of actively swimming turtles to be 211 nM ATP/gm/h. Their rate is converted to 1.888 J/gm/s in my calculations. The assimilation efficiency used in this study was obtained from a study on the bioenergetics of young turtles (Kepenis and McManus (1974). I used their assimilation estimate of 85.3% (at 25°C) as it approximates the pond temperature at the time turtles (used in stomach analyses) were collected.

Regression equations used to estimate model parameters.--Each regression has up to 3 variables, turtle weight, prey weight, and prey

density. The equations are:

$$t_c = b0 + b1(1/\text{turtle weight}) + b2(\text{prey weight/turtle weight})$$

$$t_p = b0(\text{prey weight/turtle weight}))^{b1}$$

$$\lambda_i = b0(\text{turtle weight})^{b1}(\text{prey weight})^{b2}(\text{prey density})^{b3}$$

The parameter estimates for P_i (probability of capturing prey item) involved a log-odds transformation (Draper and Smith 1981) in order to correct unequal variances.

$$\log_e(P_i/1-P_i) = b0 + b1(\log_e \text{prey weight/turtle weight})$$

Species comparisons of regression models were made using dummy variables for intercepts and slopes (Draper and Smith 1981). Data from both species were pooled if the contribution to R^2, due to the addition of dummy variables, was less than .1% and if F-tests (used to test the null hypothesis that slopes associated with dummy variables were 0) were non-significant. SAS (1982) procedures were used to calculate statistics.

Estimate of nymph densities in pond.--Methods used to estimate the abundance of Callibaetis in the pond where juvenile turtles fed are presented in detail in Snow (1984a). Head lengths of individual nymphs from benthic samples were measured. These data were used to determine the distribution of the nymph population within discrete size classes. Nymphs from stomach collections (Snow 1984a) were also

sorted into discrete size classes. The number of classes was selected using Sokal and Rolhf's (1981) proposal of forming 12 to 20 classes when transforming continuous data into discrete groups.

Model predictions were compared to actual diets of four groups of turtles feeding on Callibaetis in the pond mentioned above. The groups were C. picta hatchlings and yearlings and C. scripta hatchlings and yearlings whose stomach contents were analyzed in Snow (1984a). Encounter rate predictions are based on the regime of prey densities for nymph size classes from the pond. Each nymph size class is ranked according to the ratio of $C_h/(t_c + t_p)$. Prey size classes are incorporated into the model in rank order, as long as E_T increases, to predict the array of prey sizes that maximize net energy intake.

RESULTS

Parameter estimates.--Handling time (t_c) is hypothesized to be a function of turtle and prey weights. The proposed regression model for predicting handling time appears valid for C. picta and C. scripta (Table 1). Pooling the data from both species also produces a statistically valid model explaining 68% of the variation in t_c (Table 1). The increment in the amount of variation explained by adding dummy variables to account for interspecific differences was negligible (R^2<0.1%, Table 2). In the remainder of this study, predictions of t_c are based on pooled species data. The predictions from the regression model suggest that the t_c of small turtles is more

responsive to changes in prey size, while the t_c of large turtles changes little relative to changes in prey size (Fig. 1).

Encounter rate (λ_i, the number of individuals encountered by a turtle/s of search time) is hypothesized to be a function of turtle weight, prey weight, and prey density. The proposed regression model is statistically valid for each species and for pooled data from both species (Table 1). The contribution to R^2 as a result of adding dummy variables to the model is less than 0.1% and individual F-tests for the dummy variables are nonsignificant (Table 2). Consequently, encounter rates (λ_i) are predicted on the basis of pooled data in the remainder of the study. Encounter rates (λ_i) are predicted to increase with turtle size, prey size, and prey density (Fig. 2).

Pursuit time (t_p) is hypothesized to be a function of prey and turtle weights. The proposed regression model is statistically acceptable for predicting pursuit times for C. picta and C. scripta (Table 1). A model utilizing pooled species data is also valid. Since dummy variables used to distinguish species components of the latter model add little increment to R^2 (Table 2), parameters from the regression on pooled data are used in the remainder of the study. Based on the model, increases in prey weight tend to lengthen pursuit times for small turtles, but not for large turtles (Fig. 3).

The probability (P_i) that a juvenile turtle will capture a nymph, given that the latter is pursued, is hypothesized to be a function of the interaction between prey and turtle weights. The regression model

is valid for C. picta , C. scripta, and pooled species data (Table 1). The increments in R^2 as a result of adding dummy variables to distinquish species components were less than 0.1% (Table 2). In the remainder of this paper, capture probability (P_i) is based on pooled species data. These data suggest that capture probability increases with turtle weight and decreases with prey weight (Fig 4).

Prey profitability.--The caloric value of Callibaetis nymphs is estimated to be 5074 cal/g dry wgt (SE=94.8, n=6) or approximately 22.06 J/mg. The energetic profit (C_h) associated with each prey item was predicted over an array of prey and turtle sizes (Fig 5). Profitability is comparatively low for both large and small juveniles consuming small prey. Energetic profit rises substantially when large juveniles ingest larger prey. Energetic profits for small juveniles are less responsive to increasing prey sizes. Prey ranking based upon $C_h/(t_c + t_p)$ shows trends (Fig 6) similar to those depicted in Fig 5. However, medium-sized prey are highest ranked for small juveniles while large-sized prey are highest ranked for large juveniles.

The net energy intake (E_T) was predicted for each of four juvenile size classes (5.3, 8.8, 21.1, and 26.9 grams, respectively). These size classes match the means of juvenile size classes used in stomach content analyses (see below). Prey size classes were ranked (highest to lowest) according to the ratio $C_h/(t_c + t_p)$. Each prey size class was added by rank to the E_T model until the net energy intake was maximized. The prey size classes that promote a maximum E_T tend to

increase in size as juveniles increase in size (Fig 7). The maximum E_T increases as turtle size increases and is higher than if turtles were to feed non-selectively (Table 3).

Stomach analyses.--Head lengths of Callibaetis nymphs, found in stomachs of juvenile turtles, were measured and subsequently sorted into 17 size classes (midpoints=150 to 1750 μm at 100 μm intervals). Turtles were separated into four size classes (Table 4) according to age (hatchling or yearling) and species (C. picta or C. scripta). The proportion of large prey sizes consumed increases with increasing turtle size (Fig 7). The distribution of these proportions are significantly different (Kolmogorov-Smirnov test, Sokal and Rohlf 1981) for all comparisons between turtle size classes (Table 5).

The breadth of prey sizes in actual diets are narrower than if turtles consumed the entire range of prey in a non-selective fashion. This conclusion is substantiated by testing the null hypothesis of equality of variances (F-ratio) in comparisons between prey sizes in the habitat and prey sizes in the diets of each turtle size class. The variances in prey size associated with the habitat is greater than the variances in prey size associated with each turtle size class's diet, and the null hypothesis is rejected in each comparison ($p<.001$, Table 6).

The model predicts that turtles should consume a narrower range of prey sizes than observed. The difference between the observed and predicted diet breadths is partially due to model predictions being

based on single predator sizes (i.e., 5.3, 8.8, 21.1, and 26.9 g). Turtle size classes used to establish actual diets are composed of various sized individuals. For example, predictions for the model size class of 5.3 g are compared against actual diets of individuals ranging from 3.8 to 7.1 g (Table 4). An additional factor confounding comparisons of diet breadth predictions relative to observed breadths is that the latter is less constrained by the upper limit of potential nymph sizes.

Three additional prey groups (all Odonata nymphs: Libellulidae, Anax, Ischnura) were considered in terms of the relationship between the size of prey ingested and turtle size. Libellulid nymphs are treated as a single prey group (Erythemis, Pachydiplax, Plathemis, or Tramea) since they are morphologically very similar. The sizes of ingested libellulid prey tend to increase as juvenile turtles increase in size (Fig 8). The trend is most apparent in comparisons between the smallest and largest juvenile size classes (5.3 and 26.9 gms, respectively). Large libellulids were rarely found in stomachs of small turtles while small libellulids were seldom found in stomachs of large turtles.

The consumption of Ischnura nymphs is similar (in terms of prey size ingested) to that noted for Callibaetis and Libellulidae (Fig 8). Small juveniles had proportionally more small prey in their stomachs and large juvenile stomachs contained large Ischnura nymphs to a greater degree.

Data on the consumption of Anax nymphs provide the weakest support for any suggestion that there is a direct relationship between turtle size and the size of ingested prey. But, turtle sizes differing most in weight (5.3 vs 26.9 gms) clearly demonstrate that the smaller individuals preyed upon smaller instars while larger individuals preyed upon larger instars (Fig 8). A comparison between adjacent juvenile size classes (5.3 vs 8.8 gms) in terms of the size of prey ingested does not support the suggested relationship as vividly. Both of the above comparisons involving Anax prey may be confounded by the small sample sizes involved (see caption in Fig 8).

DISCUSSION

There is a relationship between the diet that the proposed energy intake model predicts will maximize E_T and the actual diets of Chrysemys juveniles. The model suggests that the size of Callibaetis nymphs consumed should increase with turtle size. Prey size did, in fact, increase with increasing turtle size. The model also predicts the nymph sizes that maximize E_T for the larger juveniles should be only slightly larger than the nymph sizes that maximize E_T for the smallest group of turtles considered. The disparity in the range of nymph sizes found in stomachs of larger versus smaller turtles corresponds with the prediction.

The regression equations may be over-estimating the likelihood of prey capture and encounter rates, and under-estimating pursuit times. Encounter rates, capture probabilities, and pursuit times are based on

experiments with juveniles feeding in a structureless environment. The structure associated with pond vegetation may camouflage nymphs or provide crevices in which nymphs take refuge and thus decrease the encounter rates. Reductions in encounter rates may be treated by predators as reductions in density (Werner and Hall 1974). The result of a lower perceived density is that diet breadth should increase (MacArthur 1972, Charnov 1976, O'Brien et al. 1976, Unger and Lewis 1983). The profound impact that structure can have in reducing predator efficiency has been noted by many authors (including Gause 1934, Hall et al. 1970, Glass 1971, Ware 1973, Thorp and Bergey 1981, Crowder and Cooper 1982, Minello and Zimmerman 1983).

Capture efficiency, the energy spent by a predator pursuing a given prey size, including unsuccessful pursuits, can be a major determinant of prey selection (Unger and Lewis 1983). Prey value depends on the energetic content of the prey as well as the predator's efficiency in capturing the prey. Unger and Lewis suggest that most of the relative difference in capture efficiencies between small and large fish is due to the weak swimming abilities of young fish. They maintain that as fish growth proceeds, costs of capturing different prey sizes converge resulting in prey choice being dictated by the energetic content associated with the prey rather than capture efficieny. They predicted that small predators would select smaller (and more easily captured prey) and that successively larger individuals would favor successively larger prey sizes. My results concur with the prediction. Capture efficiency is a function of predator and prey

size, and successively larger prey are consumed as turtle size increases. Also, my results appear to substantiate their conclusion that encounter rates influence diet breadth while capture efficiency determines prey choice.

Overall, dietary trends predicted by the model are consistent with actual diets of the four turtle size classes and encourage an analysis its theoretical consequences and assumptions. Similar-sized nymphs are predicted to have similar encounter rates and provide similar energetic profits irregardless of whether they were preyed upon by C. picta or C. scripta individuals. However, the predictions may be biased because they reflect similarity in foraging agility and not physiological differences. No interspecific differences were assumed to exist in two model variables: assimilation efficiency and metabolic scope (used to calculate E_s, E_c, and E_p). I am not aware of any studies that compare size-specific metabolic scopes of active submerged C. picta and C. scripta juveniles. However, Stockard and Gatten (1983) concluded that both aerobic and anaerobic metabolic scopes of active C. picta turtles in a dry chamber were less than that of Pseudemys (=Chrysemys) scripta under similar conditions. I have used Stockard and Gatten's values for the total metabolic scope of active submerged turtles. They indicate that substantial errors can accrue if metabolic scopes of turtles housed in dry chambers are substituted for metabolic scopes of active submerged turtles. They found that the total metabolic scope of submerged C. picta was over twice that of active C. picta in a dry chamber primarily because of

differences in anaerobic metabolism.

Relative prey profitabilities should remain the same even with a possible interspecific difference in metabolic scopes. But, absolute profitabilities may be altered according to the magnitude and direction of the difference in metabolic scope. Interspecific differences in absolute profitabilities would provide one of the species with the advantage of more rapid growth (all other things being equal) since greater energetic quantities would be available.

C. scripta juveniles include plant material (Najas quadilupensis) in their diets while young C. picta do not eat plant matter (Snow 1984a). Juvenile C. picta may be less efficient or incapable of processing plant material as compared to juvenile C. scripta. Herbivores tend to assimilate smaller proportions of their food (Peters 1983) and may compensate for lower assimilation efficiencies by reducing costs of food processing, reducing activity levels, or increasing food intake. Adjusting methods of food processing to lower metabolic costs associated with digesting Najas may result in a loss of efficiency in processing animal matter. An additional tradeoff in the C. scripta digestive system may exist whereby resources alloted to the production of chitinase, used in exoskeleton digestion (Jeuniuex 1963), are transfered to a system designed to reduce plant matter into usable components. The consequence should be similar to that noted for variability in metabolic scope; relative prey profitability remains the same, but absolute profitability decreases. MacArthur

(1972) noted that foragers cannot be simultaneously perfect in harvesting different kinds of food. Bartholomew (1972) and Pianka (1981) expanded this prediction into the concept of "adaptive suites" whereby a constellation of tradeoffs occur as animals increase their efficiencies in harvesting specific resources. The adaptive suite associated with digestive systems might include increased gut capacity to accomodate larger quantities of plant material (Miller 1975, Drobney 1984), and increased allocation of resources into maintenance of a larger gut. A trend is apparent in turtles whereby gut capacities increase with the degree of herbivory. Intestine lengths range from 183% of the total body length for the carnivorous Trionyx ferox to 680% for the mainly herbivorous Chelonia mydas (Jacobshagen 1937, cited in Skoczylas 1978). Hart found that C. scripta females had significantly greater intestine lengths then C. picta females of a comporable size.

If C. scripta are selecting items that maximize their net rate of energy (and it appears that nymph sizes are selected in this fashion) then consumption of Najas theoretically does not reduce E_T. Callibaetis (22.06 J/mg) are energetically richer than Najas (16.40 J/mg, Boyd 1970). The impact on E_T is greater if the percentage of extractable energy is different for these two kinds of food. Incorporating Najas into the model raises some problems, particularly in quantifying an animal's encounter rate with the plant since it is abundant in the pond. If biomass is considered as a measure of abundance, the chances of encountering anything aside from Najas are

extremely small. This raises the question of why Najas is not the most abundant item (in terms of biomass) in the C. scripta stomachs. Just as each nymph size has a unique profit associated with it, so might various structural components of Najas. For example, new growth may be easier to digest than old foliage and could be assigned different profitabilities (and different encounter rates). Silt and debris encrust older Najas in the experimental enclosure. Newer Najas foliage has a bright coloration. Possibly, juveniles may be selective in what portions of the plant they consume since only bright green Najas was found in stomachs. Given the idealized situation of a system of Callibaetis nymphs of variable sizes and Najas with foliage of variable quality, any combination of nymphs (of the appropriate size) and Najas (of the appropriate quality) may occur in diets depending on encounter rates and so long as E_T was maximized.

Reducing foraging activity levels to compensate for poor plant assimilation might produce variations in prey capture techniques between C. picta and C. scripta hatchlings. Carnivorous C. picta may exhibit behaviors characteristic of an actively searching forager while C. scripta may have characteristics more similar to a sit and wait forager. Young C. picta appear more active than C. scripta. Juvenile C. scripta in aquaria remain motionless for extended periods of time but often attack prey that come within striking distance. C. scripta may become actively searching predators if prey encounter rates are high, or they may shift to feeding on plant material when prey encounters are relatively infrequent. In this study's

experiments C. scripta actively searched for Callibaetis nymphs. Densities in the experiments were not extremely low and prey detection was not hindered by vegetation that might otherwise reduce prey encounters under more natural conditions.

Increasing food intake to compensate for low assimilation of plant matter could induce a phylogenetic divergence in foraging and related behaviors (e.g., basking). Basking facilitates digestion (Hutchison 1979, Avery 1982, Bartholomew 1982). Plant matter ingested in large quantities may prolong basking intervals and consequently reduce time available for foraging and also subject small turtles to extended periods of vulnerability to predators of basking turtles. C. scripta may be under more intense selective pressure, relative to C. picta, to minimize the likelihood of being caught by predators.

Over the long term it may be advantageous for some turtles to possess herbivorous adaptations, even though a digestive system devoted to prey digestion would be more beneficial at times. For example, large turtles may utilize plant matter rather than animal matter when it is energetically more expensive to search for prey than to feed on plant matter (Marchand 1942). The profitabilities associated with prey depend on such factors as the time required to pursue and handle the animals, and prey encounter rates. C. scripta grow to a relatively large size (c.f., Congdon and Gibbons 1983, average female plastron length=210 mm) and eventually rely heavily on plant matter (Hart 1979). C. scripta adults may have evolved

physiological, morphological, and behavioral adaptations that enable efficient use of plant matter.

Encounter rates with profitable prey may be temporally and spatially unpredictable. Stearns (1976) popularized the notion of reproductive "bet-hedging" to describe one of the tactics available to organisms faced with an uncertain future of reproductive success. By spreading out the reproductive risks temporally or spatially, an organism may increase the potential for offspring surviving to maturity. The concept of bet-hedging may also apply to foraging behavior, and may help to explain the phylogenetic variation in plant utilization. At small or intermediate sizes, the advantage of a digestive system capable of utilizing plant matter is that an alternative food source is available when encounter rates with more profitable resources drop to critical levels. This advantage becomes more important as turtles grow since the range of profitable prey appears inversely related to turtle size. Rather than allocating large amounts of resources to development of such a system at a time when it would be most useful, it might be more advantageous to balance the costs across successive life stages in a gradual but increasing degree. There is some evidence of a gradual development of such a system in C. scripta. Hart (1979) found that C. scripta intestine lengths increased with increasing body length. A gradual, as opposed to a sudden, increase in the amount of vegetation consumed may accompany the development of the system. Hart (1983) found that the proportion of plant matter consumed by C. scripta increases gradually

with turtle size. In contrast, Clark and Gibbons (1969) recognized a more sudden shift in their study. Both studies were conducted over long time intervals making it difficult to separate ontogenetic changes from seasonal changes in food levels. In effect, C. scripta may be minimizing the impact of resource shortages by "bet-hedging" with a system capable of utilizing plant matter. Unpredictable variation in preferred or energetically rich food sources may be the circumstances favoring a capacity for utilizing relatively predictable food items (Fox and Morrow 1981, McKaye and Marsh 1983).

C. picta adults are generally smaller than adult C. scripta (c.f., Moll 1979, average adult plastron length in Wisconsin=157 mm). Adult C. picta do not include large amounts of vegetation in their diets. Hart (1979) examined resource partitioning among Chrysemys turtles in southern Louisiana and found significantly more vegetation in adult C. scripta than in C. picta. Because adult C. picta are much smaller than C. scripta adults, the advantage to the former of a system requiring efficient use of plant matter may be minimal. As a consequence digestive adaptations at all C. picta life stages may favor the efficient utilization of animal prey over vegetation. This may account for the interspecific difference in juvenile utilization of Najas in my study.

Chrysemys turtles are sexually dimorphic with males being smaller than females (Bury 1979). In view of the hypotheses proposed above to

explain phylogenetic variation in plant utilization, it might also be hypothesized that male C. scripta utilize lesser amounts of plant matter relative to females. Also, adaptations that enhance digestion of plant matter may differ between sexes. Hart (1979) found significant differences in intestines lengths between sexes of a comporable size in this species.

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Table 1.--ANOVA and regression summary for parameter estimates used in model. See Table 2 for variables associated parameter estimates. Pooled refers to combined C. picta and C. scripta data.

Parameter	Species	Parameter Estimates (±SE) b0	b1	b2	b3	N	F ratio	p>F	R^2
Handling Time	C. picta	1.21±.055	10.10±0.944	39.73±1.268		1194	1824.2	.0001	.75
	C. scripta	1.03±.073	12.61±1.404	43.18±1.913		1045	654.0	.0001	.56
	Pooled	1.17±.044	10.78±0.796	40.52±1.064		2239	2382.5	.0001	.68
Encounter rate	C. picta	-1.41±.081	0.34±0.043	0.18±0.082	0.24±0.075	70	29.5	.0001	.58
	C. scripta	-1.32±.101	0.32±0.050	0.35±0.089	0.18±0.084	66	21.9	.0001	.53
	Pooled	-1.37±.063	0.33±0.032	0.26±0.060	0.21±0.056	136	49.6	.0001	.54
Pursuit Time	C. picta	1.16±.085	0.47±0.050			70	87.1	.0001	.56
	C. scripta	1.12±.095	0.48±0.052			66	87.0	.0001	.58
	Pooled	1.16±.062	0.49±0.036			136	186.7	.0001	.58
Capture Probability	C. picta	-1.29±.27	-0.51±0.07			70	53.5	.0001	.44
	C. scripta	-1.34±.33	-0.54±0.07			66	48.3	.0001	.43
	Pooled	-1.33±.20	-0.53±0.05			136	109.2	.0001	.45

Table 2.--ANOVA statistics for evaluating interspecific variation in handling time, encounter rate, pursuit time and capture probability. Dummy variable analysis (Draper and Smith 1981) is used to distinguish differences in intercept and slope coefficients. ANOVA models are included beneath each set of statistics.

Parameter	Source of Variation	df	MS	F ratio	p>F	Incremental R^2
Handling Time	b1,b2	2	5288.48	2394.06	.0001	.68
	Dummy variables					
	a0	1	0.87	0.39	.5309	<.001
	a1	1	24.43	11.06	.0009	<.001
	a2	1	5.22	2.36	.1244	<.001
	MSE	2233	2.21			
Model: t_c = b0 + b1(1/turtle wgt) + b2(prey wgt/turtle wgt) + a0(dummy intercept) + a1(dummy turtle wgt) + a2(dummy prey wgt/turtle wgt)						
Encounter Rate	b1, b2, b3	3	1.419	48.93	.0001	.54
	Dummy variables					
	a0	1	0.025	0.87	.3524	<.001
	a1	1	0.038	1.34	.2487	<.001
	a2	1	0.002	0.01	.9203	<.001
	a3	1	0.066	2.28	.1336	<.001
	MSE	127	0.029			
Model: $\log_{10} \lambda$ = b0 + b1($\log_{10}$ turtle wgt) + b2($\log_{10}$ prey wgt) + b3($\log_{10}$ prey density) + a0(dummy intercept) + a1(dummy turtle wgt) + a2(dummy prey wgt) + a3(dummy density)						

Table 2.--(continued)

Parameter	Source of Variation	df	MS	F ratio	p>F	Incremental R^2
Pursuit Time	b1	1	9.095	187.39	.0001	.58
	Dummy variables					
	a0	1	0.118	2.43	.1218	<.001
	a1	1	0.001	0.02	.8876	<.001
	MSE	132	0.048			
	Model: $\log_{10} t_p = \log_{10} b0 + b1(\log_{10}$ turtle wgt/prey wgt) + a0(dummy intercept) + a1(dummy turtle wgt/prey wgt)					
Capture Probability	b1	1	56.55	108.08	.0001	.45
	Dummy variables					
	a0	1	0.26	0.49	.4847	<.001
	a1	1	0.06	0.11	.7396	<.001
	MSE	132	0.52			
	Model: $\log_e(P/1-P) = b0 + b1(\log_e$turtle wgt/prey wgt) + a0(dummy intercept) + a1(dummy turtle wgt/prey wgt)					

Table 3.--Estimated maximum net energy (E_T) gained by turtles feeding selectively on prey items and estimated E_T gained by turtles feeding non-selectively. Energy values are in J/s.

Nature of feeding	C. picta		C. scripta	
	Hatchling	Yearling	Hatchling	Yearling
Selective	.396	1.409	.662	1.687
Non-selective	.383	1.333	.636	1.585

Table 4.--Descriptive statistics for weights of turtles sorted into size classes according to age (hatchling or yearling) and species (C. picta or C. scripta). Means are used to identify size classes in text and some tables and figures. Weights are reported in grams.

Statistic	C. picta		C. scripta	
	Hatchling	Yearling	Hatchling	Yearling
Mean	5.3	21.1	8.8	26.9
SE	0.19	0.90	0.31	1.08
N	25	25	25	25
Range	3.8-7.1	14.7-31.3	6.7-13.7	21.0-38.0

Table 5.--Kolmogorov-Smirnov Two-Sample Test (Sokal and Rolhf 1981), testing differences in distributions of Callibaetis preyed upon, between each set of juvenile turtle size classes. All distributions differ significantly (α=.05) from each other. Critical D values fill the lower left portion of the table while upper right values are D statistics based actual distributions. The sample size associated with each turtle size class are listed in parentheses.

	Turtle Size Class			
	5.3 (213)	8.8 (61)	21.1 (413)	26.9 (209)
5.3	---	.196	.366	.578
8.8	.196	---	.215	.426
21.1	.113	.186	---	.211
26.9	.131	.198	.115	---

Table 6.--Tests of equality of variances between Callibaetis sizes in diets and Callibaetis sizes in habitat. The null hypothesis that the variances are equal is rejected ($p<.001$, one-tailed F-test) in all comparisons. F-statistic is calculated using the habitat variance as the numerator. Habitat variance=174752, df=333. Head lengths are measured in micrometers.

Turtle Size	df	Variance	F statistic
5.3	222	34109	5.12
8.8	60	50114	3.49
21.1	412	57190	3.06
26.9	208	56570	3.09

Figure 1.--Estimated handling time (t_c) of Callibaetis nymphs by Chrysemys juveniles as a function of prey and turtle weights. Handling times are more responsive to prey size changes when juveniles are small. Large juveniles handle both large and small prey with nearly equal efficiency.

Figure 2.--Relationship between encounter rates (individuals/second of search time) of juvenile turtles with Callibaetis nymphs as a function of turtle and nymph weights. Density of nymphs in this example is 1/liter. Increases in both nymph and turtle weights tend to increase encounter rates.

Figure 3.--Estimate of pursuit time as a function of nymph and turtle weights. Times are longer for small juveniles pursuing large nymph relative to smaller nymphs. As turtle size increases, the disparity between pursuit times of large and small nymphs diminishes.

Figure 4.--Estimated probabilities of capturing nymphs as a function of nymph and turtle weight. Capture probabilities increase with increasing turtle size, but decrease with increasing nymph size.

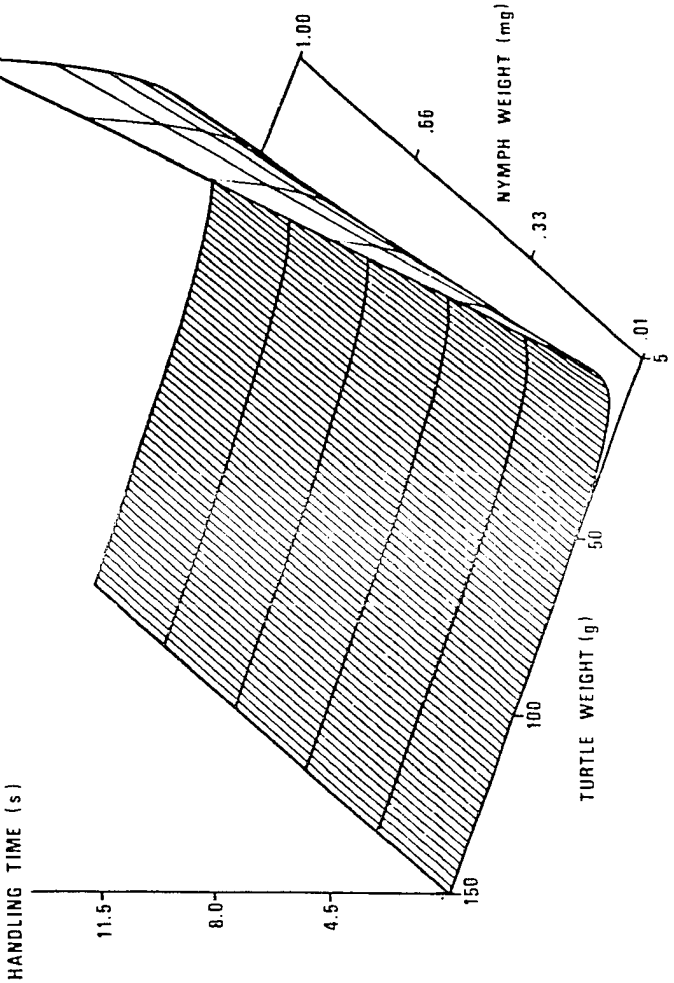
Figure 5.--Energetic profit associated with different nymph sizes as a function of turtle weight. Energetic profit is equal to the energetic content (joules) of the nymph minus the energetic costs of pursuing and handling the nymph. Large nymphs are more profitable than small nymphs. Also, larger turtles have higher profit margins than smaller turtles.

Figure 6.--Ratios of $C_h/(t_c+t_p)$ used to rank prey for inclusion into the E_T model. Ratios are generally higher for large juveniles than small juveniles for all nymph sizes. However, medium sized nymphs have the highest ratios when calculated for small turtles. Large nymphs have the highest ratios when calculated for large turtles.

Figure 7.--Percent distribution of nymph sizes in stomachs of turtles representing the four juvenile weight classes considered in the model. Percentages are given beneath bars. As turtle size increases proportionately more large nymphs are consumed. The nymph size with the highest $C_h/(t_c + t_p)$ rank is denoted by an "X" for each turtle weight class. Dashed lines span the nymph sizes that maximize E_T when they are the only sizes consumed. Total number of nymphs consumed by each turtle size class is 223, 61, 413, and 209 for weight classes 5.3, 8.8, 21.1, and 26.9 gms, respectively.

Figure 8.--Percent distribution of nymph sizes in stomachs of turtles representing the four weight classes considered in the E_T model. Distributions are provided for Anax, Ischnura, and a composit of four Libellulid species (Erythemis, Pachydiplax, Plathemis, and Tramea). Turtle weight classes are 5.3, 8.8, 21.1, and 26.9 gms; the corresponding total number of Anax nymphs consumed by each weight class is 5, 31, 40, and 9, respectively; the total number of Ischnura nymphs consumed is 41, 9, 55, and 8, respectively; the total number of libellulid nymphs consumed is 44, 23, 78, and 55, respectively.

Figure 1.


HANDLING TIME (s)
11.5
8.0
4.5
TURTLE WEIGHT (g)
150
100
50
5
NYMPH WEIGHT (mg)
1.00
.66
.33
.01

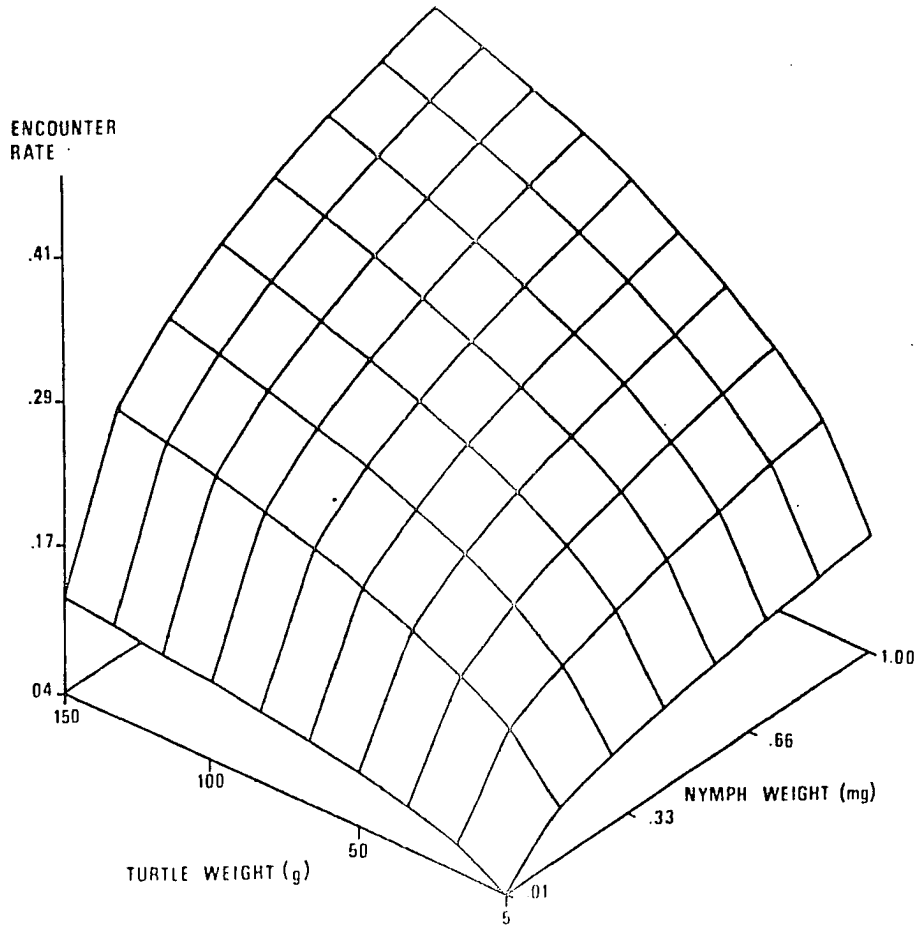

ENCOUNTER
RATE
.41
.29
.17
04
150
100
50
5
TURTLE WEIGHT (g)
01
.33
.66
1.00
NYMPH WEIGHT (mg)

Figure 2.

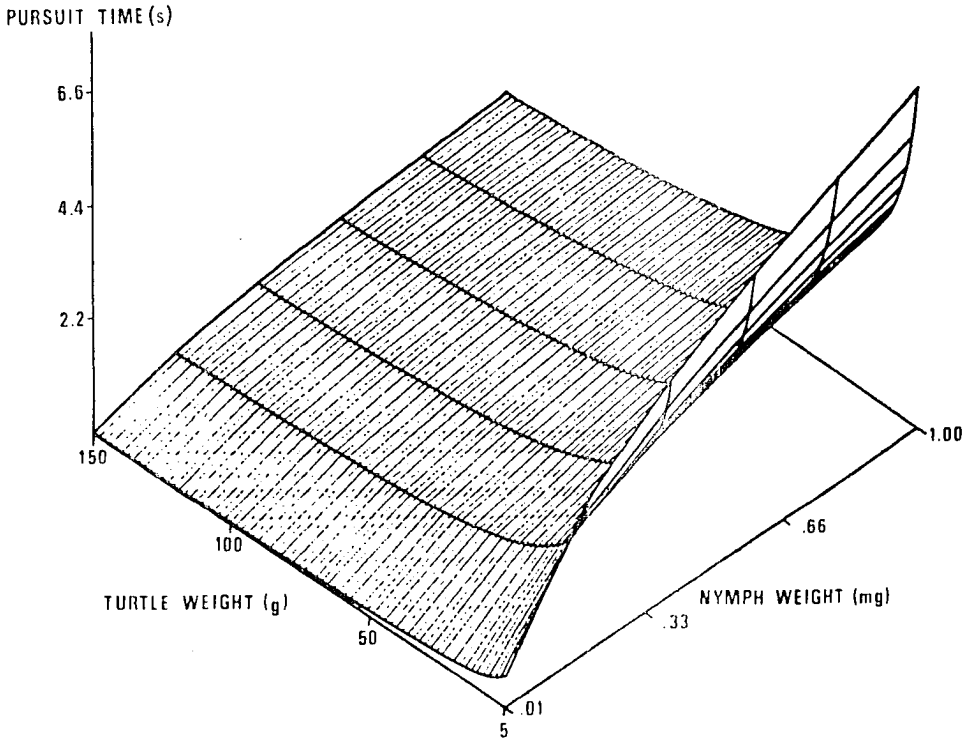

PURSUIT TIME (s)
6.6
4.4
2.2
150
100
50
5
TURTLE WEIGHT (g)
1.00
.66
.33
.01
NYMPH WEIGHT (mg)

Figure 3.

Figure 4.

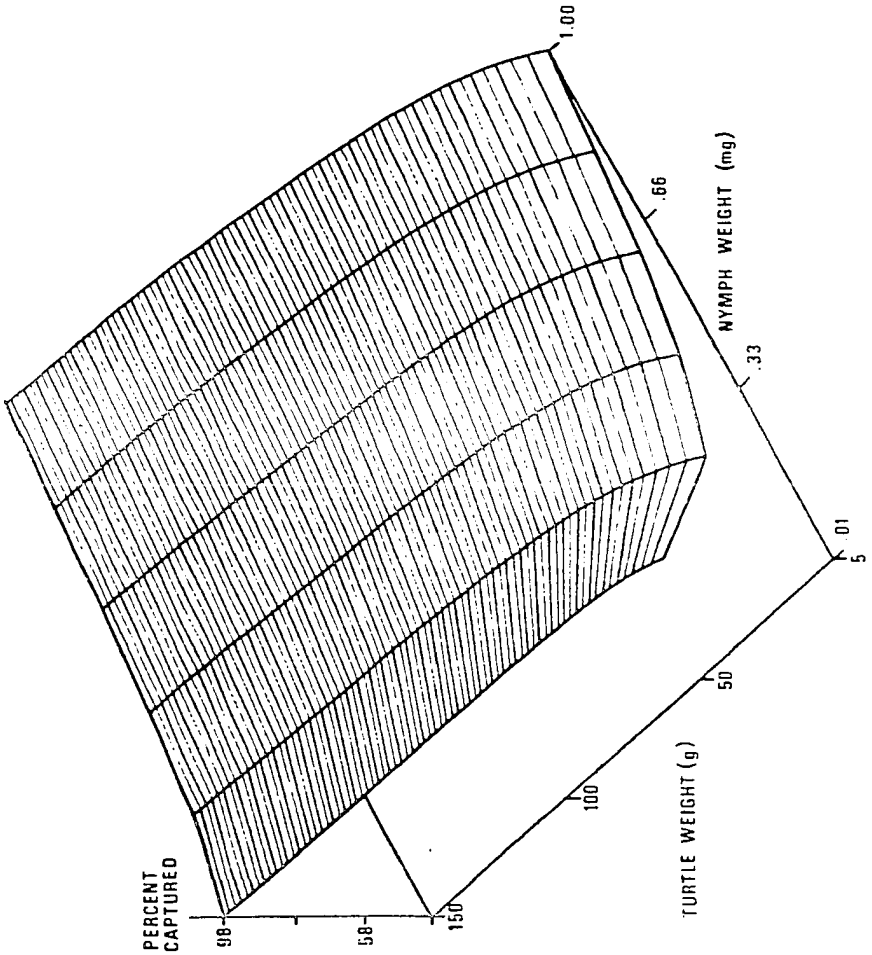

PERCENT CAPTURED
98
58
150
100
50
TURTLE WEIGHT (g)
5
.01
.33
.66
1.00
NYMPH WEIGHT (mg)

Figure 5.

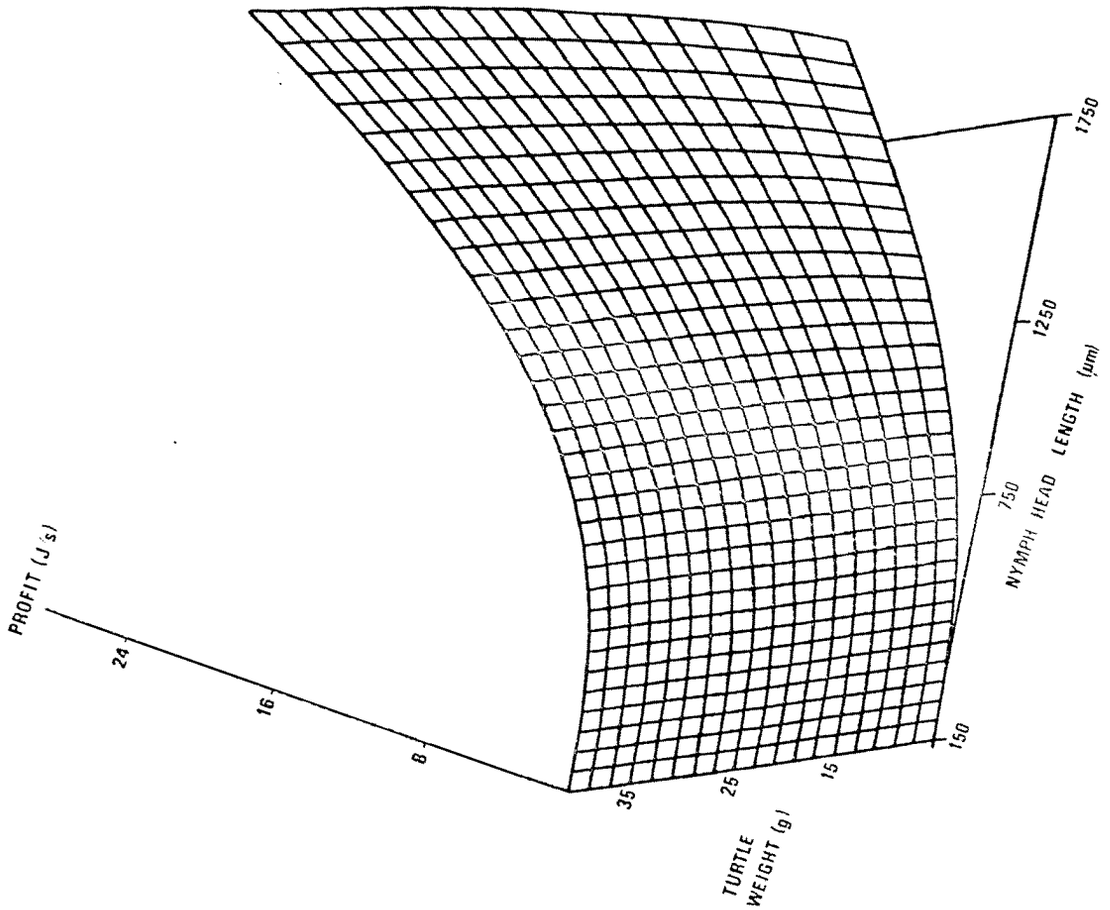
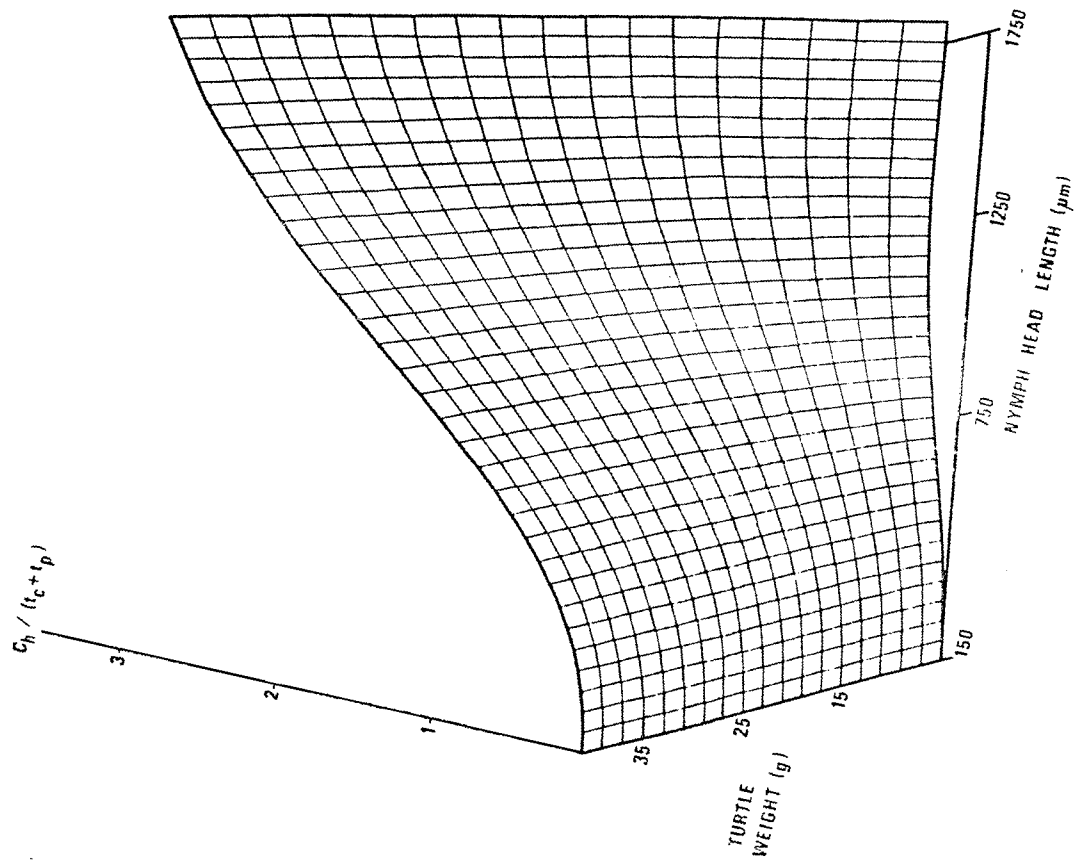

PROFIT (J/s)
24
16
8
35
25
15
TURTLE WEIGHT (g)
150
750
1250
1750
NYMPH HEAD LENGTH (μm)

Figure 6.


$C_h / (t_c + t_p)$
3
2
1
35
25
15
TURTLE WEIGHT (g)
150
750
1250
1750
NYMPH HEAD LENGTH (μm)

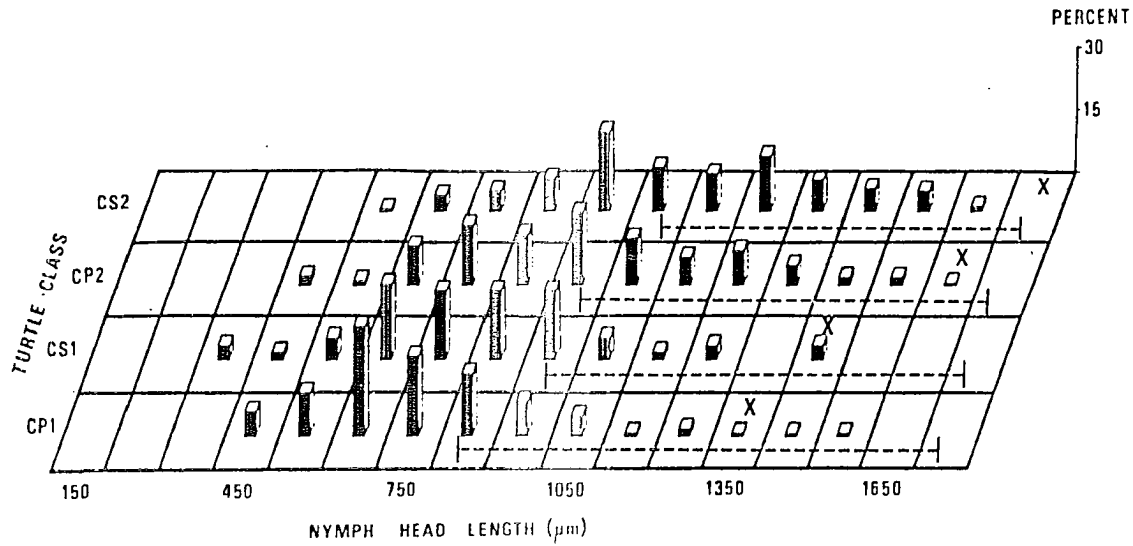
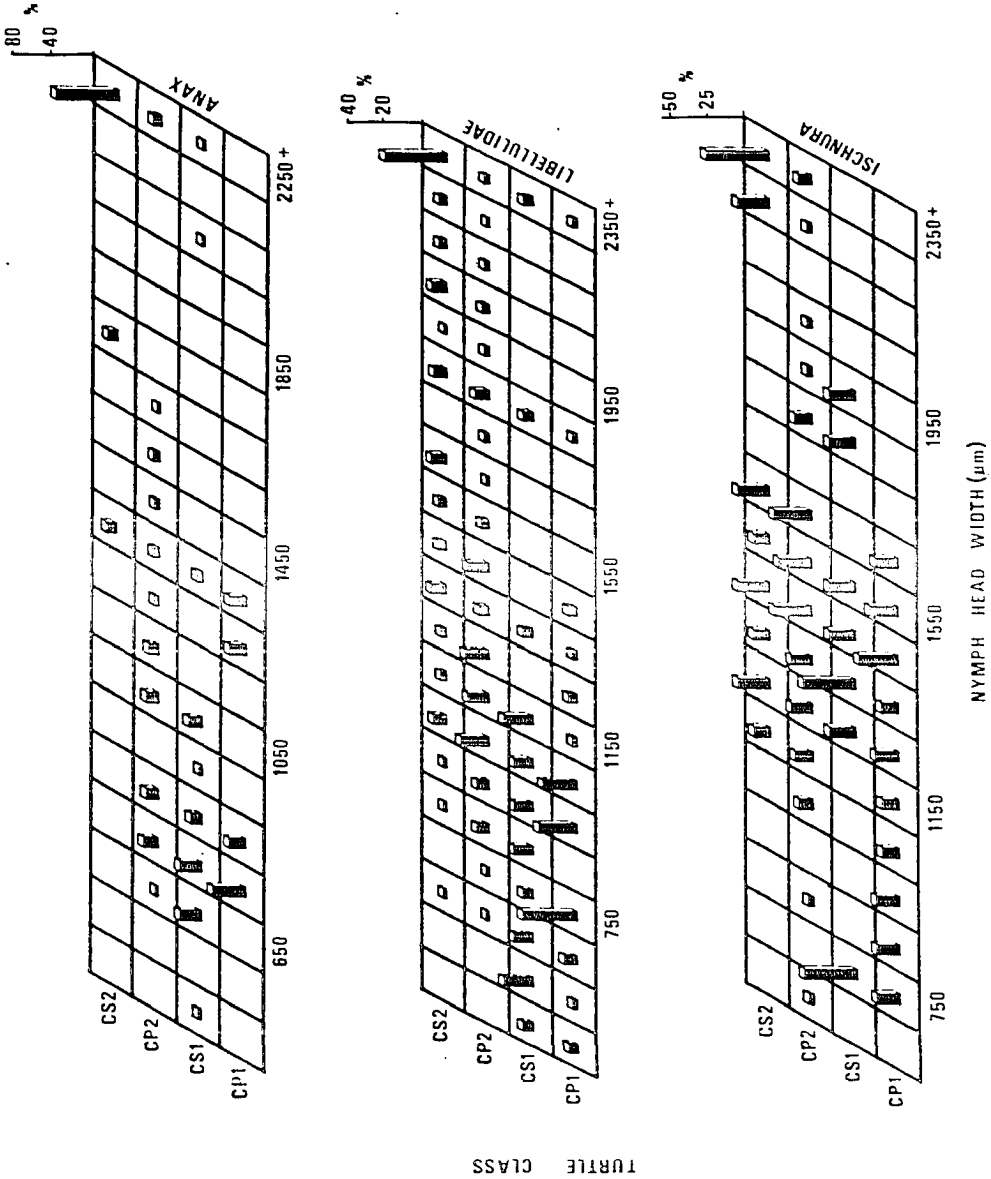

PERCENT
30
15
CS2
CP2
CS1
CP1
TURTLE CLASS
150
450
750
1050
1350
1650
NYMPH HEAD LENGTH (μm)

Figure 7.

Figure 8.


ANAX
80 %
40
650
1050
1450
1850
2250+
LIBELLULIDAE
40 %
20
750
1150
1550
1950
2350+
ISCHNURA
50 %
25
750
1150
1550
1950
2350+
CS2
CP2
CS1
CP1
TURTLE CLASS
NYMPH HEAD WIDTH (µm)

Appendix A.--Mean number of individuals in Wilding stovepipe and plankton tow samples. T-tests were used to determine if each species' abundance was statistically different between habitats. If no difference was detected (α=.05) then sample data from both habitats (for the species under consideration) are pooled and used to estimate the species' abundance in the entire enclosure. If a difference was detected then abundance estimates are calculated separately for each habitat using data only from samples collected in each respective habitat. If unequal variances (Najas vs. Typha samples) were detected then a t-test for unequal variances is used. F-ratios were examined to detect unequal variances (α=.05). Original plankton tow counts were divided by 2.88 to adjust for differences in stovepipe and plankton tow volumes. Decisions, on how the final estimate for each species' abundance in the two habitats was determined, are reported. A decision to pool data from stovepipe samples taken in both habitats is noted as 'pool-S'. 'Sep-S' indicates that the estimate of the species' abundance is based on data (stovepipe samples) collected in each respective habitat. 'Pool-P' and 'sep-P' are similar to 'pool-S' and 'sep-S', but involve plankton tow data rather than stovepipe data. See Table 2 for final density estimates. N refers to the number of samples collected.

		Stovepipe Sample			Plankton Tow			
Species	Habitat	N	Mean(SE)	F-ratio (T-test)	N	Mean(SE)	F-ratio (T-test)	Decision
DIPTERA								
Ceratopogonidae	Typha	12	4.42 (2.155)	3.21 ns	6	0.00	----	pool-S
	Najas	6	4.83 (1.701)	(-0.13 ns)	6	0.81 (0.292)	----	
Chironomidae								
Ablabesmyia	Typha	12	2.75 (1.045)	2.64 ns	6	1.67 (0.433)	14.05 *	pool-S
	Najas	6	2.83 (0.910)	(-0.05 ns)	6	0.12 (0.115)	(3.48 *)	

Appendix A (continued).

Anatopynia	Typha	12	0.00	----	6	0.17 (0.118)	----	pool-S
	Najas	6	0.17 (0.167)	----	6	0.00	----	
Chaoborous	Typha	12	0.67 (0.333)	----	6	0.00	----	pool-S
	Najas	6	0.00	----	6	0.81 (0.519)	----	
Clinotanypus	Typha	12	0.00	----	6	0.00	----	sep-S
	Najas	6	2.33 (0.494)	----	6	0.00	----	
Cryptochironomus	Typha	12	0.00	----	6	0.00	----	pool-S
	Najas	6	1.17 (1.167)	----	6	0.00	----	
Labrundinia	Typha	12	0.17 (0.112)	3.74 ns	6	1.21 (0.462)	----	sep-S
	Najas	6	1.17 (0.307)	(-3.77 **)	6	0.00	----	
Microtendipes	Typha	12	0.08 (0.083)	2.00 ns	6	0.17 (0.077)	1.13 ns	pool-S
	Najas	6	0.17 (0.167)	(-0.50 ns)	6	0.12 (0.073)	(0.54 ns)	
Polypedilum	Typha	12	0.75 (0.411)	----	6	0.29 (0.226)	----	sep-S
	Najas	6	0.00	----	6	0.00	----	
Procladius	Typha	12	0.33 (0.256)	23.06 ***	6	0.00	----	sep-S
	Najas	6	4.17 (1.740)	(-2.18 ns)	6	0.00	----	
Rheotanytarsus	Typha	12	0.33 (0.225)	59.23 ***	6	0.00	----	sep-S
	Najas	6	8.50 (2.446)	(-3.32 *)	6	0.00	----	

Appendix A (continued).

Culicidae								
Culex	Typha	12	0.00	----	6	4.04 (1.503)	44.05 ***	sep-P
	Najas	6	0.00	----	6	0.00	(2.47 (.0549))	
Anopheles	Typha	12	0.00	----	6	1.15 (0.330)	32.80 **	sep-P
	Najas	6	0.00	----	6	0.06 (0.056)	(3.29 *)	
Stratomyidae	Typha	12	0.00	----	6	0.17 (0.077)	----	pool-P
	Najas	6	0.00	----	6	0.00	----	
Tabanidae								
Chrysops	Typha	12	1.92 (0.557)	2.98 ns	6	0.00	----	pool-S
	Najas	6	3.50 (1.360)	(-1.29 ns)	6	0.00	----	
Acilius	Typha	12	0.17 (0.112)	----	6	0.00	----	pool-S
	Najas	6	0.00	----	6	0.00	----	
ODONATA								
Aeshnidae								
Anax	Typha	12	3.00 (0.640)	----	6	1.50 (0.563)	0.25 ns	sep-S
	Najas	6	0.00	----	6	0.33 (0.333)	(-1.78 ns)	

Appendix A (continued).

Coenogrionidae								
Ischnura	Typha	12	6.25 (2.115)	6.35 **	6	4.67 (1.021)	0.68 ns	pool-S
	Najas	6	2.83 (0.792)	(-1.51 ns)	6	2.33 (0.843)	(-1.76 ns)	
Libellulidae*	Typha	12	23.75 (4.732)	11.91 *	6	1.67 (0.558)	0.74 ns	sep-S
	Najas	6	9.17 (1.939)	(-2.85 *)	6	1.17 (0.447)	(-0.68 ns)	
EPHEMEROPTERA								
Baetidae								
Caenis	Typha	12	1.00 (0.348)	51.08 ***	6	0.75 (0.423)	4.94 ns	sep-S
	Najas	6	17.50 (3.519)	(-6.71 **)	6	2.60 (0.941)	(-1.79 ns)	
Callibaetis	Typha	12	17.83 (4.194)	7.79 *	6	14.16 (3.944)	5.88 ns	pool-S
	Najas	6	9.50 (2.125)	(-1.77 ns)	6	3.33 (1.626)	(2.54 *)	
HEMIPTERA								
Belostomatidae								
Belostoma	Typha	12	0.83 (0.083)	----	6	0.00	----	pool-S
	Najas	6	0.00	----	6	0.00	----	

Appendix A (continued).

Notonectidae								
Buenoa	Typha	12	1.58 (0.570)	(5.85 ns)	6	3.12 (0.938)	2.52 ns	pool-S
	Najas	6	1.33 (0.333)	(0.38 ns)	6	2.19 (0.591)	(0.83 ns)	
Hebridae	Typha	12	0.00	----	6	0.12 (0.073)	----	pool-P
	Najas	6	0.00	----	6	0.00	----	
Mesovelidae								
Mesovelia	Typha	12	0.17 (0.167)	(2.00 ns)	6	0.00	----	pool-S
	Najas	6	0.17 (0.167)	(1.20 ns)	6	0.00	----	
COLEOPTERA								
Dytiscidae								
Tropisternus	Typha	12	0.33 (0.256)	----	6	0.00	----	pool-S
	Najas	6	0.00	----	6	0.00	----	
Halipidae	Typha	12	0.00	----	6	0.00	----	pool-S
	Najas	6	0.17 (0.167)	----	6	0.00	----	
Hydroptilidae								
Berosus	Typha	12	0.75 (0.279)	1.47 ns	6	0.00	----	pool-s
	Najas	6	1.67 (0.477)	(0.81 ns)	6	0.00	----	

Appendix A (continued).

Hydroptilinae	Typha	12	0.00	----	6	0.46	(0.231)	(8.89 *)	pool-P
	Najas	6	0.00	----	6	0.17	(0.077)	(1.19 ns)	
HYMENOPTERA	Typha	12	0.00	----	6	0.06	(0.058)	----	pool-P
	Najas	6	0.00	----	6	0.00		----	
ARACHNIDA	Typha	12	0.00	----	6	0.06	(0.058)	----	pool-P
	Najas	6	0.00	----	6	0.00		----	
HYDRACARINA	Typha	12	0.00	----	6	0.46	(0.263)	13.00 *	pool-P
	Najas	6	0.00	----	6	0.12	(0.073)	(1.27 ns)	
GASTROPODA									
Physidae									sep-S
Physa	Typha	12	86.50	(16.912)	1.30 ns	6	0.00		
	Najas	6	174.17	(27.293)	(-2.89 *)	6	0.00		
COPEPODA	Typha	0				6	344.67	(156.23)	12.14 *	sep-P
	Najas	0				6	3822.50	(544.30)	(-6.14 ***)	

Appendix A (continued).

CLADOCERA									
Ceriodaphnidae									
Ceriodaphnia	Typha	0			6	121.50	(47.633)	35.36 **	sep-P
	Najas	0			6	1257.83	(283.260)	(-3.96 **)	
OSTRACODA	Typha	0			6	53.33	(13.76)	324.98 ***	sep-P
	Najas	0			6	737.67	(248.12)	(-2.75 *)	
CRUSTACEA									
Astacidae	Typha	12	0.08 (0.083)	----	6	0.00		----	pool-S

* Libellulidae = Erythemis, Pachydiplax, Plathemis, and Tramea.

Appendix B. Number of prey of each category in stomachs of individuals caught in the Typha habitat. N/A indicates habitat counts are not available.

Taxon	ID #	Stomach Counts				Habitat Count
		CP1	CP2	CS1	CS2	
Ceratopogonidae	1	7	10	34	1	160.5
Ablabesmyia	2	40	37	27	12	97.8
Chaoborus	3				1	0.0
Clinotanypus	4		3			82.0
Crytochironomus	5		2			13.7
Labrundinia	6	1	1	1		6.0
Microtendipes	7	4	3			3.9
Polypedilum	8		1	1		26.4
Culex	9	38	18	59	21	142.2
Anopheles	10	10	37	2	13	40.5
Stratomyidae	11			1		3.2
Anax	12	4	38	28	7	105.6
Ischnura	13	34	49	9	4	179.9
Libellulidae	14	34	74	22	29	835.9
Caenis	15	89	82	38	39	35.2
Callibaetis	16	180	394	57	163	530.0
Belostoma	17				1	2.1
Buenoa	18	1	1	1	1	52.8
Hebridae	19			1		2.1
Tropisternus	20				1	7.7
Berosus	21		1		1	31.3
Hydroptilinae	22	83	5	8	2	11.3
Hydracarina	23	1				10.2
Physa	24	1	4	1	1	3044.3
Simocephalus	25	4	76	59	1	39.8
Ceriodaphnia	26		9669	16834	60470	15323.1
Ostracoda	27	22	18	35		8986.4
Noteridae	28	2	5	3		N/A
Najas	29					N/A

Appendix C.--Number of each prey category in stomachs of individuals from the Najas habitat.

Taxon	ID #	Stomach Counts CP1	CP2	CS1	CS2	Habitat Count
Ceratopogonida	1		48			160.5
Ablabesmyia	2	13	2	1		97.8
Chaoborus	3					0.0
Clinotanypus	4		2		1	0.0
Crytochironomus	5					13.7
Labrundinia	6	1				41.9
Microtendipes	7			1		3.9
Polypedilum	8	1				0.0
Culex	9	1	36	8		0.0
Anopheles	10	2	11			0.0
Stratomyidae	11					3.2
Anax	12	1	2	3	2	0.0
Ischnura	13	7	6		4	179.0
Libellulidae	14	10	4	1	26	322.7
Caenis	15	90	4		13	615.9
Callibaetis	16	43	19	4	46	530.0
Belostoma	17					2.1
Buenoa	18		3			52.8
Hebridae	19					2.1
Tropisternus	20					7.1
Berosus	21					31.3
Hydroptilinae	22	2	2			11.3
Hydracarina	23	1	2			10.2
Physa	24					6130.0
Simocephalus	25		2	10		39.8
Ceriodaphnia	26	221		29	5572	1480.1
Ostracoda	27	3		6		649.7
Noteridae	28					N/A
Najas	29					N/A

APPENDIX D

The following program is used in the timing and recording of foraging events (handling, pursuing, and searching). It is written specifically for use with the ISAAC/Apple computer system (Model 91A, Cyborg Corp., Newton, MA). It is written in the compatible languages of LABSOFT and APPLESOFT. See the user's guide for the ISAAC/Apple system for details on LABSOFT.

Lines 10 to 40 creates a data set "FEEDDATA" on computer disk where input data are subsequently stored.

```
10  REM  DATA SET BUILDER
15  HOME
20 D$ = "": REM  CNTL D
25  PRINT D$:"MON I.O.C"
30  PRINT D$:"OPEN FEEDDATA"
40  PRINT D$:"WRITE FEEDDATA"
```

Lines 42 to 46 are LABSOFT commands (refer to user's guide for explanation).

```
42  & CLRTIMER
44  & BPOLL.(TV) = Q.(XM) = 65535
45  & TIMERIN.(TV) = FRACT
46  & BEEP
```

Lines 47 to 50 create a character variable "N$" that identifies the foraging event being recorded. Line 51 is available for future use.

```
47  IF Q = 1 THEN N$ = "SEARCH "
48  IF Q = 2 THEN N$ = "PURSUIT"
49  IF Q = 3 THEN N$ = "HANDLE "
50  IF Q = 4 THEN N$ = "SURFACE"
51  IF Q = 5 THEN N$ = "FIVE    "
```

Lines 60 to 69 record real time from an internal clock in hours "HR", minutes "MN", and seconds "SC". All data (foraging event "N$" and time) are then combined into a single variable (A$). Line 70 prints A$ and FRACT (length of previous interval) into the data set FEEDDATA. Note: FRACT is internally controlled and resets to zero after approxiately 16 seconds.

```
60  & TIME TO HR.MN.SC
61 Q$ =  STR$ (Q): IF  LEN (Q$) = 1 THEN Q$ = "0" + Q$
62 HR$ =  STR$ (HR): IF  LEN (HR$) = 1 THEN HR$ = "0" + HR$
63 MN$ =  STR$ (MN): IF  LEN (MN$) = 1 THEN MN$ = "0" + MN$
64 SC =  INT (SC):SC$ =  STR$ (SC)
66  IF  LEN (SC$) = 1 THEN SC$ = "0" + SC
67 A$ = N$ + " " + HR$ + " " + MN$ + " " + SC$
69 FRACT = FRACT / 1000
70  PRINT A$.FRACT: GOTO 42
90  PRINT D$:"CLOSE FEEDDATA"
```