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EFFECTS OF BODY SIZE ON THE PREDATOR–PREY INTERACTION BETWEEN PUMPKINSEED SUNFISH AND GASTROPODS¹

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Abstract. Body size is known to play a critical role in determining patterns of prey selection. In this study, we examined the diets of pumpkinseed sunfish (*Lepomis gibbosus*) from three Michigan lakes. Pumpkinseeds have highly developed pharyngeal jaws specialized for crushing gastropods, and in our study lakes gastropods consistently contributed >80% of the prey mass in pumpkinseed diets. However, the average dietary composition and prey selection among snail taxa and size classes varied considerably among dates and sites. We hypothesized that this variation was influenced by changes in the size structure of the snail community. We used laboratory studies to quantify the effect of snail (and fish) size on three important components of the predator–prey interaction: encounter rates, attack probabilities, and capture successes. We then used these laboratory data to predict prey selection observed in the field. For most of our field situations, a simple model (based on size-specific encounter rates only) explained a large percent (71%) of the observed variation in prey selection. However, in those cases where some of the snails were resistant to predation, due to crushing resistance or gape limitation, this simple model was a very poor predictor of prey selection. A more complex model (based on encounter rates and size refuges) successfully explained 46% of the variance in these cases where snails were relatively invulnerable. Finally, we compared estimates of attack probabilities with predictions from optimal foraging theory and found qualitative agreement in that fish ignored prey of low profitabilities and became more selective as the quality of the environment improved. However, the incorporation of variable attack probabilities into the foraging model resolved only a small part of the observed residual variation in selectivities because snails with low profitabilities were already underrepresented in the diet due to their low encounter rates or capture successes. This study demonstrates that predator–prey interactions in size-structured populations can create apparently complex variation in prey selection, but that this variation can be largely understood within a framework that simultaneously considers the dynamics of prey size distributions and how components of the foraging interaction scale with body size of the predator and prey.

Key words: body size; encounter rates; gastropods; *Lepomis*; littoral; optimal foraging; predator–prey; prey selection; size-structured populations.

INTRODUCTION

A predator's choice of prey serves as a primary link connecting the dynamics of species on different trophic levels (Brooks and Dodson 1965, Paine 1966, Murdoch and Oaten 1975, Hassel 1978). Prey choice and foraging rates not only determine the energy gained and therefore influence the growth, survival, and fecundity of predators (Turnbull 1962, Mittelbach 1988, Osenberg et al. 1988), but by definition they also influence the mortality of prey. These effects and the feedback between them remain a central focus for the understanding of population dynamics and community structure (Rosenzweig 1973, Holt 1977, Levins 1979, Oksanen et al. 1981).

Foraging theory, developed extensively since the seminal work by Holling (1959a, b) and Watt (1959), is a potentially powerful tool that can be used to link the mechanistic understanding of prey choice at the individual level with patterns that emerge at the population and community levels (Wilson 1976, Werner 1977, Tilman 1982, Mittelbach et al. 1988). Clearly, this connection between different levels of organization is an important one to make in ecology, but it is often hindered by the complexity inherent in natural systems. For example, prey species each possess unique sets of traits that influence a predator's prey preferences (Schmitt 1981, 1982, Morgan 1987). Further, predators often exhibit strong preferences within a single prey species (Mittelbach 1981, Bence and Murdoch 1986, Folkvord and Hunter 1986). The construction of a general framework in which to view prey selection, and the extension of this framework to population and community patterns, hinges upon determining the functional basis of this variation in the predator–prey

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relationship. Because prey selection is equal to the relative per capita mortality rate imposed on a prey type by the predator (Chesson 1978, 1983, Vanderploeg and Scavia 1979), prey selection by the predator and predation risk for the prey (i.e., the mortality incurred via the predator) can be viewed from similar perspectives within the same general framework.

Prey selection is determined by the product of three important functions: the encounter rate between predators and prey, the probability that a predator attacks an encountered prey item, and the probability that the predator successfully consumes an attacked prey item (O'Brien 1979, Greene 1983). Previous studies in aquatic systems show that each of these functions, which could be even further subdivided, are often related to prey (and predator) body size (Elnor and Hughes 1978, Mittelbach 1981, Pastorak 1981, Wright and O'Brien 1984, Bence and Murdoch 1986, Wainwright 1987), although different prey (and predator) species often vary in the way the relationships scale with body size (Swift and Fedorenko 1975, Breck and Gitter 1983, Folkvord and Hunter 1986, Wainwright 1988). Thus, a general model of prey selection might consist of a few relatively simple functions, where complexity is present primarily in the way the parameters of these functions scale with body size for each of the interacting species. Because body size also influences individual fecundities (Bagenal 1978, Perron 1982, Peters 1983, Osenberg 1988), it may well serve as a common variable linking models of prey selection with models of population dynamics based on size-specific birth and mortality rates (VanSickle 1977, Kirkpatrick 1984, Werner and Gilliam 1984, Kooijman 1986).

In this paper, we explore patterns of prey selection by pumpkinseed sunfish (*Lepomis gibbosus*), a specialized molluscivore in the family Centrarchidae. In field studies, we show that pumpkinseeds feed primarily on gastropods (see also Seaburg and Moyle 1964, Sadzikowski and Wallace 1976, Keast 1978, Laughlin and Werner 1980, Mittelbach 1984) but that dietary patterns and prey selection among gastropods are highly variable from time to time (or site to site). We then use a series of laboratory studies to measure important size-related predator and prey traits that influence encounter rates, attack probabilities, and capture successes. By incorporating these data into a series of general models, increasing in their level of complexity, we demonstrate how prey selection in the field is influenced by these components and how the effect of each key trait scales with body size.

FIELD STUDIES

Study sites and natural history

Pumpkinseed diets were examined in three small (6–22 ha) hardwater lakes (Culver Lake, Palmatier Lake, and Three Lakes II) near the Kellogg Biological Station in southwestern Michigan (see Osenberg et al. 1988).

The fish communities of these lakes are typical of small glacial lakes in the northcentral United States, and centrarchids, notably bluegill (*L. macrochirus*), pumpkinseed, and largemouth bass (*Micropterus salmoides*), compose well over half of the total fish biomass (Brown and Ball 1942, Hall and Werner 1977, Werner et al. 1977). Of the ≈ 20 species of fish occurring in these lakes, pumpkinseeds are the only significant molluscivore (C. Osenberg and G. Mittelbach, *personal observations*), because they possess highly modified pharyngeal jaws and strong molariform teeth, which allow them to efficiently crush the shells of gastropods and extract their soft tissues (Lauder 1983, Mittelbach 1984).

Eleven gastropod species occur in the three study lakes (see Table 1), where they are found primarily on the surface of littoral vegetation, which extensively covers the littoral habitat (there is no, or very little, bare sediment or rocks) and is dominated by the macroalga *Chara*. The snails vary considerably in their shell morphologies and maximum body masses (Clarke 1981, Osenberg 1988). In addition, snail population densities and size structures are seasonally dynamic and variable among the 11 species due to differing patterns of reproduction, growth, and mortality (Osenberg 1988). Below, we document how patterns of diet selection by pumpkinseeds change in response to this variation in the snail community.

Methods

We examined dietary patterns and prey selection in 166 pumpkinseeds that were collected by seining on six dates between August 1983 and June 1985 (Table 2). Only one of three study lakes was sampled per date, and therefore the variation we observe among these collections cannot be attributed to effects of either dates or lakes, per se. However, we are interested in providing general explanations of the variation in dietary patterns among collections, rather than isolating the specific effects of dates or lakes. Thus, we typically refer to the six samples as being derived from different dates, acknowledging that some samples were also collected in different lakes. Collected fish ranged in size from 52 to 131 mm standard length (SL). Pumpkinseeds < 50 mm SL rarely feed on gastropods (Mittelbach 1984) and were not collected. Fish were sampled between 0900 and 1100. Large fish (generally > 80 mm SL) were stomach pumped (Seaburg 1957), and smaller fish, which do not stomach pump easily, were preserved in 4% buffered formaldehyde. Preserved fish were later dissected for diet analysis. Comparison of these two techniques showed that stomach pumping was unbiased and > 90% efficient in removing prey (Osenberg 1988).

Prey from stomach samples were identified, counted, and measured. Nongastropod prey were identified to family or genus, and linear measurements were converted to dry mass using length–mass regressions. Gastropods were identified to the lowest possible taxo-

TABLE 1. Gastropod species and pooling scheme for dietary analyses of pumpkinseeds. Also shown are the approximate adult tissue dry masses for each snail species. All species occur in each of the three study lakes, except *Viviparus*, which occurs only in Three Lakes II.

Class	Family	Species	Prey category	Adult mass (mg)
Prosobranchia	Hydrobiidae	<i>Amnicola limosa</i>	<i>Amnicola</i>	0.5–1.5
		<i>Amnicola walkeri</i>	<i>Amnicola</i>	0.1–0.3
		<i>Marstonia lustrica</i>		0.3–0.8
		<1.5 mm	<i>Amnicola*</i>	
		≥1.5 mm	<i>Marstonia</i>	
	Valvatidae	<i>Valvata tricarinata</i>	<i>Valvata</i>	1.0–2.0
	Viviparidae	<i>Viviparus georgianus</i>	<i>Viviparus</i>	>20
Pulmonata	Physidae Planorbidae	<i>Physa</i> †	<i>Physa</i>	2.0–10.0
		<i>Gyraulus parvus</i>	<i>Gyraulus</i>	0.1–0.4
		<i>Gyraulus deflectus</i>	<i>Gyraulus</i>	0.6–3.0
		<i>Promenetus exacuous</i>	<i>Gyraulus</i> ‡	0.2–1.5
		<i>Helisoma anceps</i>	<i>Helisoma</i>	10.0–20.0
		<i>Helisoma campanulata</i>	<i>Helisoma</i>	10.0–20.0

* Prosobranch snails in fish guts were identified by their opercula. Opercula of *Marstonia* of <1.5 mm shell height were indistinguishable from *Amnicola* and were assigned to the latter genus.

† *Physa* is probably represented by only one species in these lakes, but due to ambiguities and difficulties in the systematics (e.g., Te 1975), we do not refer to a specific epithet.

‡ Pulmonate snails were identified by shell, body, and/or foot characteristics, but *Promenetus* could not be distinguished from *Gyraulus*.

onomic level, typically genus. Only gastropod prey were identified from fish collected during 1983. Because pumpkinseeds crush the snails' shells, snail sizes could not be assessed directly by measuring the shell. For prosobranch snails, we counted and measured opercula because they are not digested. Opercular diameter was converted to shell height or shell diameter using regressions based on snails collected from the study lakes. Opercula could be identified to genus, with the exception of the opercula of *Marstonia*, which at small sizes closely resembled the opercula of *Amnicola*. Therefore, *Marstonia* <1.5 mm (shell height) were included in the *Amnicola* prey category (Table 1). For pulmonate snails (which lack opercula), the length of the foot was measured. The foot has greater integrity than other soft parts of the snail and could be clearly identified and measured in the stomach samples. Pulmonate snails were identified to genus, although *P. exacuous* and *Gyraulus* were very similar and were combined into a single category: *Gyraulus* (Table 1). Foot lengths were converted to shell height or shell diameter using regressions of foot length on snail size. All measurements of snail size were converted to tissue dry mass (excluding shell and operculum mass) using length–mass regressions.

In addition to the data from the stomach samples, we also counted and measured opercula collected from the intestines of preserved fish. However, no data for pulmonates were taken from the intestines of preserved fish because pulmonates could not be consistently identified or measured in these samples. Thus, data from intestine contents were used to increase sample sizes only when comparisons were restricted to prosobranch snails.

Immediately before collecting fish, snails were sampled from the same area of the lake. Snails were collected by gently creating an opening in the *Chara* mat

and inserting a 20.3 cm diameter brass sieve (mesh size = 0.5 mm) under an undisturbed part of the *Chara*. We then placed a similar diameter stovepipe above the *Chara*, and pushed the stovepipe down onto the sieve, thus collecting the vegetation and snails that occurred within the 0.0324 m² area of littoral habitat. A total of 8–16 cores were collected per sampling date (Table 2), and these were combined into one pooled sample. The collected vegetation was rinsed to remove the snails and the residue was preserved in 4% buffered formaldehyde. Snails were sorted from the residue, identified to species, counted, and all or up to ≈300 snails per species were measured for each date.

Prey selectivities for fish feeding on several different snail types were calculated using Manly's index (Manly 1974, Chesson 1978, 1983; see Table 3 for a summary of symbols used in this paper):

$$\alpha_i = (d_i/N_i) / \sum_{j=1}^k (d_j/N_j) \quad (1)$$

where $i = 1, 2, \dots, k$

and where k is the number of prey categories, d_i is the number (or proportion) of prey of type i in the diet sample and N_i is the density (or proportion) of prey of type i in the environment. Based on Eq. 1, a vector of k selectivity values is obtained, one for each of the prey types (α_1 through α_k). Notice that each of the k selectivities is standardized by a common denominator such that the selectivities within a single vector sum to 1. Thus, α_i ranges from 0 to 1, with random selection being indicated by $\alpha_i = 1/k$. If a predator feeds randomly ($\alpha = 1/k$), the composition of its diet simply reflects the relative abundances of prey in the environment. Selectivity can be interpreted as a relative per capita mortality rate, mediated through the predator, on the k prey types (Vanderploeg and Scavia 1979).

TABLE 2. Study sites and collection information. Fish size is given in millimetres standard length (mm SL). Cores gives the number of separate vegetation cores (0.0324 m² per core) that were collected and pooled to form a single resource sample per date.

Lake	Date	No. fish	Size range (mm SL)	Cores
Three Lakes II	19 August 1983	9	56–80	8
Three Lakes II	4 September 1984	21	59–109	10
Three Lakes II	17 May 1985	63	54–131	16
Three Lakes II	6 June 1985	32	52–115	10
Culver Lake	30 August 1984	20	69–128	8
Palmatier Lake	17 August 1984	21	60–124	10

Rare prey types (those with <20 snails collected in a resource sample: each sample contained >1100 snails) were excluded from calculations of selectivities, and diet samples with low numbers of snails were also excluded. The threshold that was used depended on the particular analysis and will be provided along with the results.

We observed the feeding activity of pumpkinseeds on 10 dates in Three Lakes II and on 3 dates in Culver Lake. Observations were made from the surface using mask and snorkel. This technique worked well and did not affect the fish, which appeared to behave naturally while being observed. Fish were haphazardly selected and followed for 5–10 min (less time if they were lost). We estimated the size of each fish to the nearest 5 mm and recorded their activities with a stopwatch (e.g., handling time, rejection time, search time, time spent interacting with other fishes: see below, Laboratory Experiments, for discussion of these activities). We observed 161 fish that we estimated to range in size from 80 to 130 mm SL.

For statistical analyses, patterns expected to follow allometric relationships were analyzed by regression or analysis of covariance with fish size (or snail size) as the covariate (SAS 1985: PROC REG or PROC GLM). Data were log transformed to achieve linearity. For responses that were not expected to follow simple allometric relationships, the fish were divided into four, ≈ 20 mm, size categories (50–69, 70–89, 90–109, and 110–131 mm SL) and these data were analyzed using analysis of variance (SAS PROC GLM). Proportions were arcsine square-root transformed, while most other data were log transformed to reduce mean-variance correlations. Selectivity vectors (with $k > 2$) were contrasted using multivariate analysis of variance (SAS PROC GLM with the MANOVA option). In order to test for deviations of a selectivity vector from the random expectation ($\alpha_i = 1/k$ for all i), Hotelling's T^2 statistic was calculated (BMDP3D, Dixon 1981).

Results

Pumpkinseeds fed on a variety of littoral prey including gastropods, chironomids, other insect larvae,

and Cladocera. Snails, however, contributed >80% of the total prey dry mass (excluding snail shells and opercula) in the fish diets: averaged over all dates and fish sizes, $\bar{X} = 89.0\%$, 95% CI = 84.2–93.0%, $n = 157$ (see Osenberg 1988). Seaburg and Moyle (1964), Sadzikowski and Wallace (1976), and Mittelbach (1984) also found that large pumpkinseeds feed primarily on gastropods in lakes in Michigan and Minnesota. In general, the total mass of snails in the stomachs of fish increased with fish size (Fig. 1a), although the slopes varied among the six collection dates (ANCOVA, $F_{5,165} = 3.04$, $P < .05$). Heterogeneity of slopes suggests that fish size varied in importance among dates with respect to its effect on feeding rate on snails.

The mean size of snails (measured as tissue dry mass) in the diet also showed a general increase with fish size for each of the major snail taxa, and again, the effect of fish size varied among collections (Fig. 1b shows data for *Ammnicola*; Osenberg 1988 provides other examples). The variable effect of fish size appeared to be related to the size-frequency distribution of snails available on each of the dates (Fig. 1c). For example, the snail samples collected during May and June in

TABLE 3. Definition of important symbols used in the text. Units are given parenthetically.

d_i	number of prey type i in a fish's diet or in a group of fishes' diet
N_i	density of prey type i in the environment (number per square metre)
k	number of prey categories among which selectivity is examined
α_i	selectivity of a fish (group of fish) for prey type i when foraging in an environment with k prey types available
a_i	instantaneous encounter rate between a fish and prey type i (per second)
λ_i	total encounter rate between a fish and prey type i (number per second) = $a_i N_i$
$P_i(g)$	probability that a snail of type i can be taken into the fish's mouth given an attack
$P_i(c)$	probability that a snail of type i can be crushed given it is taken into the fish's mouth
$P_i(s)$	probability that an attack on prey type i is successful = $P_i(g)P_i(c)$
$P_i(a)$	probability of attack given an encounter with prey type i
C_i	crushing resistance of prey type i (newtons)
h_i	handling time per snail of prey type i : successful attacks (seconds)
r_i	rejection time per snail of prey type i : unsuccessful attacks (seconds)
H_i	total handling time per snail of prey type i including successful and unsuccessful attacks (seconds) = $P_i(s)h_i + [1 - P_i(s)]r_i$
m_i	tissue dry mass per snail of type i (milligrams)
SL	fish size (standard length in millimetres)
M	fish wet mass (grams)
R	metabolic rate of a fish (joules per second)
e_i	energy reward (gross or net) offered by an item of prey type i : $e_n = e_g - RH_i$ (joules)
e_i/H_i	profitability of prey type i (joules per second)
E/T	rate of (net or gross) energy acquisition to a predator (joules per second, see Eq. 10): optimal foraging rates are indicated by E/T^*

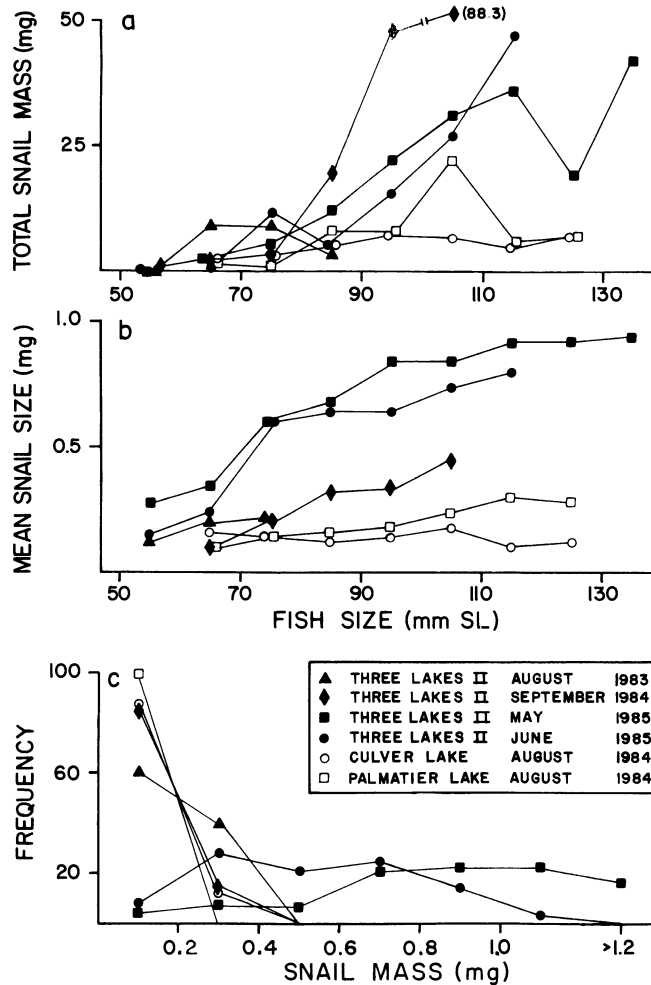


FIG. 1. (a) Total dry mass of snails in fish stomachs collected on six dates. Regressions of snail mass [$\log_{10}(x + 0.1)$] on fish standard length, SL [$\log_{10}(\text{SL})$] were significant ($P < .001$) for collections in Three Lakes II on 4 September 1984, 17 May 1985, and 6 June 1985, but not significant ($P > .1$) for the collection in Three Lakes II on 19 August 1983 or for collections in Culver or Palmatier Lakes. Untransformed data (based on 166 fish) were pooled into means within 10-mm size classes for clarity of presentation. (b) Mean size of *Amnicola* in fish diets. For each fish, a mean snail mass was calculated and these data were \log_{10} transformed and analyzed with analysis of covariance and linear regression. Slopes were heterogeneous among dates (ANCOVA: $F_{5,140} = 9.39, P < .001$) and separate regressions were significant ($P < .01$) for each collection except the one from Culver Lake ($P > .7$). Data presentation is the same as in (a). (c) Size-frequency distributions for *Amnicola* collected in resource samples on each of the six collection dates. Frequency is scaled to sum to 100 for each distribution, and values < 2 are shown as zeros. Sample sizes for each date are > 200 .

Three Lakes II contained relatively large *Amnicola* (all snails were born the previous year), while the samples collected during midsummer in Culver and Palmatier Lakes contained small *Amnicola* born the previous month (Osenberg 1988 discusses the phenology of the snail populations). Distributions from August and September in Three Lakes II were intermediate. Thus, the effect of fish size was seen most clearly on dates when the snail distribution was biased toward larger snails (compare Fig. 1b and 1c), and this might have also contributed to the differences in total ingestion rate or stomach contents (Fig. 1a).

Prey selection by pumpkinseeds varied extensively among collections as evidenced by the different selectivities for prosobranch and pulmonate snails (Fig. 2). On a finer scale, there was also significant variation among dates in the pattern of selection among snail taxa (Fig. 3). No single snail taxon was consistently preferred. Instead, a single prey taxon was most preferred on no more than two of the six dates, leading to four different snail taxa (*Amnicola*, *Valvata*, *Gyraulus*, and *Physa*) being most preferred on at least one of the six dates. Like the earlier patterns shown in Fig. 1, these patterns of selectivity appear to be related to

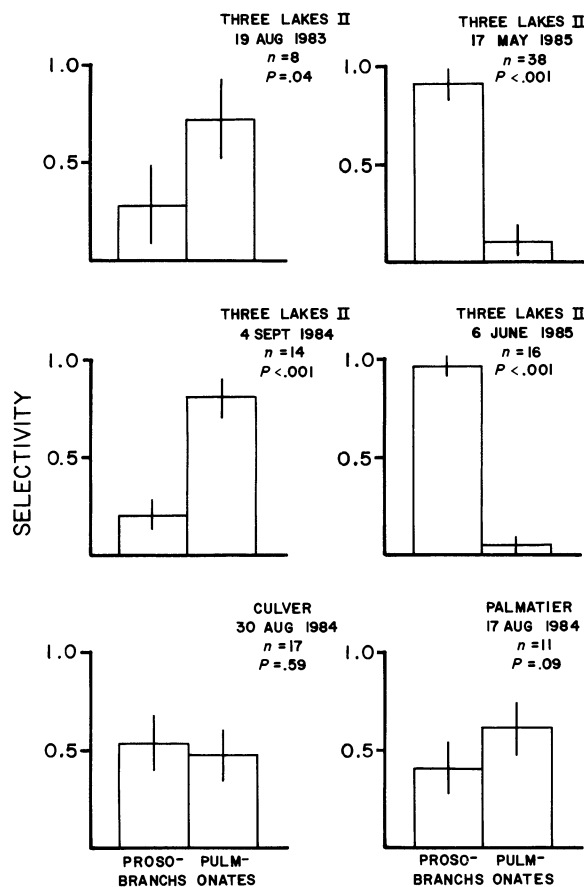


FIG. 2. Selectivities (means and 95% CI) between proso-branch and pulmonate snails for each of six collection dates. Random prey selection (i.e., in proportion to the representation in the environment) would be indicated by selectivities equal to 0.5. Sample sizes (number of fish with >10 snails in diet) and the probabilities that each selectivity vector represents random feeding are given. Within each date, selection did not vary among the four 20-mm size classes of fish (ANCOVA: $P > .05$ for each date).

shifts in the size distributions of snails among dates. For example, *Physa* was most preferred in the September sample from Three Lakes II, and its size-frequency distribution was skewed most strongly toward larger sizes (Fig. 4a). Similarly, *Amnicola* was most preferred in the June sample from Three Lakes II, and it was the *Amnicola* distribution that was skewed most strongly toward larger sizes on this date (Fig. 4b). These patterns suggest that the variation in selectivities might be explained by examining how size selection varied among dates.

Prey size selection, within a snail taxon, also exhibited variation among dates (Fig. 5). In addition, on several dates, different sized fish showed varying selectivity. In developing these analyses, it was necessary to pool data from all fish within a size class in order to obtain sufficient numbers of snails of a given taxon

in a diet sample (but see Chesson 1984 for a cautionary note). Notice that selectivity generally increased with snail mass, although the eight selection vectors for *Amnicola* from May and June in Three Lakes II, by contrast, either were hump-shaped or decreased with snail mass. On these two dates, the size distributions of *Amnicola* were relatively broad (Fig. 1c), and the largest snails may have entered a size refuge, thus causing the selectivity vectors to become hump-shaped and dependent on fish size (Fig. 5). On the other dates, only small *Amnicola* were available (Fig. 1c), due to patterns of reproduction (see Osenberg 1988), and we observed that size selection was a positive function of *Amnicola* size and that fish size had little influence on size selectivity (Fig. 5).

These data reveal that dietary patterns and prey selection were extremely variable, and depended, in part, on the effects of fish size, and on the size distributions of prey. It was not possible to describe a simple hierarchy of preference among the different snail taxa (Figs. 2 and 3), nor was it possible to describe a simple effect of fish size on prey selection (Fig. 5) or dietary content (Fig. 1). Instead, the data suggest that any one of the available snail taxa could, on certain dates, be the most preferred. Because fish exhibit strong size selection within snail species (Fig. 5) and because snail size distributions are extremely variable over the season (Figs. 1c and 4; Osenberg 1988), it is plausible that much of the variation in dietary patterns and prey selection might be attributable to variation in the size structure of the snail community among lakes and/or through time within a lake. The additional effect of fish on dietary patterns and prey selection also appears to depend on size structure of the snail community. Thus, it is likely that by understanding how fish size and snail size each influence components of the predation process, we might be able to resolve these complex dietary patterns. In the following sections, we use laboratory studies to explore the effects of predator and prey size on specific components of the predator-prey interaction. In particular, we examine how each of these components (e.g., encounter rates and capture successes) scale with body size (of sunfish and/or snails), and then determine ways in which these data can be resolved into functionally simple and general relationships. We then synthesize these results into models of prey selection whose predictions we compare with observed patterns of prey selection.

LABORATORY EXPERIMENTS

Methods

Encounter rate (the number of prey detected per unit of predator search time) is probably the most fundamental component of any foraging model because it sets the initial baseline against which all other components of the predator-prey interaction operate. Despite their importance, the rates at which predators

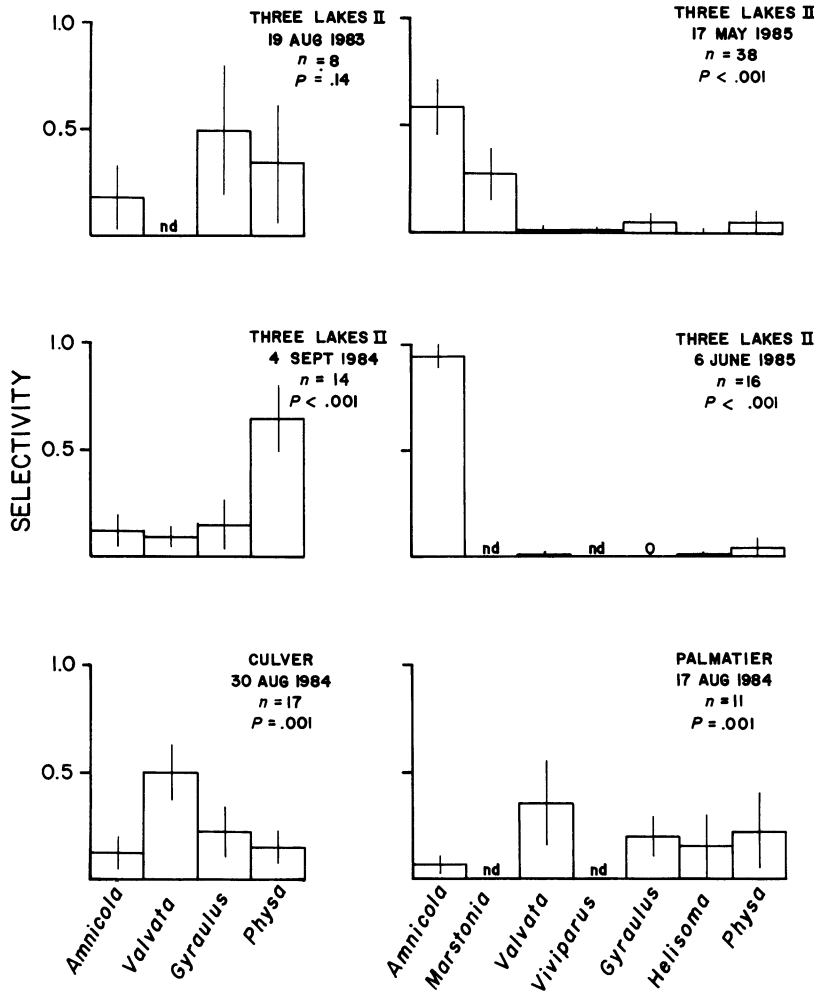


FIG. 3. Selectivities (means and 95% CI) among snail species for each of six collection dates. Random selection would be indicated by selectivities equal to $1/k$ (i.e., the reciprocal of the number of snail taxa present on a date). Sample sizes (number of fish with >10 snails in diet) and the probabilities that each vector represents random feeding are given. nd indicates that the snail taxon was absent (or too rare to include) on the given date. Selectivity for *Gyraulus* was 0 on 6 June 1985. Selectivities differed among the four fish size classes on two of the six dates (MANOVA: $P < .05$ for August in Culver and Palmatier Lakes); therefore selectivities calculated for those dates represent population averages and not necessarily selection by any particular size class of fish.

encounter different prey types have rarely been measured, due in part to the inherent difficulty in determining when an encounter has occurred. Indeed, it is often difficult to determine when a forager has encountered (i.e., discovered or detected) a prey item unless it exhibits an unambiguous response to the prey item. An attack provides the clearest indication that an encounter has occurred. However, attack rates will generally differ from encounter rates under field conditions because attack rates are the product of two factors: encounter rates and the probability that an encountered item is attacked. When many different prey types co-occur, a predator can choose to ignore encountered items of a particular prey type (e.g., based

on availability of other prey types as predicted by optimal diet models: Charnov 1976).

In our laboratory studies, we took several steps to increase the confidence with which we could observe prey encounters and therefore estimate encounter rates between fish and snails. First, because an attack provides the least ambiguous indication that an encounter occurred, we designed our experiments so that encounter rates could be estimated by attack rates. We maximized the likelihood that attack probabilities were close to one by placing only a single snail type (i.e., of a given species and size) into a foraging arena (see below, Experiment 1). Thus, we used single prey trials to isolate the effect of encounter rates without the con-

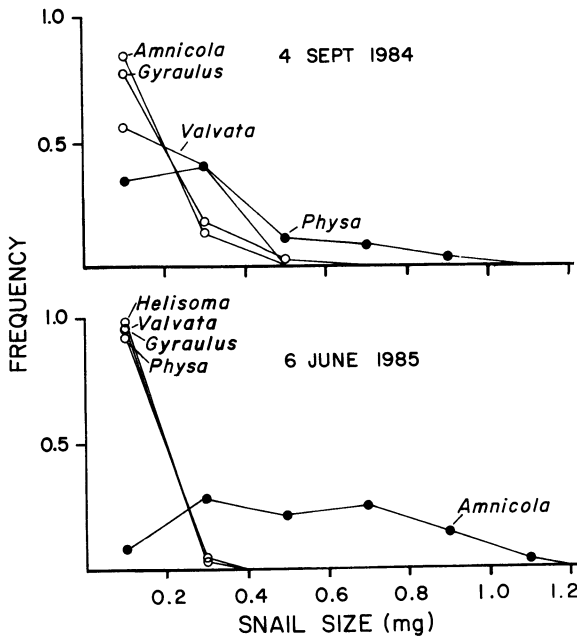


FIG. 4. Size-frequency distribution of major snail taxa on two collection dates in Three Lakes II. In each panel, solid symbols are used for the snail group that was most preferred by pumpkinseeds on that date (mean selectivity values shown in Fig. 3).

founding influence of decisions made by the predator, which become problematic when multiple prey types occur within the foraging environment. We also used fish that had been starved prior to the start of a feeding trial, thus increasing the fish's motivation and increasing the probability that the fish would attack an encountered prey item. (See Mittelbach [1981] for another example of this approach.)

The second important feature of our system that helped us estimate encounter rates concerns fish feeding behavior. Pumpkinseeds search for prey while hovering just above the vegetation, often with their bodies pitched slightly forward. Upon encountering a prey item, a fish flares its fins out, pitches further forward, and attacks the prey item or returns to a semihorizontal position and swims away. This very stereotypic behavior enabled us to detect encounters in our laboratory trials even in those few instances when no attack occurred (<4% of all encounters). Thus, we were able

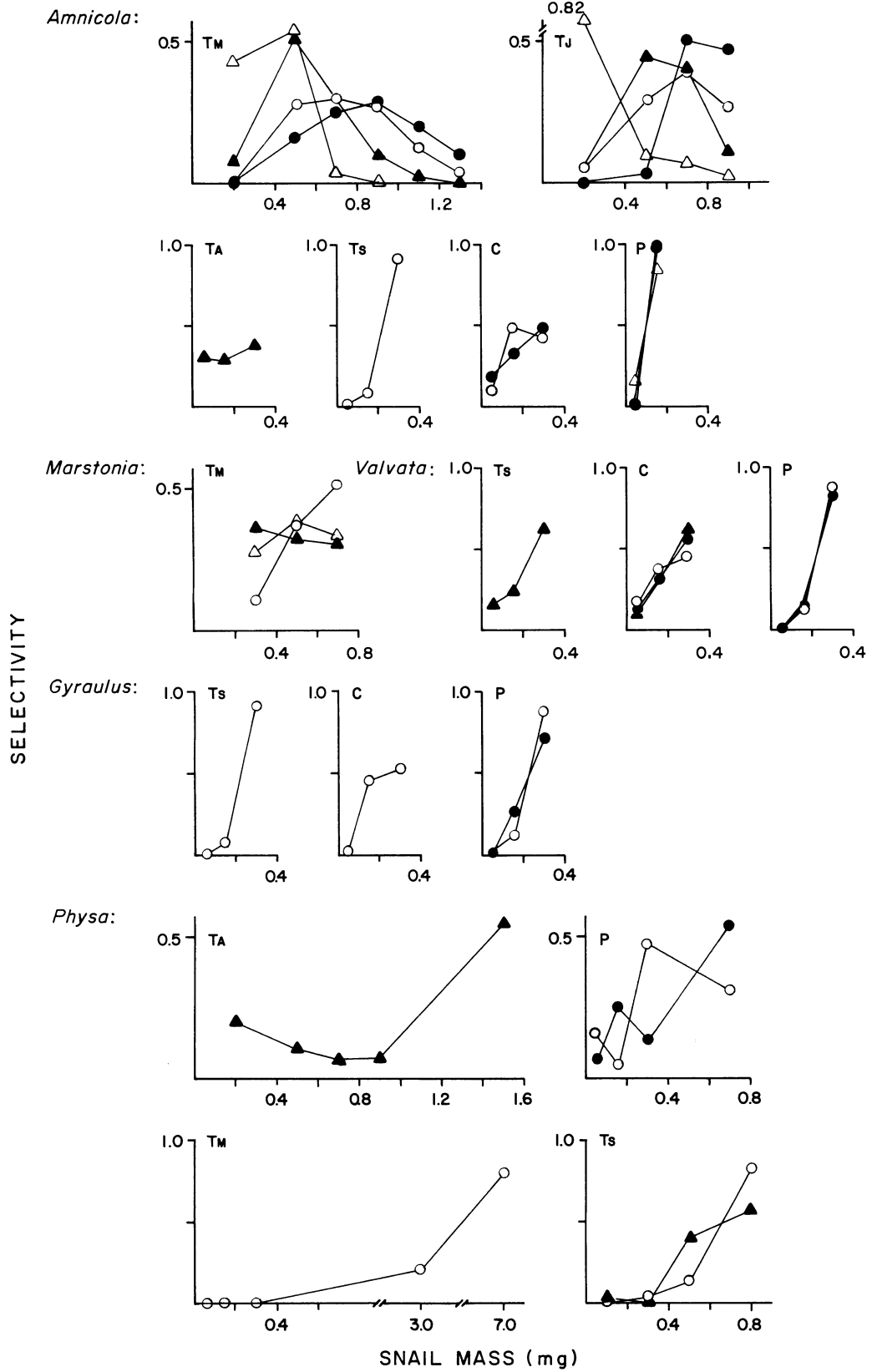
to estimate encounter rates between sunfish and prey reliably due both to the clear behavioral changes exhibited during an encounter and due to the experimental design which maximized the likelihood that an encounter would be followed by an attack. We next provide details of our experimental methodology.

Experiment 1

Encounter rates were estimated in a large (214-L) aquarium into which a bottom layer of 10 cm of rinsed *Chara* was placed: in the field, most snails occur within the top 10 cm of the *Chara* mat and most attacks by sunfish are directed at prey occurring on *Chara* (C. Osenberg, *personal observation*). Two pumpkinseeds (109 mm SL each) were kept in separate holding areas within the aquarium, where water temperature was maintained between 22.0° and 23.5°C. Doors separated the holding areas from the experimental arena, which measured 0.539 m². Fish were acclimated to feeding in the arena before the experiment started, and each fish was starved at least 6 h before being used in a trial. Snails were sorted by size and species, and a given density of a single snail type (defined by size and taxon) was introduced into the arena. Snails ranged in tissue dry mass from ≈0.1 mg up to 0.8 mg for *A. limosa*, 1.1 mg for *V. tricarinata*, 1.6 mg for *Gyraulus*, and 9.0 mg for *Physa*. Snail densities were 150 snails per arena (278 snails/m²) for *A. limosa* and *V. tricarinata*, and 50 snails per arena (93 snails/m²) for *Physa* and *Gyraulus* (both *G. parvus* and *G. deflectus* were used, but their representation in each trial varied depending on the size class). We used greater densities for the two prosobranchs because we expected encounter rates to be lower (and therefore difficult to estimate at low snail densities) for these two smaller species (see below in this section for definition of encounter rate). These densities fall within the natural range of densities observed in the study lakes. In addition, prosobranchs are consistently more abundant than pulmonates (Osenberg 1988).

Snails were added to the experimental arena and given 2 h to disperse within the *Chara* before the start of a trial. One pumpkinseed was released into the arena and each trial ran from 5–12 min depending on the amount of prey depletion. Depletion averaged 7% and never exceeded 37% (only 6% of trials had >20% depletion). During a trial we recorded each encounter

FIG. 5. Patterns of size selection for four size classes of fish. Each panel shows the size selection for one snail taxon on one of the six dates. Data are based on pooling data from all fish within each of four size classes, thus each selectivity vector is based on one pooled sample and no estimate of error is available. Therefore no statistical analysis of the data is given. Individual selectivity values for each fish size class are connected with a solid line. Selectivities were calculated only for fish groups with >10 snails in the diet sample (for pulmonate taxa), or >25 snails (for prosobranch taxa). Fish size classes are denoted by different symbols (Δ = 50–69 mm, ▲ = 70–89 mm, ○ = 90–109 mm, ● = 110–131 mm). Letters in the top left corner of each panel refer to the lake and collection date: C = Culver Lake, P = Palmatier Lake, TM, TJ, TA, Ts = Three Lakes II during May, June, August, and September, respectively (exact dates are given in Table 2).



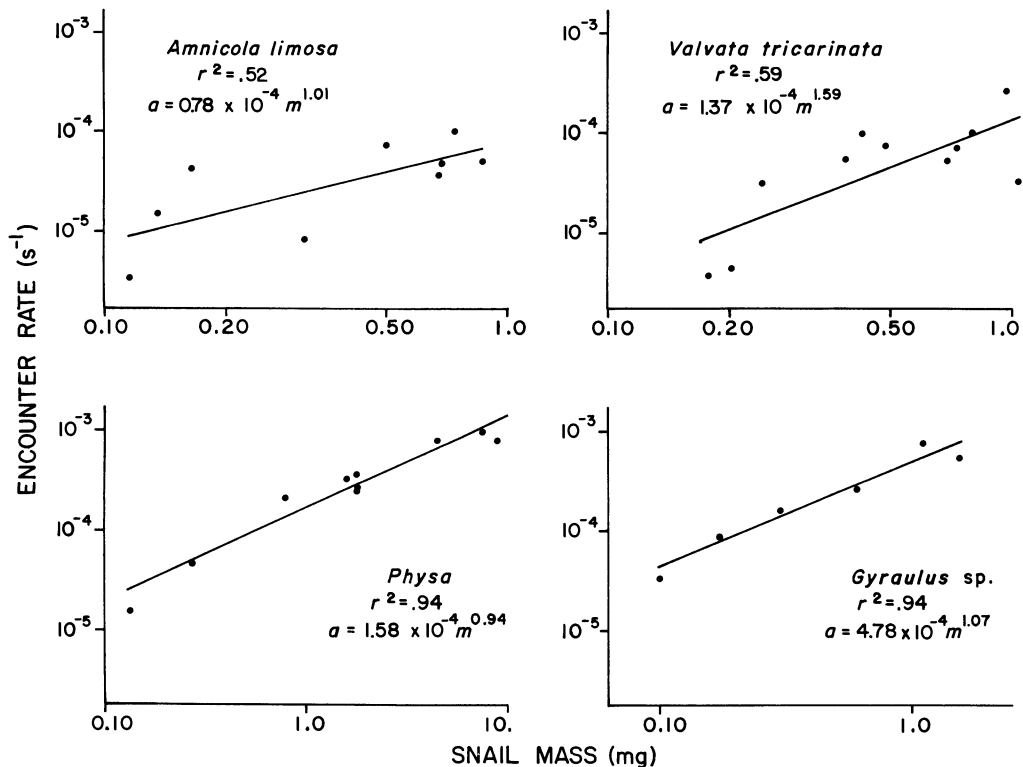


FIG. 6. Encounter rate (a) as a function of snail mass (m) for four snail taxa. Linear regressions for log-log transformed data are given. Each regression is significant at $P < .02$. Data are based on Experiment 1, which used pumpkinseeds (109 mm SL each) in individual trials. r^2 gives proportion of variance in a explained by m .

with a snail, each attack on a snail, whether the attack was successful, how much time elapsed from the start of an attack until the fish resumed search activity (referred to as handling time if the attack was successful and rejection time if unsuccessful), and how much time the fish spent in nonforaging related activities (e.g., interacting with the second fish through the plexiglass walls that separated them). Following a trial, consumed snails were replaced and given ≈ 1 h to disperse, and then the other fish was introduced into the arena and observed. After 1–3 trials per fish, the *Chara* and snails were removed. New *Chara* was rinsed and added to the arena along with a new set of snails.

We ran 131 trials. Instantaneous rates of encounter (a) were estimated for each of these trials based on an exponential model that accounted for depletion (e.g., Murdoch et al. 1984):

$$a = [\ln(N_{\text{start}}) - \ln(N_{\text{end}})]/pS \quad (2)$$

where N_{start} and N_{end} are the snail densities at the start and end of the trial, p is the proportion of encounters that resulted in the consumption of a snail (i.e., depletion of the snail population), and S is the total search time during the foraging trial. p was calculated as the ratio of the number of successful attacks divided by the total number of encounters (those followed by an

attack plus those that were not). Because the encounter rate estimated by Eq. 2 is a per capita rate, it can be converted to a total encounter rate between a predator and a prey type by multiplying by the density of the snail type (i.e., $\lambda = aN$, where λ is the total rate of encounter). Thus, a is identical to the “instantaneous rate of discovery” discussed by Holling (1959b) in the development of Type II functional responses. We refer to a simply as the encounter rate.

Preliminary analyses showed that the two fish did not differ in their encounter rates; therefore, encounter rates that were estimated from all trials within a set (i.e., sequential trials without complete replacement of the snails and *Chara*) were averaged (usually $n = 4$, 2 per fish) to obtain one estimate of the encounter rate per set. The 131 trials thus produced 36 independent estimates of encounter rates, which were examined for effects of snail size and taxon.

Experiment 2

Results from Experiment 1 also yielded information on whether attacked snails were successfully consumed, how long it took a fish to handle a snail that it successfully consumed (handling time), and how long fish spent handling a snail that it eventually rejected (rejection time). Size refuges, handling times, and re-

jection times were further examined in another laboratory experiment using the same four snail taxa: *A. limosa*, *V. tricarinata*, *Gyraulus*, and *Physa*. Pre-measured snails (ranging from very small sizes [≈ 0.1 mg] up to maximum adult sizes: e.g., Table 1) were offered individually to 1 of 29 pumpkinseeds that were kept in separate aquaria and ranged in size from 48 to 132 mm SL. If the fish attacked the snail, we recorded if the attack was successful or, if the attack was unsuccessful, whether the snail was too big to fit into the fish's mouth or whether the fish spit the snail out (presumably indicating that the snail could not be crushed). We also recorded the time it spent handling or rejecting the snail.

Crushing experiment

The final set of laboratory data involved measuring the mechanical strength of the snail shells as functions of their sizes. Shell strength was measured by placing a snail on a small platform on the bottom of a plexiglass tube. A slightly smaller tube, also with a bottom, was placed inside the first and on top of the snail. Sand was slowly poured into the inner tube until the snail shell was crushed. The mass of the sand and tube was determined and converted to newtons. A wide range of snail sizes was used for each species, and the relationship between crushing resistance and snail mass was estimated using an allometric relationship for each of the species.

RESULTS

Encounter rates

Encounter rates increased with snail mass (Fig. 6). Analysis of covariance revealed no differences in the scaling of encounter rate with snail mass across species (based on regressions of $\log_{10}(a)$ on $\log_{10}(m)$: $F_{3,28} = 1.00$, $P < .40$). However, the adjusted means did differ among the groups ($F_{3,31} = 9.07$, $P < .001$), due entirely to the greater adjusted mean of *Gyraulus*. The greater encounter rate for *Gyraulus* appears to have resulted from a laboratory artifact. As snails were transferred to the aquarium during the setup of the experiments, *Gyraulus* (but no other snails) trapped air bubbles under their shells. The air bubble, which was visible through the shell, reflected light and made the snails much more noticeable to the observer. In the study lakes, which generally lack emergent vegetation, *Gyraulus* rarely traps air within its pulmonary sac. Therefore, it is likely that our estimates of encounter rates between fish and *Gyraulus* were artificially high. Repeating the ANCOVA with only *Physa*, *Valvata*, and *Amnicola*, showed that the three species did not differ significantly in their relationships between encounter rates and snail mass (slopes: $F_{2,24} = 1.33$, $P > .25$; adjusted means: $F_{2,26} = 1.15$, $P > .30$; effect of mass: $F_{1,26} = 54.58$, $P < .001$).

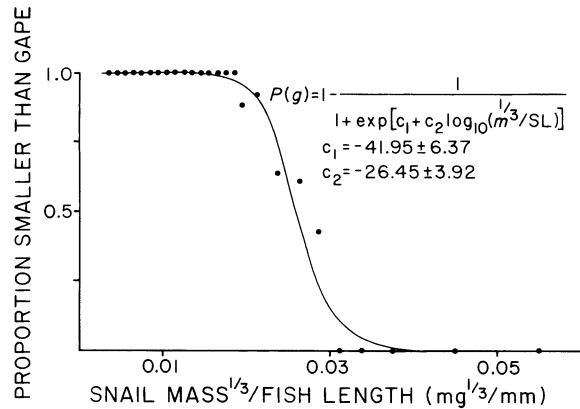


FIG. 7. Size refuge based on the occurrence of gape limitation during Experiment 2. Points give the proportion of snails within a range of the independent variable that were smaller than the gape of a fish [$P(g)$]. Original data ($n = 1110$), which were binary (i.e., a given snail was either smaller or larger than the gape), were grouped into categories for clarity of presentation. The equation estimated by logistic regression on the original data is given, as are the standard errors of the estimates. Results are based on 29 fish that ranged in size from 48 to 132 mm standard length (SL) and snails that ranged from 0.08 to 95 mg dry tissue mass (m).

Size refuges and crushing resistance

Following an attack, a snail can escape death if it is too large to be taken into the fish's buccal cavity (i.e., the fish is gape-limited; Zaret 1980) or if its shell is too thick to crush (i.e., the fish is crushing-strength-limited). Because snail species differ in their morphologies and shell thicknesses, the relationship between gape or crushing limitation and snail size might vary among snail species. Our primary goal in analyzing the size refuge data was to construct general functional relationships that appropriately scaled prey and predator sizes into simple models that transcended the differences among species.

Mouth gape in pumpkinseeds increases linearly with fish standard length (Laughlin 1979). Thus, gape limitation should scale with the ratio of prey length to predator length. The average linear dimension of a prey item increases as the cube root of its mass (assuming mass is proportional to the cube of length) and should be relatively independent of species identity. Thus, gape limitation should scale simply with the ratio of the cube root of snail mass to fish length. Indeed, as this index of the relative size of prey to predator increased, gape limitation became more severe and snails often escaped attacks (Fig. 7). Among the snail taxa used in Experiments 1 and 2, only *Physa* in Experiment 2 ever escaped via gape limitation; other snails were all too small.

The ratio of prey-to-predator size is commonly used to scale many aspects of the predator-prey relationship, for example handling times and size refuges (Werner

TABLE 4. Relationships between crushing resistance (C , measured in newtons) and snail size (L , length, in millimetres, or m , mass, in milligrams).

Species*	n	Size range	Crushing resistance regression coefficients				
			Size basis†			Length basis‡	
			a	b	r^2	c	d
<i>A. limosa</i>	43	0.6–4.9	1.039	1.97	.92	15.87	0.779
<i>A. walkeri</i>	20	0.7–2.5	0.925	1.74	.85	10.29	0.688
<i>M. lustrica</i>	20	0.9–4.5	1.558	1.02	.80	7.21	0.421
<i>V. tricarinata</i>	26	1.3–4.5	0.285	2.74	.88	10.53	0.828
<i>Physa</i> (lab)	23	2.6–11.0	0.104	0.89	.74	0.43	0.340
<i>Physa</i> (field)	21	1.6–14.8	0.883	1.15	.77	5.43	0.438
<i>H. anceps</i>	18	1.9–10.8	0.110	2.33	.93	3.39	0.855
<i>H. campanulata</i>	20	1.9–14.8	0.031	2.78	.91	1.93	1.141
<i>G. parvus</i>	20	1.2–3.9	0.150	3.21	.93	45.97	1.454
<i>G. deflectus</i>	14	1.2–7.0	0.122	2.71	.95	9.80	0.996
<i>P. exacuous</i>	14	1.4–5.2	0.310	0.71	.44	0.93	0.260
<i>V. georgianus</i>	20	4.0–13.0	0.259	1.91	.82	4.16	0.583

* Genus names given in full in Table 1.

† Snail size was originally measured in linear units (shell height was measured for *Physa* and all prosobranchs except *Valvata*, and maximum shell diameter was measured for Planorbids and *Valvata*). Size range gives the range of snail sizes (mm) used in the crushing experiments. Linear regressions were fit to log-transformed data, and linear regression parameters were transformed back to the allometric form of the equation: $C = aL^b$. Each regression was significant at $P < .01$.

‡ Length-mass regressions were used to translate the shell length relationships into mass-specific relationships: $C = cm^d$, where m is measured in milligrams dry tissue mass.

1977, Mittelbach 1981, Bence and Murdoch 1986). However, gape limitation is one of the few processes for which this scaling is a priori expected to be appropriate (see previous paragraph). Crushing limitation need not follow such a simple relationship. Indeed, unless crushing resistance of snail shells and crushing ability of fish increase linearly with size (of snails and fish) then the use of the ratio of prey-to-predator length will be incorrect and will mask important sources of variation in the data. Therefore, we next explore the relationships between snail size and crushing resistance and between fish size and crushing ability in order to develop a method for scaling the simultaneous effects of snail size and fish size on crushing limitation.

Crushing resistance of snails increased significantly with snail size for all 12 prey types examined (Table 4). Linear regressions of log-transformed data explained >70% of the variation in crushing resistance for each species except *Promenetus* ($r^2 = 44\%$). Two relationships were obtained for *Physa*: one for snails collected from lakes and one for snails cultured in the laboratory. Both types of snails were used in Experiments 1 and 2 and since the source for each snail is not known, we assume that the average crushing resistance of *Physa* used in the laboratory trials was intermediate to these two extremes ($C = 0.49L^1$; see Table 4).

The data from Experiment 1, which were obtained from two fish of the same size (109 mm SL), show that the proportion of snails that were crushed declined with snail mass for each species except *Physa*, which were always successfully attacked (Fig. 8a). Notice that the curves in Fig. 8a appear to be species-specific when expressed in terms of snail mass: i.e., some species escaped at small body mass (e.g., *A. limosa* and *G.*

parvus) while some escaped only at large body mass, or not at all (e.g., *Physa*). However, when expressed with respect to crushing resistance, a general relationship was obtained that appeared to apply equally well to each of the species (Fig. 8b). These data suggest that a single relationship between crushing limitation and crushing resistance can be used for all snail species.

To explore how crushing ability scaled with fish size, we used the data from Experiment 2, divided the data from the 29 fish into 10-g fish mass intervals (0–10 g up to 100–110 g) and examined the relationship between crushing limitation (i.e., $P(c)$, the probability that a snail could be crushed) and crushing resistance for each size class of fish. Logistic regression was used to fit an equation to the data (SAS Proc Catmod), and from these equations we calculated the crushing resistance (of a snail) that separated snails that could be crushed more than half of the time from snails that could not be crushed at least half of the time: i.e., the crushing resistance at which $P(c) = 0.5$. The effect of snail size was not significant for large fish classes (>60 g) because these fish could generally crush even the largest snails that were offered (i.e., $P(c)$ was constant and equal to 1.0). Therefore, we used only the results from the six smallest fish classes (0–10 g up to 50–60 g) and explored how the crushing resistance at which $P(c) = 0.5$ varied with fish mass (the mean within a 10-g class). The relationship was fit with a power function and was approximately linear (exponent of power function = 1.07, $n = 6$, 95% CI = 0.88–1.25, $r^2 = 0.98$), suggesting that the crushing ability of a fish was directly proportional to its mass. If a doubling in snail crushing resistance requires a doubling in fish crushing ability, in order to maintain a constant crushing probability, then a general index of crushing limitation can be ex-

pressed as the ratio of snail crushing resistance to fish crushing ability (i.e., fish mass). The proportion of attacked snails that were crushed in Experiments 1 and 2 declined with the ratio of crushing resistance to fish mass and the relationship was fit extremely well by logistic regression (Fig. 9).

The efficacy of gape limitation and crushing limitation for each snail species exposed to different sizes of predators was explored by combining the results from Figs. 7 and 9. From these relationships, we determined the mass, for each species, at which the probability of escaping through gape limitation, or crushing limitation, was equal to 50%: i.e., $P(g) = 0.5$ or $P(c) = 0.5$. These solutions were found for a range of fish sizes (50–140 mm SL). The predicted relationships between snail mass and fish size were the same for each snail species based on gape limitation, but the relationships for crushing limitation varied among species due to differences in how crushing resistance scaled with snail mass. Crushing limitation was likely to occur at smaller snail sizes than gape limitation (Fig. 10). The only exception was for *Promenetus exacuous*, which has one of the thinnest shells (Table 4). Additionally,

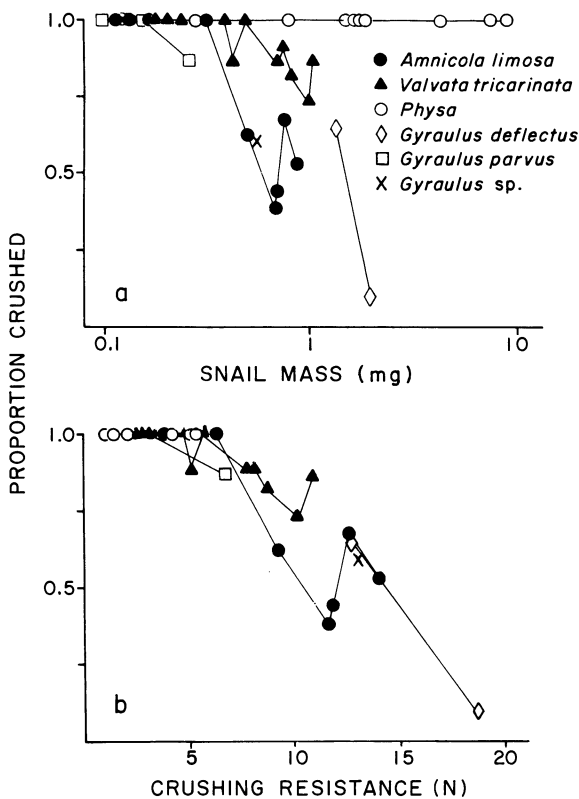


FIG. 8. Size refuge mediated through crushing resistance in Experiment 1. Given are the proportion of attacked snails in each size class that were successfully crushed (no snails escaped through gape limitation): (a) based on snail mass, (b) based on crushing resistance. The data for *Gyraulus* sp. came from trials in which there were approximately equal numbers of *G. parvus* and *G. deflectus*.

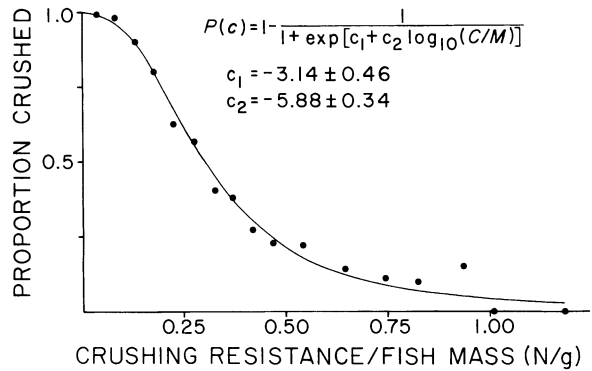


FIG. 9. Proportion of snails crushed ($P(c)$) for data from Experiments 1 and 2 combined. Only snails that were taken into the fish's buccal cavity were used ($n = 1538$). The equation estimated by logistic regression is given, as are the standard errors of the estimates. Binary data were grouped into categories for clarity of presentation (see also Fig. 7). Data are based on fish that ranged from 4 to 105 g live mass (M) and snails with crushing resistances (C) that ranged from 1 to 28 N.

many snail species never escape from some size classes of sunfish because they rarely, if ever, achieve the necessary body mass (compare Table 1 and Fig. 10). For example, in order to escape [$P(c) < 0.5$] from a 100-mm SL fish, *A. walkeri* must have a mass of at least 1.34 mg; however, we have never collected an *A. walkeri* > 0.5 mg.

Handling and rejection times

Data from Experiments 1 and 2 and from field observations were used to examine the effects of snail size and fish size on handling times (defined by successful attacks) and rejection times (defined by unsuccessful attacks). Comparison of the handling times from the two fish used in Experiment 1 with handling times from seven fish of comparable size (100–119 mm SL) used in Experiment 2, showed that the effect of snail size differed significantly between the two data sets for all four snail taxa (Fig. 11). In each case, handling time increased more slowly when many snails were available (i.e., Experiment 1) than when only one snail was available (i.e., Experiment 2). Snail size explained, on average, only 7% of the variation in handling time in Experiment 1, while snail size explained an average of 33% of the variance in Experiment 2.

We concluded that the differences in handling times in these two experiments were likely due to the presence of multiple snails in Experiment 1. In Experiment 2, we presented snails singly to a fish, and a new snail was not offered until the fish had finished feeding on the first snail; thus, there was little motivation for a fish to complete handling time and look for a new snail in this experiment. Most previous studies of the relationship between fish size, prey size, and handling time have also presented prey as in Experiment 2 and have generally found that handling time increases with prey

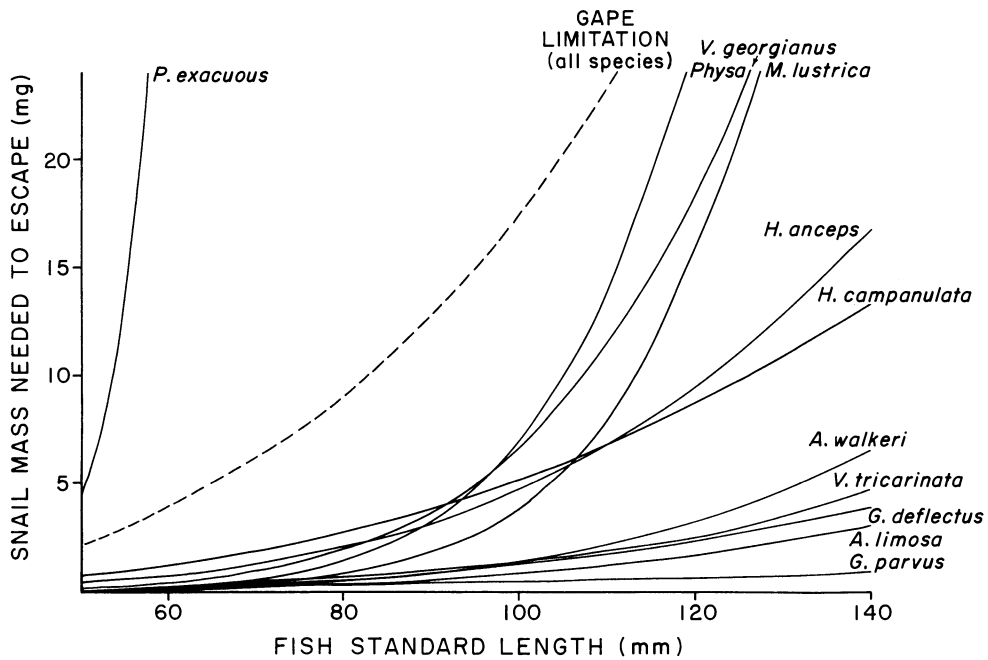


FIG. 10. Relative importance of gape limitation (---) and crushing limitation (—) for each snail species in relationship to size of the predator. Lines show results from Figs. 7 and 9 where snails have probabilities equal to 0.5 of being rejected by the predator due to gape limitation or crushing limitation. The line for *Physa* is based on estimates of crushing resistance from lake collections; the line for the laboratory culture lies near the line for *P. exacuouus*. Lines give theoretical expectations, although snails do not necessarily reach sufficient size under field conditions to enter a refuge (e.g., compare figure with adult sizes listed in Table 1).

size (see Mittelbach 1984 and Stein et al. 1984 for examples with sunfish and snails). We were somewhat surprised by the results of Experiment 1, and it caused us to look back at a series of experiments (G. Mittelbach, *personal observation*) conducted in 1983. In these experiments, two pumpkinseeds (78 and 82 mm SL) were offered three sizes of *Physa* (0.26, 0.56, and 1.60 mg tissue dry mass per snail) under a similar protocol to that of our Experiment 1 (3–4 trials per fish per snail size). When we reanalyzed these data, we also found that snail mass (m) had no significant effect on handling time ($\log_e(\text{handling time}) = 1.89 - 0.0776m$, $r^2 = 0.02$, $P > .5$, $n = 21$). Thus, while a positive relationship between prey size and handling may exist for some predator-prey interactions, our data suggest that snail size does not have a strong effect on pumpkinseed handling times under natural conditions.

Due to the potential bias in handling times observed in Experiment 2 (Fig. 11), we were unable to address the effect of fish size directly. Two indirect lines of evidence suggest that fish size probably has a small effect on handling times under natural conditions. First, we analyzed the handling times from our field observations of pumpkinseed foraging using analysis of covariance (dates were treatment groups and fish size was the covariate). This analysis showed that handling time was not related to fish size ($F_{1,123} = 0.11$, $P > .70$). Although larger fish tend to consume larger snails (Fig.

1b), our previous data suggest that snail size has little effect on handling times under natural conditions (i.e., differences in snail size do not confound the interpretation of the ANCOVA). Thus, we conclude that fish size also has a negligible effect on handling times.

We also examined the relationship between crushing limitation and handling times for each set of trials in Experiment 1. We used this information to infer the effect of fish size because one of the primary roles of fish size is its effect on crushing ability. In situations where all attacked snails were crushed, observed mean handling times were variable, ranging from 3.5 to 11.4 s (Fig. 12). However, there was much less variation among groups in which some of the snails were not crushed, and there appeared to be an overall mean handling time that described the data without reference to the magnitude of the size refuge. The observed handling times in the field match these laboratory data quite well (Fig. 12), and together suggest that there is an upper limit to the amount of time a fish spends attempting to crush a snail when other snails are present in the environment. Therefore, as the crushing resistance of prey increases, fish reject a greater portion of snails (Fig. 9), but maintain a relatively constant handling time of 8–11 s (Fig. 12). These data suggest that fish size might have little effect on handling time (based on successful attacks) or on rejection times (see next paragraph). Fish size does, however, influence a

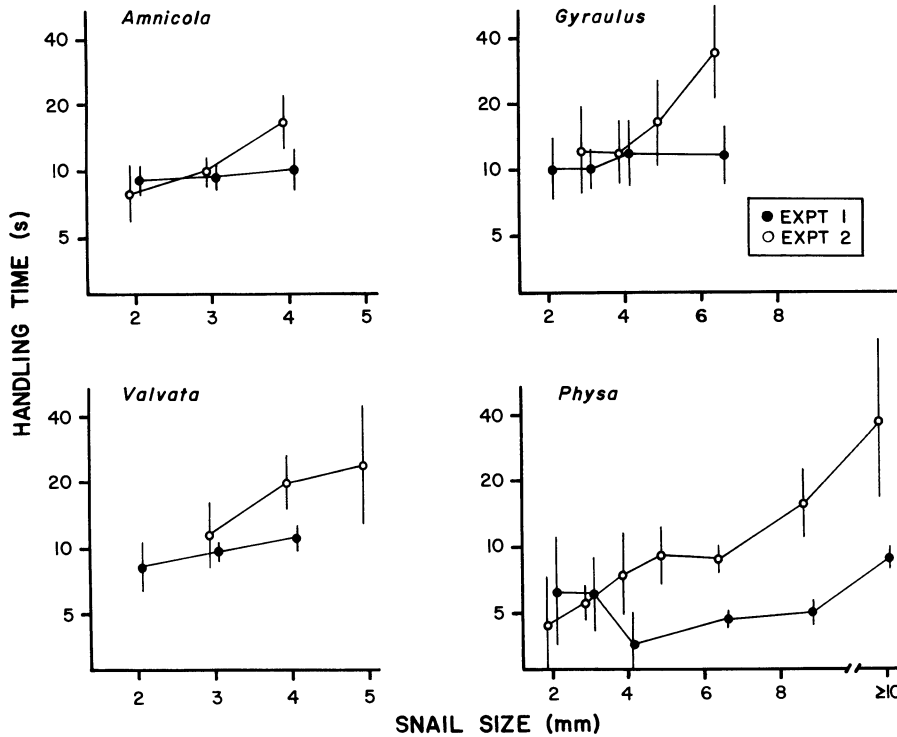


FIG. 11. Handling times (means and 95% CI) from Experiments 1 and 2. Fish sizes were 109 mm SL (two fish) in Experiment 1 and 100–119 mm SL (seven fish) in Experiment 2. Data were grouped into snail size classes for clarity of presentation. Analysis of covariance showed that the slope in the relationship between log(handling time) and snail size was significantly greater in Experiment 2 than in Experiment 1 for all four comparisons ($P < .05$ for each test). Sample sizes ranged from 31 to 210 snails per taxon per experiment.

fish's probability of crushing a snail (Fig. 9). Therefore, the total handling time required by a fish to successfully crush one snail of a particular type decreases with fish size.

Rejection times were independent of snail mass (ANCOVA, $F_{1,125} = 2.39, P > .10$) and snail taxa ($F_{2,125} = 1.07, P > .30$) in Experiment 1. In Experiment 2, snail mass also had no significant effect on rejection times ($F_{1,255} = 1.82, P > .10$), although rejection times differed among snail species ($F_{3,255} = 6.01, P < .001$). In addition, fish size had no detectable effect on rejection times ($F_{1,255} = 2.90, P < .05$). Rejection times recorded in the field agreed very well with the laboratory data (Fig. 13), although field data were insufficient to permit analysis of fish size effects.

The differences detected in handling times (and perhaps rejection times) between Experiments 1 and 2 suggested that crushing probabilities might also have differed between the two laboratory studies. In Fig. 14, we show all data from Experiment 1 and compare them with data from a similar range of crushing resistance per unit fish mass (C/M) extracted from Experiment 2 (Experiment 1 provided a narrower range of these values). Crushing limitation was similar in the two experiments (Fig. 14). Of the seven size categories shown in Fig. 14, only one provides evidence that crushing

limitation differed between the data sets. This is based entirely on the largest size of *Gyraulus* used in Experiment 1, and is exacerbated by a slight hump in the data from Experiment 2 (i.e., the data for this category appear to be out of line compared to the smaller sizes and the next larger size).

DEVELOPMENT AND TESTING OF THE FORAGING MODEL

In this section, we use the laboratory data to develop a series of increasingly complex foraging models, from which we attempt to predict patterns of diet selection observed for pumpkinseeds collected in the field. Expanding Holling's disk equation (Holling 1959a, b) to include attack probabilities and multiple prey types, the foraging rate (FR) of a predator on prey type i can be modelled as

$$FR = a_i N_i P_i(a) P_i(s) / [1 + \sum_{j=1}^k a_j N_j P_j(a) H_j] \quad (3)$$

where $i = 1, 2, \dots, k$

and where foraging rate equals the number of prey of type i killed by a predator per unit foraging time, N is the density of a prey type, a is the encounter rate (i.e., aN is the total encounter rate), $P(a)$ is the probability

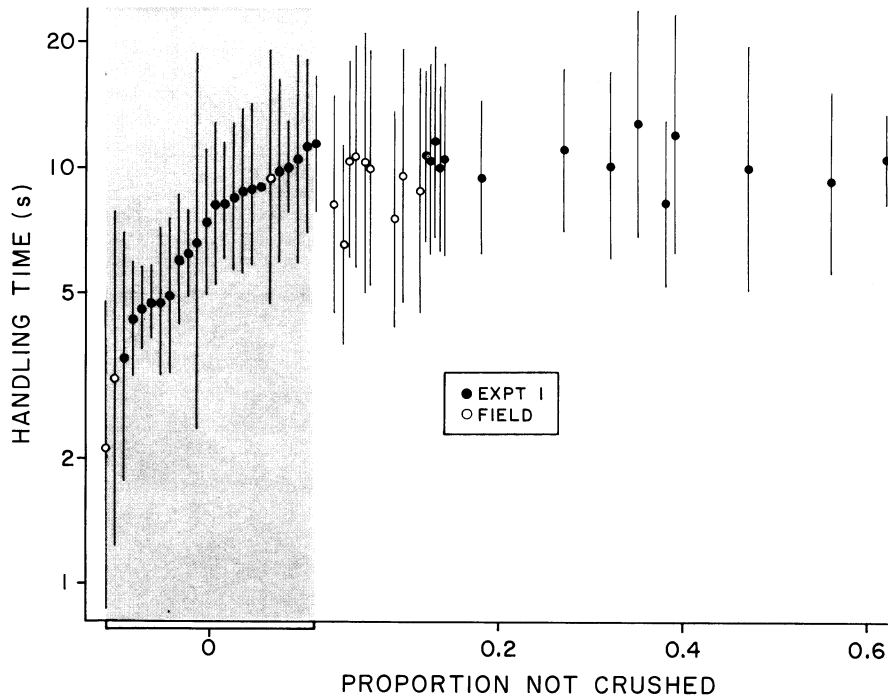


FIG. 12. Handling times (means \pm 1 SD) from Experiment 1 and field observations in relationship to the proportion of attacks that resulted in successful consumption of a snail. Handling times are based only on successful attacks. Each set of trials from Experiment 1 is represented with one datum, although one point is excluded in which only two snails were eaten and both were probably swallowed without being crushed. Each mean from the field is based on observations conducted on a single date. The data within the shaded region are sets (or dates) in which all attacks were successful (i.e., no snails were rejected). These data are ordered by increasing mean handling time. Handling times are based on sample sizes of 2–49 snails per set for Experiment 1 and 12–260 snails per date for field observations.

that the predator attacks an encountered prey item, $P(s)$ is the probability that an attack results in the successful consumption of the prey item, and H is the total handling time allocated to the successful capture of one prey item (i.e., including successful and unsuccessful attacks). Therefore, the predicted proportion of the diet consisting of prey type i is

$$\hat{p}_i = a_i N_i P_i(a) P_i(s) / \sum_{j=1}^k a_j N_j P_j(s) \quad (4)$$

where $i = 1, 2, \dots, k$

and the predicted prey selection, which is equal to the standardized ratio of the prey contribution in the diet compared to the environment (Chesson 1978, 1983), is

$$\hat{\alpha}_i = a_i P_i(a) P_i(s) / \sum_{j=1}^k a_j P_j(a) P_j(s) \quad (5)$$

where $i = 1, 2, \dots, k$.

In the following sections (Models 1, 2, and 3), we use the results from the laboratory experiments, and from the literature, to estimate the components in Eq. 5 as functions of snail and fish sizes. We then use these functions to predict patterns of prey selection based upon the densities and size distributions of snails in

resource samples. In particular, we are interested in determining to what extent each of the components of the predator–prey interaction (i.e., a , $P(a)$, and $P(s)$) contribute to observed patterns of prey selection.

We assessed the performance of the foraging model by comparing how well the model predicted prey selection relative to a model of random prey selection. Recall that each selectivity vector (one per fish or group of fish) is composed of k selectivity values (one for each of k prey types). Random selection is indicated by $\alpha = 1/k$ for each selectivity value. We devised an index (I) similar in definition to r^2 calculated in linear regression:

$$I = 1 - \left\{ \sum_{j=1}^n \sum_{i=1}^{k_j} (\alpha_{j,i} - \hat{\alpha}_{j,i})^2 / \sum_{j=1}^n \sum_{i=1}^{k_j} [(\alpha_{j,i} - (1/k_j))^2] \right\} \quad (6)$$

where $\alpha_{j,i}$ is the observed selectivity for the i^{th} prey type in the j^{th} selection vector, $\hat{\alpha}_{j,i}$ is the predicted selectivity based on the foraging model, k_j is the number of prey categories in vector j , $1/k_j$ is the mean selectivity for the j^{th} vector (i.e., the expectation under random foraging), and n is the number of selectivity vectors in the data set. The second term is the residual sums of squares

of the foraging model divided by the residual sums of squares of the random model (i.e., analogous to the total sums of squares in linear regression). This term is then subtracted from 1 to yield I (the explained sums of squares). Unlike r^2 , I ranges from $-\infty$ to 1.0. Negative values can arise because the foraging model is developed independently of the observed data and can actually provide a worse fit to the data than can the random model; this is not possible in regression analysis where the regression model always fits better than the mean of the observed data. Thus, when the foraging model performs worse than the random model, $I < 0$, and when the model performs better than the random model, $I > 0$. $I = 1$ indicates that the foraging model perfectly predicts the observed data. Because the α_i 's are not independent, we do not apply statistical tests to these I values. Instead, we use the I 's as a simple way to describe the relative performance of the different foraging models.

Our principal aim in this section is to compare the performance of three models in predicting the patterns of size selection given in Fig. 5. In the first model, we based predictions only on consideration of encounter rates. In the second model, we also incorporated the effects of size refuges, and in the third model we further incorporated the effect of attack probabilities. In the final portion of this section, we compare how the third and most complete model also predicted patterns of selection among snails of differing taxa as well as size.

Model 1

The simplest model we developed was based only on consideration of how encounter rate scaled with prey size. Encounter rates were assumed to increase with snail mass according to the results of the analysis of covariance based on *A. limosa*, *V. tricarinata*, and

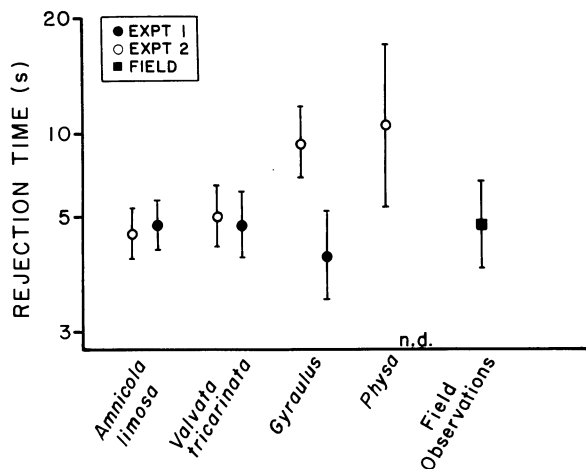


FIG. 13. Rejection times (means and 95% CI) for four snail taxa from Experiments 1 and 2 and from field observations. *Physa* were never rejected in Experiment 1. Data are based on samples of 31–86 rejections per group.

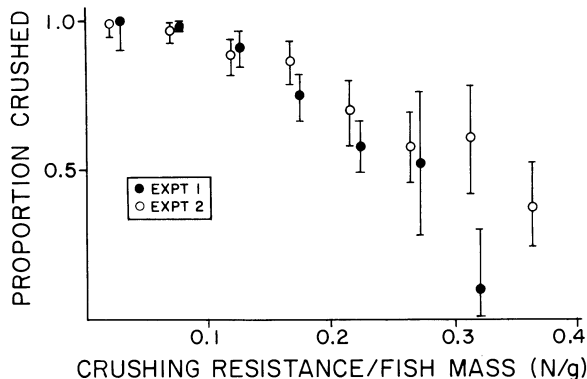


FIG. 14. Comparison of the size refuge based on crushing limitation from Experiments 1 and 2. Proportion of snails that were successfully crushed (given they were taken into the buccal cavity) is plotted along with 95% CI based on the binomial distribution. Sample sizes per datum range from 31 to 291 snails.

Physa (Fig. 6; see Results: Encounter Rates). The results from this analysis yielded the following relationship

$$a = 0.00001062m^{1.063} \tag{7}$$

which we assumed was applicable to all snail taxa and to fish of all sizes.

To assess how well size-specific encounter rates alone predict the observed patterns of size selection depicted in Fig. 5, we simplified Eq. 5 to

$$\hat{\alpha}_i = a_i \sum_{j=1}^k a_j \tag{8}$$

where $i = 1, 2, \dots, k$

(i.e., by assuming that $P(a)P(s)$ in Eq. 5 was constant among all snail size classes; Table 5). We used this model to generate the predicted selectivities among snail size classes for each group of fish (collected on a given date and in one of the four fish size classes) by using the midpoints of the fish size categories (60, 80, 100, 120 mm SL) and estimating the average value of a for a snail within each of the k prey categories (using the size distributions of snails in the resource samples and the allometric relationship between snail size and encounter rate). In this simple model, selectivity was independent of fish size (a was assumed a function only of snail size), so predictions were identical for all fish groups within a date. In subsequent models (Models 2 and 3), which incorporated attack and capture probabilities, predictions differed among fish of different sizes. We then compared these predictions, based on Eq. 5, to the observed selectivities shown in Fig. 5.

This simple model (Model 1; Table 5) explained 53% of the observed variation in selectivities in the entire data set (Fig. 15). In addition, we divided the observed set of selectivity vectors into two categories: those in which the snails in the largest size class could, on av-

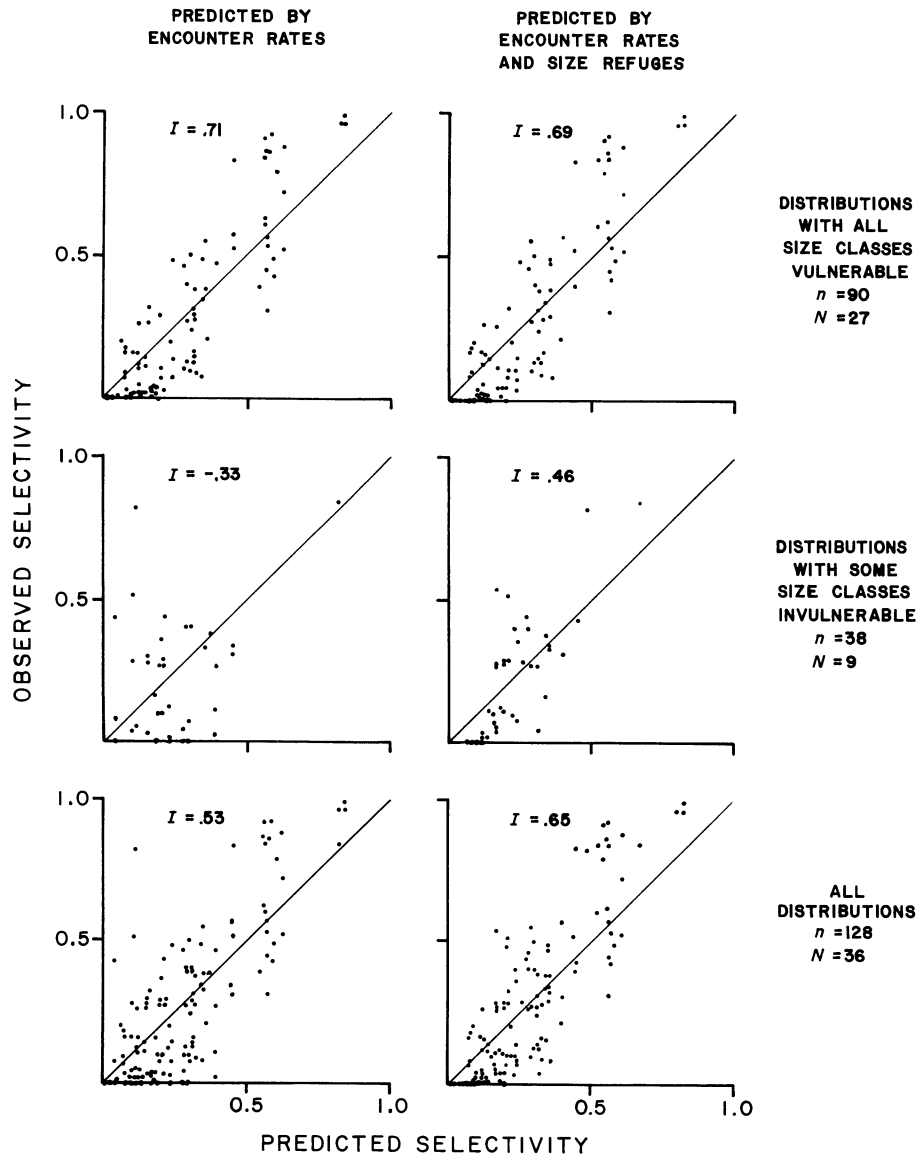


FIG. 15. Comparison of observed and predicted size selectivities using Model 1 (incorporating size-specific encounter rates) and Model 2 (which additionally incorporated size-specific refuges) (see Table 5). The top graphs give the results from situations in which even the largest snail class was easily eaten ($P(s) > 0.5$), while the middle graphs give the results from situations in which the largest snail class (and possibly smaller ones) were relatively difficult to capture successfully ($P(s) < 0.5$). The bottom graphs give the results for all selectivity vectors. I is the performance of the foraging model in explaining variation in selectivities relative to a random model (Eq. 6). The diagonal line gives the expectation if the model was a perfect fit to the data. N = number of selectivity vectors. n = number of individual selectivities. The observed selectivities are plotted in Fig. 5.

erage, be successfully consumed by a pumpkinseed whose size corresponded to the midpoint for a fish group (i.e., $P(s) > 0.5$ for a 60, 80, 100, or 120 mm SL fish), and those in which the largest size class could not, on average, be successfully consumed ($P(s) < 0.5$). We refer to these two groups as relatively vulnerable and invulnerable, respectively. Nine of the selectivity vectors (a total of 38 selectivity values) in Fig. 5 were classified as invulnerable (the vectors for *Ammnicola* in

May and June in Three Lakes II for the three smaller fish classes, the vector for *Ammnicola* in Palmatier Lake for the smallest fish class, and the vectors for *Marstonia* for the two smaller fish classes), while the other 27 vectors (90 selectivity values) were classified as vulnerable (i.e., most snails in even the largest snail class could be eaten with probabilities exceeding 0.5). The encounter rate model explained 71% of the variation within the vulnerable category, but performed worse

TABLE 5. Equations for general functions used in foraging Models 1, 2, and 3 (see Eqs. 5, 8, and 9). The column headed "Model" indicates which equations were used in each of the models. Assumptions for a model of random selection ($\alpha_i = 1/k$ for all i) is also given. See Table 3 for descriptions of the terms.

Function		Model
a	= constant = $0.0001062m^{1.063}/s$	random 1, 2, 3
$P(g)$	= constant = $1 - 1/\{1 + \exp[-41.95 - 26.45 \log_{10}(m^{1/3}/SL)]\}$	random, 1 2, 3
$P(c)$	= constant = $1 - 1/\{1 + \exp[-3.140 - 5.885 \log_{10}(C/M)]\}$	random, 1 2, 3
$P(a)$	= constant = $1/\{1 + \exp[-2.332 - 6.579 \log_{10}[(e_g/H)/(E_g/T^*)]\}$	random, 1, 2 3

than the random model ($\alpha_i = 1/k$ for all i) when predicting selectivities for distributions that included invulnerable snails ($I = -33\%$, Fig. 15).

Model 2

We next incorporated the effects of size refuges in the model by modifying Eq. 5 to include the effect of size refuges as well as encounter rates:

$$\hat{\alpha}_i = a_i P_i(s) / \sum_{j=1}^k a_j P_j(s) \quad (9)$$

where $i = 1, 2, \dots, k$.

Using the same procedure as outlined above for Model 1, we used Eq. 9 to generate predicted size selectivities for each of the fish classes on each of the collection dates. Incorporating size refuges (Model 2: Table 5) into the model increased the total variance explained by the foraging model from 53 to 65%. More importantly, this model dramatically increased the performance of the model when some size classes were invulnerable ($I = 46\%$ vs. $I = -33\%$ for Model 1). As expected, the first two models (Eqs. 8 and 9) performed similarly when snails had not reached a size refuge (i.e., for vulnerable distributions, $I \geq 69\%$). These results demonstrate that both encounter rates (which increase with snail size) and the ability of fish to consume attacked snails (which declines with snail size and increases with fish size) can be important. Depending on the distribution of snail sizes in the environment (e.g., Fig. 1c) and on the fish size, the resulting patterns of selection can be monotonically increasing, decreasing, or hump-shaped (Fig. 5).

Model 3

In developing the first two models, we assumed that attack probabilities ($P(a)$) were equal among all snail sizes (e.g., $P_i(a) = 1.0$ for all i). Some of the residual variation in Fig. 15 might be attributable to variation in the probability that fish attack encountered snails that differ in size. The best conceptual framework from which to generate an expected pattern for attack prob-

abilities comes from standard optimal diet theory (e.g., Charnov 1976, Stephens and Krebs 1986). The theory predicts that in environments with many prey types available, predators should ignore encountered prey whose net energy return is less than the environmental average, and that predators should always attack prey that offer a greater net energy return. Two problems had to be resolved before we could examine our data and determine if attack probabilities were varied in accord with optimal diet theory. First, an optimization model had to be specified and the values of important parameters (e.g., handling times) determined. Second, we needed to develop a technique to estimate attack probabilities from the laboratory and field data, neither of which directly yielded estimates of attack probabilities.

Optimal diet models have been published in many forms (e.g., Werner and Hall 1974, Charnov 1976). The model we construct is similar to that developed for the bluegill sunfish (Mittelbach 1981), where net energy gained per fish per unit foraging time is estimated as:

$$E_n/T = \left[\sum_{i=1}^k e_{gi} a_i N_i P_i(a) P_i(s) - RT \right] / T, \quad (10)$$

where $T = 1 + \sum_{i=1}^k a_i N_i P_i(a) H_i$, e_{gi} is the gross (i.e., assimilable) energy gained from an item of prey type i , a_i is the encounter rate between a fish and prey type i , N_i is the density of prey type i (i.e., aN is the total rate of encounter), $P(a)$ is the probability that an encountered prey is attacked, $P(s)$ is the probability that an attacked prey is successfully consumed, R is the metabolic rate of a fish, T is the total foraging time that results from 1 s of search (i.e., 1 s of search plus all associated handling and rejection time), and H_i is the expected total handling time per consumed item of prey type i (and includes the combined effects of handling time, rejection time, and capture success) (see Table 3). In general, the foraging rate is simply equal to the total amount of assimilable food (snail tissue) that can be collected by a pumpkinseed during 1 s of

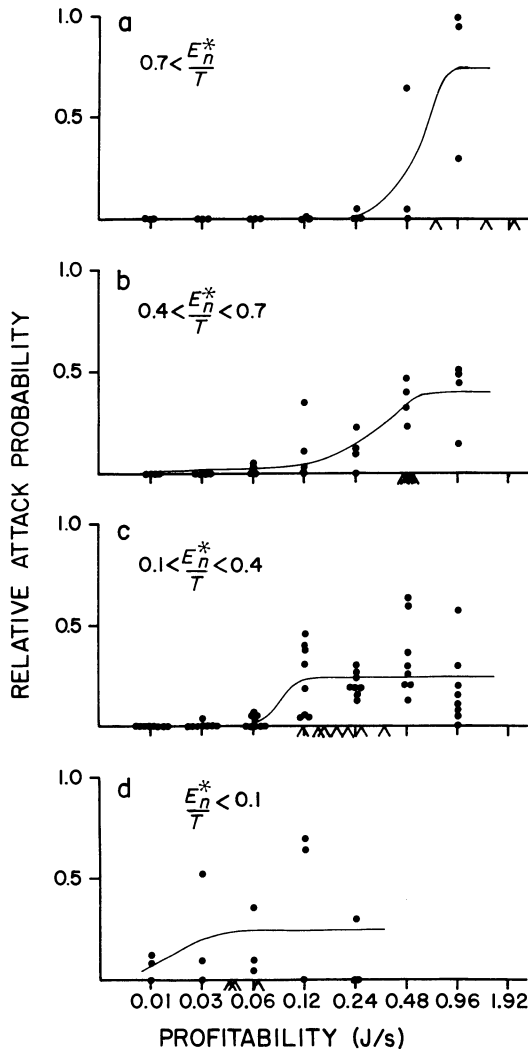


FIG. 16. Relationship between relative attack probability (α' , calculated using Eq. 11) and prey profitability (e_n/H) as influenced by variation in the net rate of energy return (E_n/T^*) for an optimally foraging fish. A total of 18 vectors of α' were calculated, each consisting of 5–7 separate values of α' . These vectors were obtained from each available combination of fish size class and date of collection. Results were grouped depending on the estimate of E_n/T^* for the date/fish group. Particular values of E_n/T^* for each data set are indicated by the arrowheads beneath the horizontal axis. Data in panel (d) were obtained from the smallest fish size class (which consistently had lower estimates of E_n/T^*), while data in each of the other three panels were obtained from at least two of the three larger size classes (which overlapped considerably in their estimates of E_n/T^*). Due to the lower range of profitabilities available to the fish in (d), only five profitability classes were defined. Lines were fit to the equation $\alpha' = M/1 + \exp[c_1 + c_2(e_n/H)]$ by nonlinear regression.

search time, minus the energy cost of foraging (RT), divided by the total foraging time that results from 1 s of search time. The optimal solution to Eq. 10 can be found by ranking prey by increasing profitabilities

(i.e., the ratio of net energy gain per total handling time: e_n/H , where $e_n = e_g - RH$; Table 3) and determining the diet breadth that maximizes E_n/T (see Charnov 1976). The solution yields an estimate of the optimal (maximal) net foraging rate (symbolized E_n/T^*) as well as the predicted pattern of how $P(a)$ should vary with prey profitability: if $e_n/H > E_n/T^*$, then $P(a) = 1.0$, else $P(a) = 0.0$ (see Charnov 1976 and Stephens and Krebs 1986 for discussion of predictions and assumptions of these models).

Densities, encounter rates (a), and capture probabilities ($P(s)$) were estimated for each snail type collected in the resource samples (e.g., Table 5) in order to calculate E/T^* . However, based on preliminary trials, the inclusion of two snail types, which are only rarely eaten by pumpkinseeds, influenced the estimates of E/T^* . These snails (large *Helisoma* [>6 mm shell diameter, or ≥ 2.1 mg] and *Viviparus*) typically occur deep within the *Chara* (C. Osenberg, *personal observation*). Encounter rates with these snails are likely to be much lower than those we estimated using Eq. 7. Indeed, the fact that these snails, which are uncommon in the field, compose very little of the snail biomass in pumpkinseed diets, suggests that their actual influence on E/T^* should be small. Therefore, we set encounter rates with these prey equal to zero in the model.

To complete the specification of the model, we estimated gross energy content of a snail as the tissue dry mass of the snail times 20 J/mg (Stein et al. 1984) times an assimilation efficiency of 70% (Ware 1975, Elliott 1976). Rates of energy loss were based on metabolic rates of pumpkinseeds during summer months (Evans 1984) and an energy conversion rate of 13.6 J per milligram of oxygen (Elliott and Davison 1975). We also assumed that metabolic rates were similar during all phases of the foraging process. Rejection time (needed to estimate total handling time, H) was assumed constant and equal to 6 s, which is in good agreement with the field data and most of the laboratory data (Fig. 13). We set successful handling time (also needed to estimate H) equal to 9 s per snail (invariant among snail taxon, snail size, and fish size), based upon the results of Experiment 1 and the field observations (Figs. 11 and 12). Based on these assumptions and the resource samples (which gave estimates of snail densities and size structure), we used Eq. 10 to estimate E_n/T^* for 60, 80, 100, and 120 mm SL fish (corresponding to the midpoints for the four 20-mm fish size classes) on the six collection dates.

Observed attack probabilities, though not directly available from the field data, can be inferred by applying Manly's index (Eq. 1) in the following manner. If feeding by fish reflects the combined effects of encounter rates, size refuges, and attack probabilities, and if the feeding rate on prey type i can be modelled according to Eq. 3, then a new index of selectivity can be defined as

$$\alpha'_i = [a_i N_i P_i(a) P_i(s) / a_i N_i P_i(s)] / \left[\sum_{j=1}^k a_j N_j P_j(a) P_j(s) / a_j N_j P_j(s) \right]$$

$$\alpha'_i = P_i(a) / \sum_{j=1}^k P_j(a) \quad (11)$$

where $i = 1, 2, \dots, k$.

In deriving this index, we assumed that the composition of a fish's diet reflected the relative values of $aNP(a)P(s)$ (see Eq. 4). To cancel terms whose importance we have already explored (i.e., a , and $P(s)$), we divided $aNP(a)P(s)$ by $aNP(s)$, thus isolating the effect of $P(a)$ (Eq. 11). Finally, we standardized each ratio by the sum of the ratio over all prey types (as shown in the denominator in the precursor to Eq. 11). Relative values of $aNP(a)P(s)$ were estimated from the gut contents, and values of $aNP(s)$ were estimated using Model 2 (Eq. 9; Table 5). Thus, the standardized ratios of these two terms provide estimates of relative attack probabilities (α' , Eq. 11). In theory, if pumpkinseeds behaved optimally and the model was properly specified, relative attack probabilities (α') should vary discontinuously from zero for prey with low profitabilities to $1/k^*$ for prey with greater profitabilities (i.e., if $e_n/H < E_n/T^*$, then $\alpha' = 0$, else $\alpha' = 1/k^*$, where k^* is the number of prey classes within the optimal diet). In addition, the cutoff point between prey with $\alpha' = 0$ and prey with $\alpha' = 1/k^*$ should be equal to E_n/T^* .

We defined prey types based on their profitabilities (using seven profitability classes, except when only fewer were available), and calculated selectivities among

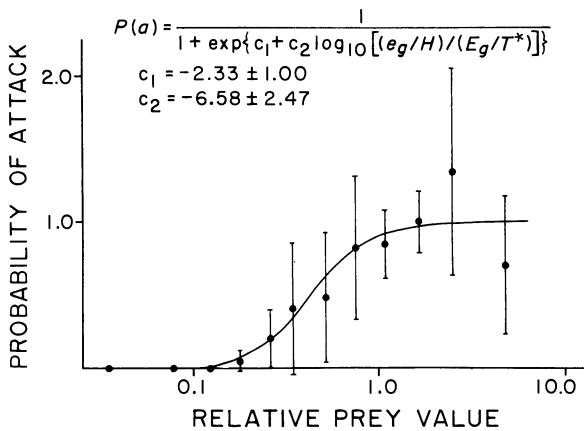


FIG. 17. Probability of attack as a function of the relative value of the prey items. Data were taken from Fig. 16 and transformed as described in the text (see Development and Testing of the Foraging Model: Model 3). The equation estimated by nonlinear regression is given. For presentation, data were grouped into categories and means and 95% CI determined (sample size is 10 per datum). Fitted parameter values and their standard errors are shown.

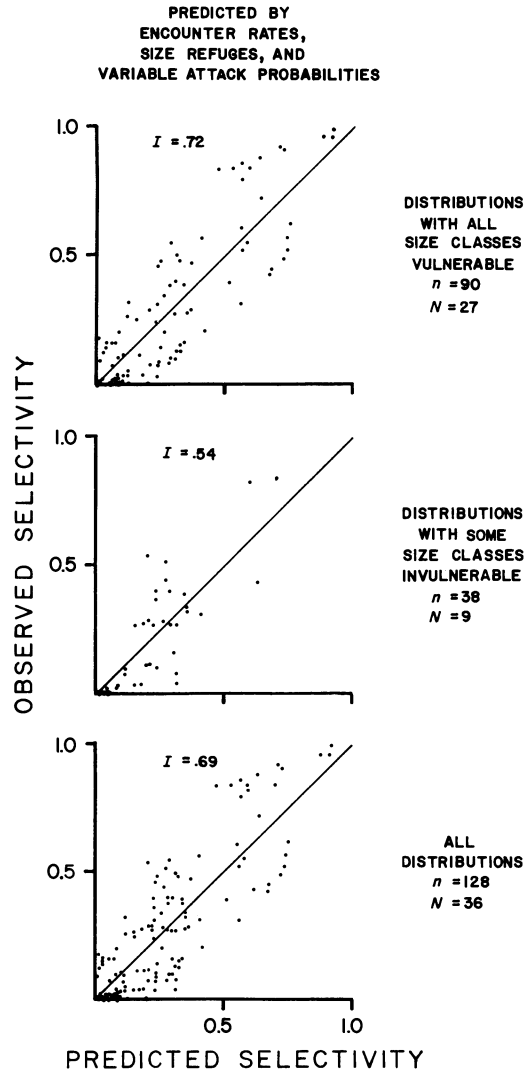


FIG. 18. Comparison of observed and predicted size-selectivities using Model 3 (see Fig. 15 and Table 5).

these classes for each of the four fish size classes on each of the six dates, which yielded 18 selection vectors (all with >25 snails in the diet sample; six vectors based on <10 snails were excluded). To facilitate the comparison we grouped the 18 vectors into four categories corresponding to increasing values of E_n/T^* . We then compared the patterns of observed relative attack probabilities (α' , Eq. 11) with the patterns predicted by optimal diet theory. If the variation in selectivity that remained after including the effects of encounter rates and size refuges (Model 2), was related to profitabilities, then our new index (Eq. 11) should scale positively with profitability.

Relative attack probabilities (α' , Eq. 11) increased with profitability, and the transition between prey with low attack probabilities and high attack probabilities

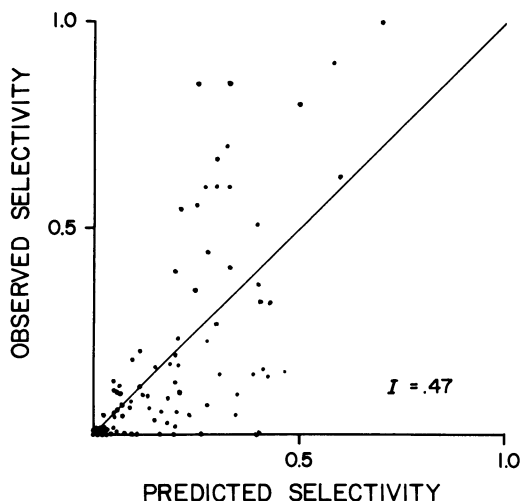


FIG. 19. Comparison of observed selectivities on snail types defined by size class and taxon with those predicted by Model 3 (see Fig. 15).

increased with E_n/T^* (Fig. 16). For example, in the situations with low E_n/T^* (Fig. 16d), snails with low or medium profitabilities were attacked as often as were snails with greater profitabilities. However, in situations where E_n/T^* was relatively large (Fig. 16a), the snails with low and medium profitabilities were ignored ($\alpha' = 0$) and only the most profitable snails were attacked. Therefore, it appears that fish varied their attack probabilities in qualitative accord with optimal foraging theory. However, as in previous studies of prey selection (e.g., Lacher et al. 1982; see also Stephens 1985) prey with $(e_n/H) < (E_n/T^*)$ were included in the diet, and it appears that attack probabilities, rather than showing an abrupt increase from 0 to 1 showed a continuous increase (although it is difficult to assess this critically with the available data).

We concluded from this analysis that attack probability, $P(a)$, is an important component of the foraging interaction between pumpkinseeds and snails. To incorporate attack probabilities into the foraging model (Eq. 5), we derived a general empirical relationship (since the quantitative predictions of the optimal diet model were not met) relating the probability of attack to the profitability of the prey. We first fit nonlinear regressions ($\alpha' = M / (1 + \exp(u))$, where $u = c_1 + c_2(e_n/H)$, and M , c_1 , and c_2 are constants fit by regression) to the four data sets in Fig. 16. The asymptote of this equation, M , is an estimate of the maximum relative attack probability (theoretically, $1/k^*$), which should correspond to an absolute attack probability of 1.00. Therefore, absolute attack probabilities ($P(a)$) were estimated as α'/M for the data in Fig. 16. Prey value was standardized across the different levels of E_n/T^* by using the ratio of gross prey profitability to the gross foraging rate: i.e., $(e_g/H)/(E_g/T^*)$, thus providing an

index of relative prey value. Operationally, the use of gross rewards (rather than net rewards) has little effect on the model but was necessary to avoid statistical problems arising when both net terms (e_n/H and E_n/T^*) were negative (e_g/H and E_g/T^* are always > 0). We then submitted these data to nonlinear regression: $P(a) = 1 / (1 + \exp(u))$, where $u = c_1 + c_2 \log_{10}[(e_g/H)/(E_g/T^*)]$, and c_1 and c_2 were fit by regression. Log-transformed data were fit better than nontransformed data. This method, justified for its empirical use, provided an excellent description of the data (Fig. 17), and could be easily incorporated into the foraging model (Model 3, Eq. 5, Table 5), although unlike the previous models, Model 3 used field data in its development and is therefore not independent of the field patterns.

The new model explained slightly more of the variance in selectivities than did the model without variable attack probabilities ($I = 69\%$ in Fig. 18 vs. $I = 65\%$ in Fig. 15), although the improvement was slight considering the strong patterns evident in Figs. 16 and 17. Most noticeably, incorporating variable attack probabilities improved the predictions for invulnerable size distributions ($I = 54$ vs. 46%), and it reduced the apparent bias in the model; notice that the points in Fig. 15 tend to fall along a line with slope > 1 , whereas the data in Fig. 18 fall much closer to a line with slope = 1.

Thus far, we have used the model only to predict size selection within snail taxa. We performed a final test of Model 3 by comparing predicted and observed selectivities based on prey taxa as well as size. Each prey item was assigned to a taxonomic category as well as a size class (i.e., < 0.5 mg, 0.5 – 1.0 mg, 1.0 – 2.0 mg, 2.0 – 4.0 mg, etc.). Finer divisions of sizes were not made due to limited numbers of prey items that had to be placed in a potentially large number of prey categories (e.g., prosobranch data from intestine samples could not be used in this analysis, which greatly reduced the number of prey items in each diet sample). Due to the relatively broad size categories, most taxa were represented by only one or two size classes on any particular date. Thus, the test was largely one of species selection, where predictions were based upon differences in the size structure of each snail taxa as well as the way in which a , $P(s)$, and $P(a)$ scaled with size for each snail taxa. Model 3 explained 47% of the observed variation (compared to the random model) in prey selection (Fig. 19).

DISCUSSION

The components of the pumpkinseed–snail interaction that were measured in the laboratory were quite successful in predicting and explaining observed patterns of prey selection under natural conditions. Each of the three primary foraging components (encounter rates, attack probabilities, and capture probabilities) were found to scale with body size of prey, and each component increased the explanatory power of the

model. Encounter rates, which increased with snail size, played a major role in determining prey selection. However, on dates when some snails had grown into the size refuge, only a model incorporating both encounter rates and capture probabilities accurately predicted prey selection. Together, these two functions create a risk curve that is hump-shaped, with intermediate size snails at greater risk than smaller or larger snails of the same species (Pastorak 1981, Greene 1983, 1986, Fig. 20). Of course, the predator's size affects the location of this hump (e.g., due to changes in the predator's crushing ability), and different snail species also differ in the location of the hump due to differences in the way crushing resistance scales with body size among the snail species. Similarly, prey profitability is a hump-shaped function of snail size because of the conflicting effects of snail size on the components of profitability: energy content and total handling time (H). Small snails have very low energy content, and therefore very low profitabilities, while very large snails offer large potential energy rewards, but they can only rarely be successfully eaten, thus producing a very low profitability also. Therefore, $P(a)$ will also be hump-shaped, although its position will depend on E/T^* , which is determined by many factors, including the densities and size distributions of snails. These processes are summarized in Fig. 20. Notice that Models 1 and 2 differ qualitatively in their predictions of size selection (monotonic vs. humped), but that Models 2 and 3 both predict hump-shaped selection curves: incorporating variable attack probabilities simply shaves off the tails of the hump-shaped curve.

Several recent papers have suggested that size selection should, in theory, be hump shaped, but that natural distributions of prey may not provide enough range in prey sizes to permit the detection of hump-shaped selection under field conditions (Scott and Murdoch 1983, Schmitt and Holbrook 1984, Bence and Murdoch 1986). The data on size selection by pumpkinseeds confirms this suggestion. In our study, hump-shaped selection curves were rarely observed in the field; selection was usually monotonically increasing, due to the rarity of large prey (a point also stressed by Scott and Murdoch 1983). Only on rare occasions, when the snail size distributions were broad relative to the feeding abilities of the fish, could the underlying hump-shaped relationship be documented. Therefore, it appears that a complete understanding of prey selection can best be obtained from a perspective that simultaneously considers the feeding abilities of the predator, the scaling of risk to prey size, and the dynamics of prey size distributions in the environment.

Variation in size structure of the snail community can have major effects on the dietary patterns of pumpkinseeds (Figs. 1–5). For example, in Fig. 4, we showed the size-frequency distributions of snails on two dates in Three Lakes II when selectivities were very different (Fig. 3). The variation in prey selection between these

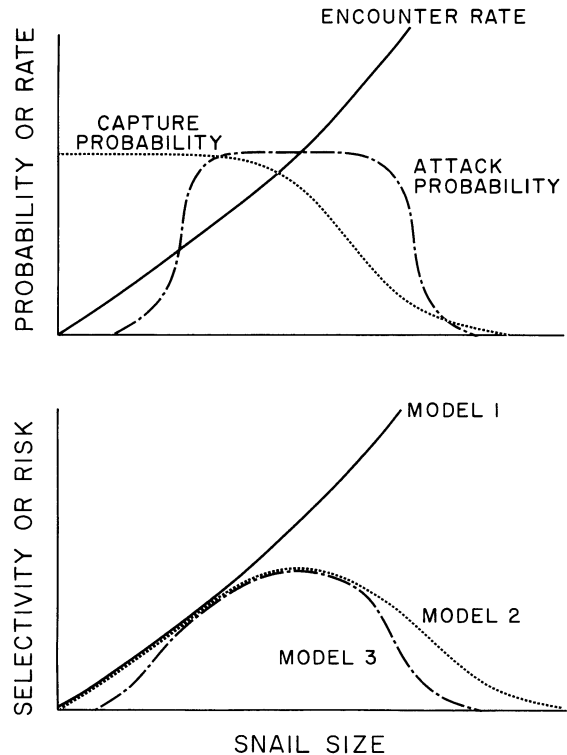


FIG. 20. Schematic representation of the foraging models. (a) The three primary components of the foraging models (encounter rates, capture probabilities, and attack probabilities) as functions of snail size. (b) Predictions of prey selection (or prey risk) as functions of snail size for the three foraging models (see Table 5). Random selection would be indicated by a horizontal line (i.e., independent of size).

two dates can be easily understood by considering that encounter rates increase with prey size and that the size distributions of taxa shifted between the two dates. In September, *Physa* were relatively large and therefore had a high selection coefficient due to large encounter rates. In June, *Amnicola* was selected (i.e., incurred the highest risk) because all other species were small (having recently hatched out from eggs) and thus incurred much lower encounter rates. The slight size refuge enjoyed by the large *Amnicola* was not enough to reduce its risk in the face of high encounter rates.

Thus, dynamics of size structure in the snail community can have profound effects on the prey selection by pumpkinseeds. Differences in the snail community among sites can also influence dietary patterns. For example, the snail communities in Culver and Palmatier Lakes tend to be dominated by smaller snails than occur in Three Lakes II. In addition, the snail communities in all lakes are biased toward smaller snails during August (which is when Culver and Palmatier Lakes were sampled). On these two dates, there were only small effects of fish size on total snail biomass in the diet (Fig. 1a) and on mean snail mass in the diet

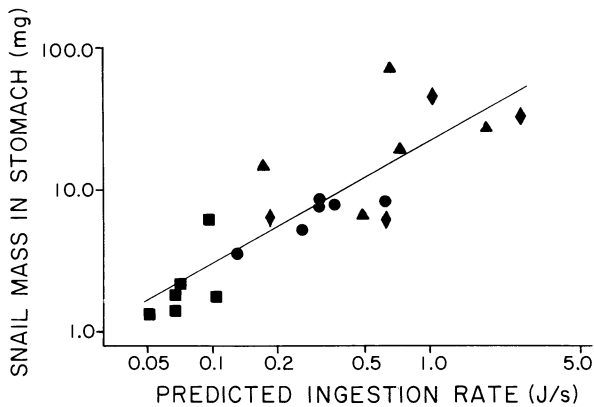


FIG. 21. Total snail mass in stomach as a function of predicted ingestion rate. Data are based on means for fish within the four size classes. The regression analysis for the complete data set was highly significant and the relationship was not different from linear (log-log regression: $r^2 = 0.71$, $n = 21$, $P < .001$, slope = 0.86, 95% CI on slope = ± 0.26). Symbols denote fish size classes: ■ = 50–69 mm SL, ● = 70–89 mm SL, ▲ = 90–109 mm SL, ◆ = 109–131 mm SL.

(Fig. 1b). Data from Three Lakes II showed consistent effects of fish size. These differences arose for at least two reasons. First, because snails were larger in Three Lakes II, size refuges were more important than in Culver and Palmatier Lakes. Thus, larger fish should have consumed larger snails because of their better crushing ability. Second, the effects of the size refuges caused E/T^* to increase more rapidly with fish size in Three Lakes II than in Culver and Palmatier Lakes; thus, larger fish dropped a greater range of small snails from their diets, further increasing the trends in mean snail size. The complex dietary patterns and selectivities observed in this system were only understood as a result of the simultaneous consideration of how prey and predator morphologies influenced key components of the predator–prey interaction and how shifts in the size structure of the snail community altered the relative importance of these processes.

Development of the foraging models required that we greatly simplify the natural complexity inherent in any field situation. Despite these simplifications, the models provided much insight into the importance of several key processes that influence the predator–prey interaction between pumpkinseeds and snails. One assumption that we made was that encounter rates could be modelled as a simple function of snail size. Clearly, encounter rates can also be influenced by other factors. For example, fish size is known to influence encounter rates with zooplankton (O'Brien et al. 1976, Mittelbach 1981) because larger fish generally possess better visual acuity (Li et al. 1985). However, in highly structured environments such as the littoral zone of lakes, the fish size advantage can disappear (Werner et al. 1983b). Microhabitat use by snails could also modify encounter rates with predators, as could differences in coloration

or activity, although, to the extent that these factors scale with body size, their effects are probably included in our measurements and description of encounter rates. A more comprehensive model would need to explore and possibly incorporate these (and other) additional sources of variation in encounter rates.

Encounter rates might also vary through the formation of search images or through patch selection by fish, both of which would produce encounter rates that are density and/or frequency dependent. The possible role of these two factors is seen in Fig. 19 where prey with low risk tended to be avoided more than predicted, while prey at high risk were selected more than predicted. These biases were not seen in the size selection patterns (Fig. 18), suggesting that unexplained sources of variation in risk might be greater among species than among size classes within species.

The difference in the accuracy of the model in predicting size selection (Fig. 18) vs. species selection (Fig. 19) might be the result of the different spatial scales over which snail densities and size distributions vary. Using data collected over several months in 1983 from a study site in Three Lakes II, we examined how the coefficients of variation, cv , (one simple way to express patchiness) varied when measured for density and for mean snail size for each species. The cv 's for densities ($128.4\% \pm 18.6$; \bar{X} and 95% CI) were three to eight times as great as the cv 's for mean mass ($44.7\% \pm 9.9$) and mean size ($16.0\% \pm 3.3$). These data suggest that small patches of the littoral zone are likely to differ more with respect to snail densities than with respect to average snail sizes. Additionally, for each date we examined the correlations between the densities of the common snail species; of 24 correlations, only 2 were significant at $P < .05$. Therefore, species were relatively independently distributed within this study site. If a fish concentrated its search in one particular patch, it was likely to see a very different species composition compared with a nearby patch, although the size distributions of any snail species would be fairly similar between the patches. This suggests that investigation of patch selection might provide additional insights into the determinants of prey selection by pumpkinseeds. Schluter (1981) reached a similar conclusion after reviewing studies that tested optimal diet theory under field conditions in which multiple prey species were available.

Most studies of prey selection make no attempt to quantify encounter rates, probably because encounter rates are often difficult and time-consuming to measure. However, as this and other studies have shown (Mittelbach 1981, Wright and O'Brien 1984), the explicit consideration of prey encounter rates can be critical in accurately explaining patterns of selection. For example, Stein et al. (1984) studied prey selection by another molluscivorous sunfish (*L. microlophus*), and concluded that optimal foraging theory was not useful in predicting patterns of prey choice they observed in

the laboratory. In one sense, we agree with Stein et al. that foraging profitability alone might not explain a large fraction of the observed variation in prey selection by predators (indeed, it did not in our study; Fig. 15 vs. Fig. 18), and that the optimal aspect of many foraging models might be unnecessary. However, Stein et al. did not measure encounter rates and capture probabilities, and without accurately assessing the effects of these components of the foraging process, the additional role of prey profitability cannot be easily assessed. This raises the general problem of testing optimal foraging predictions by examining the correlation between diet selection and prey profitability. In many situations, components of the predator-prey interaction are correlated; e.g., encounter rates and prey profitabilities both increase with prey size under many conditions (Werner and Hall 1974, O'Brien et al. 1976, Mittelbach 1981, this study). Thus, the observation that a predator's diet is biased, for example, in favor of larger prey cannot be interpreted as evidence that the predator only attacked more profitable (i.e., larger) prey. The effects of encounter rates and other passive components of the interaction (e.g., capture success) must first be incorporated into the model.

In addition to testing the importance of various mechanisms or processes that influence a predator-prey interaction, foraging models can also be useful tools for understanding population dynamics and/or individual performance of predators and prey. For example, we used the foraging model (Model 3) to predict the rates of prey ingestion for fish on each of the six collection dates. The predicted ingestion rates were strongly correlated with the snail biomass in the stomachs of fish (Fig. 21: $r^2 = 0.71$, $n = 21$, $P < .0001$), suggesting that the model correctly predicted relative feeding rates of fish. However, the relation in Fig. 21 is somewhat suspect because of the use of different size classes of fish. That is, stomach capacity increases with fish size and predicted ingestion rate also generally increases with fish size; therefore, prey mass in the stomach and predicted ingestion rate might be correlated but not functionally related. To factor this out, we performed an analysis of covariance (on \log_{10} -transformed data) using the three largest size classes of fish, which overlapped in their predicted ingestion rates. Slopes (i.e., the scaling effect of ingestion rate) were similar among the three groups ($P > .75$), and adjusted means did not differ among the fish size classes ($P > .20$). The predicted ingestion rate (the covariate) did, however, explain a significant portion of the variation in snail mass in the fish stomachs ($P = .03$). Therefore, the model provided a good description of the relative feeding rates of fish and might be a useful tool to predict the growth rates of fish or the degree of food limitation using measures of resource abundance in different environments (see Osenberg et al. 1988, Mittelbach 1988, and Mittelbach et al. 1988 for similar examples with bluegill). In another study (Osenberg 1988), this same

model was used to predict relative mortality rates of snails exposed to predation by pumpkinseed sunfish, and the predictions of the model were significantly correlated with the observed effects of pumpkinseeds in a field experiment in Palmatier Lake.

Due to the important role of prey size in determining prey selection by predators (and the predation risk of prey), individual growth rates of prey should have large influences on their survival because growth rates determine the time spent at each size and therefore how long prey incur each level of risk (Werner et al. 1983a, Werner and Gilliam 1984). The shape of the risk curve (e.g., Fig. 20) determines the effect that growth rate has on the survivorship of prey during a particular time interval. For example, if risk decreases with prey size, then an increase in growth rate will result in a greater survivorship over a time interval (Craig 1982, Travis 1983). However, if risk increases with prey size, as it does under many situations (Fig. 6; Mittelbach 1981, 1988, Li et al. 1985), then the survival during a time interval will necessarily decrease with increasing growth rate. Thus, by increasing the prey's growth rate (e.g., by increasing the abundance of its resources), the mortality of the prey could actually increase. This is neither a numerical nor a functional response by the predator, but rather a simple consequence of the simultaneous effects of growth rate on prey size and of prey size on risk.

This interaction between growth and predation risk could have important consequences for population dynamics of size-structured prey (Botsford 1981, Hastings 1983, McNair 1987). In these populations, the survival rate of cohorts from birth to reproduction will be simultaneously determined by growth rates and size-specific risk (see VanSickle 1977, Werner et al. 1983a). The integration of these survival rates with fecundities, which are also often strongly influenced by body size and, therefore, individual growth rates, will describe the population dynamics. This argument suggests that in size-structured populations, the factors that directly affect growth rate (e.g., temperature, food abundance, or competitor density) and the factors that directly affect mortality rates (e.g., predator density) are inextricably linked: it is not possible to dichotomize population dynamics into being governed by one set of factors vs. another. There has been, and continues to be, debate over whether populations and/or communities are affected by, for example, competition vs. predation (Connell 1983, Shoener 1983, Sih et al. 1985), or bottom-up vs. top-down processes (McQueen et al. 1986). Indeed, in size-structured populations, where mortality rates are typically size-specific, the effects of bottom-up and top-down processes will necessarily interact, and it is this interaction that demands attention from ecologists. Because body size provides a simple way to scale many processes that influence a species' ecology, and because body size can be used as a common variable uniting separate demographic components that

determine population dynamics, an explicit focus on body size might provide a powerful way to develop ecological models that necessarily incorporate the simultaneous effects of diverse processes and interactions.

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