

Ecology: Vol. 65, No. 3, 1984, pp. 702-715.

ISSN 0012-9658

doi: 10.2307/1938042

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USING TIME AND ENERGETIC MEASURES OF COST IN ESTIMATING PREY VALUE FOR FISH PREDATORS¹

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Abstract. In the predator-prey interaction between redear sunfish (*Lepomis microlophus*) and benthic, freshwater snails (*Physa*, *Helisoma*, and *Oxytrema*), we document selective predation among genera and sizes of prey and use optimal foraging theory in an attempt to explain diet selection. In experiments, sunfish strongly selected against *Oxytrema* and weakly discriminated between *Physa* and *Helisoma*, with *Physa* most often chosen; size selection within any genus did not occur. Among genera, selection results were consistent with differences in shell strength and a time cost/benefit (C/B) construct operationally defined as handling time divided by prey dry mass. Within any genus, neither shell strength (smallest snails had weakest shells) nor time C/B (largest snails had minimal C/B) provided predictions consistent with results from selective-predation experiments. To explain this discrepancy, we measured metabolic costs of handling and energy content of prey. Dividing net energy of prey (E , generated by subtracting the energetic cost of handling from prey energy content) by handling time (T) yielded values of E/T that were similar for *Physa* and *Helisoma*. Within either genus, E/T was always highest for largest snails. Thus, this construct also provided predictions inconsistent with our experimental results. Only an energetic C/B ratio, in which the energetic costs of handling were divided by the energetic value of the prey, was consistent with selection of *Physa* over *Helisoma* and no size selectivity within either genus. Whether predators add prey to their diet based on this construct is unknown at present. The lack of concurrence between theoretical predictions of how prey should be ranked by predators (i.e., according to energy gained per unit time expended) and our experimental results suggests these constructs should be re-evaluated. Unless we know the discriminatory ability of our predators (in terms of how fine a difference in prey types they can assess) and the currency used in making decisions, C/B or E/T constructs provide little insight into diet selection by predators.

Key words: behavior, foraging costs; *Helisoma*; *Lepomis microlophus*; optimal foraging; *Oxytrema*; *Physa*; selective predation; snails; time and energy.

INTRODUCTION

Fish predators, through selective consumption of prey, dramatically influence community structure of freshwater systems (for a review, see Zaret 1980). To predict the impact of these predators, we must understand, in some mechanistic sense, selective predation. In this paper, we explore factors that control selective consumption by a molluscivorous predator, the redear sunfish (*Lepomis microlophus*), of three genera of freshwater, benthic snails.

Predation by both invertebrates (mostly crabs) and vertebrates (mostly fishes) has been invoked as an important mortality factor for both marine (Kitching et al. 1966, Vermeij 1978, 1979, Palmer 1979) and freshwater molluscs (Eisenberg 1966, Gillespie 1969, Covich 1976, Vermeij and Covich 1978, Covich 1981). Long-term historical evidence suggests that molluscivores influence species diversity (Covich 1976) and prey morphology (Vermeij 1977b). Changes in prey morphology generally involve increases in shell thickness and ornamentation coincident with increases in predation intensity (Vermeij 1977b, Palmer 1979).

From field observations and laboratory experiments, various investigators have documented the importance of thick shells in reducing susceptibility to prey-crushing predators (Ebling et al. 1964, Spight and Lyons 1974, Spight 1976, Vermeij and Currey 1980).

Although shell thickness appears related to survival, investigators have not specifically examined how shell thickness actually influences selection by a predator (but see Elner 1978). Thus, to explore this relationship, we use an optimal foraging approach. Theoretically, prey should be ranked by prey energetic value per unit handling time, and should be added to the diet of a predator in decreasing order of some measure of energetic benefit of prey, divided by handling time for that prey (Pyke et al. 1977). In work with fishes, Werner (1974) has suggested using handling time divided by prey dry mass (H_i/M); those prey with minimal H_i/M should be consumed first, with prey added in increasing order of this cost/benefit (C/B) ratio. This construct has been successful in predicting prey selection in the field and laboratory (Kislalioglu and Gibson 1976, Stein 1977, Elner and Hughes 1978, Gillen et al. 1981). More recent work has centered on measuring prey utility on the basis of energy gained per unit time (E/T), suggested by many investigators (for a review see Pyke et al. 1977), and summarized by Mittelbach (1981) in his work with bluegill (*Lepomis macrochirus*) foraging in

¹ Manuscript received 6 July 1982; revised 28 February 1983; accepted 7 April 1983.

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a small Michigan lake. The optimal foraging model developed in his study accurately predicted prey selection by large bluegills, immune to predation pressure, in the field. An additional method of assessing prey utility is to assume that H_i is a measure of energetic cost of handling and, as above, B is energetic benefit of the prey, as in Sherry and McDade (1982). In their work, they assume that prey should be added to the diet not in increasing order of H_i/M , but rather in increasing order of an energetic cost/energetic benefit ratio. Although this construct has not been justified on theoretical grounds, we use it here as another method by which prey may be ranked by a predator. Thus, in this paper, to document and explain predation by redear sunfish, we (1) describe the predatory interaction between redear sunfish and three genera of freshwater snails, (2) examine selective predation by sunfish among genera and individual sizes of snails, and (3) evaluate both proximate (shell strength and morphology) and ultimate (through the use of C/B and E/T ratios) factors that might explain selective predation by this molluscivore.

EXPERIMENTAL ANIMALS

Redear sunfish are important predators on gastropods (Chable 1947, Huish 1957, Trautman 1957, Carothers and Allison 1968, Cross and Collins 1975, Pflieger 1975), hence their common name the shell-cracker sunfish. Although field data are scanty, most evidence suggests that molluscs contribute substantially to the diet of redear sunfish. Carothers and Allison (1968) found that redear sunfish readily eat pond snails, *Physa* spp. and *Lymnaea* spp., in laboratory aquaria, even choosing these snails over dragonfly nymphs and chironomid larvae. In plastic swimming pools containing aquatic plants, populations of snails were reduced 81–99% within 1 d after introduction of redear sunfish (Carothers and Allison 1968).

For prey, we chose three genera of snails: *Physa*, *Helisoma*, and *Oxytrema*. These genera (1) are common in freshwater habitats of North America, (2) overlap with redear sunfish over a broad geographic range, and (3) exhibit a wide range of shell strengths and morphology. Of the pulmonates, *Physa* is conspiral with a thin-walled shell and a large inflated body whorl. By comparison, *Helisoma* has a moderately thickened shell and is planispiral. Our single representative from the Prosobranchia, *Oxytrema*, is heavy walled with a conical shell (Fig. 1). Internal shell bracing also varies. Both *Physa* and *Helisoma* lack a thickened columella whereas *Oxytrema* has robust support structures (Fig. 1). We used four species: *Physa integra* (see Te 1975), *Helisoma anceps*, *H. trivolvis*, and *Oxytrema semicarinata* (identified by C. Stein, Museum of Zoology, The Ohio State University). These species also differ in external morphology, but exhibit a similar range of sizes up to 15 mm, total length (except for *Oxytrema* which reaches 20–25 mm).

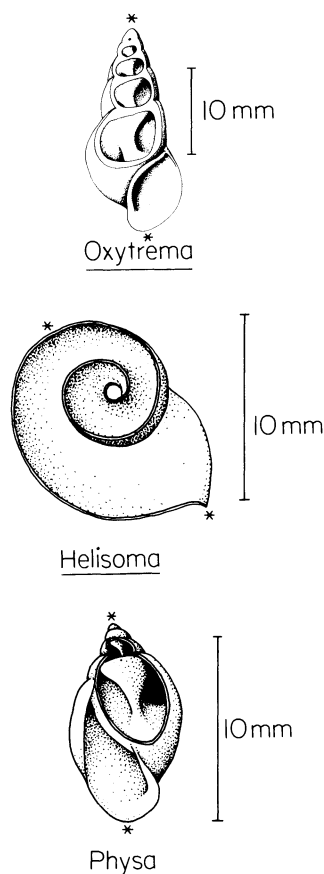


FIG. 1. Cutaway view of three genera of snails: *Physa*, *Helisoma*, and *Oxytrema*, revealing internal architecture and shell thickness. Length measurements were taken between the asterisks (*). Drawing by David M. Dennis, College of Biological Sciences, The Ohio State University.

Redear sunfish (130–220 mm, total length) were collected from Ross Lake, Ross County, Ohio, USA. *Physa integra*, *Helisoma anceps*, and *Oxytrema semicarinata* were collected from the Scioto River, Franklin County, Ohio, whereas *Helisoma trivolvis* were collected from Caldwell Lake, Ross County. In predation experiments, we did not distinguish between *H. anceps* and *H. trivolvis*; these two species were similar in outward appearance and in shell-crushing resistance (see Results), but differed in size, with *H. trivolvis* the larger species. Animals were held in flow-through and standing-water aquaria at 19°–21°C with a constant photoperiod of 16 h light: 8 h dark. Snails were fed trout pellets; fish were fed a combination of beef heart and snails. Experiment tanks were either 250-L flow-through aquaria or 300-L standing-water aquaria in a controlled environment room; within any experiment, tanks used were the same size.

THE SUNFISH-SNAIL INTERACTION

In this section, we describe the interaction between redear sunfish and these three genera of benthic snails.

TABLE 1. Proportion of shell ingested and ejected by redear sunfish consuming *Physa* and *Helisoma* during 30–45 min feeding experiments. No data were available for *Oxytrema* because they were rejected by redear sunfish after unsuccessful crushing attempts. Percents of shell ingested and ejected did not add to 100% because of the techniques used to arrive at these numbers. Because we could not weigh shell and tissue separately before feeding sunfish, we had to rely on shell mass estimated by subtracting tissue mass (see Fig. 7) from whole snail mass (tissue plus shell). These estimated shell masses contributed, along with incomplete recovery of shell material from stomach and tank, to the discrepancy between our estimates and 100%.

Genus	Snail characteristics		Number of trials	Percent of shell ($\bar{x} \pm SD$)	
	Size (mm)	Number eaten		Ingested	Ejected
<i>Physa</i>	6	20	2	22.3 \pm 12.5	77.1 \pm 7.3
	8	20	2	25.0 \pm 6.3	90.4 \pm 10.0
	10	28	3	11.4 \pm 5.5	89.1 \pm 3.2
Summary statistics		68	7	18.4 \pm 9.3	86.1 \pm 8.2
<i>Helisoma</i>	6	31	4	22.5 \pm 8.0	79.4 \pm 10.3
	8	10	1	13.9	95.7
	10	16	2	6.7 \pm 2.1	70.0 \pm 2.8
	12	3	1	4.4	100.0
Summary statistics		60	8	15.2 \pm 9.8	81.6 \pm 12.8

Because amount of shell ingested may differ among genera and sizes of snails, and hence influence energy per unit mass consumed, we also quantified the proportions of shell ingested by sunfish for *Physa* and *Helisoma*.

Methods

During the initial stages of work, we observed redear sunfish consume *Physa*, *Helisoma*, and *Oxytrema*. In addition, we determined the relative proportions of snail shell ingested and ejected by sunfish during predation. Sunfish were satiated with either *Physa* or *Helisoma*, then starved for 24 h. At this time, all snails, shells, and shell fragments were removed from the tank. 10 snails (within 1-mm length classes) of a single genus were added and the sunfish allowed to feed for 15–45 min. Fish were then removed, anesthetized, and their stomachs flushed with water (Seaburg 1957); based on comparisons with stomach analysis, this technique removed 95–100% of the contents of the stomach. From the stomach contents, snail shell was separated from tissue; this comprised the ingested portion. Ejected fragments of shell were siphoned from the tank. All shells were dried for 48 h at 80° and weighed to the nearest milligram.

Results and discussion

In aquaria, redear sunfish readily ate snails. Fish picked up snails, transferred them to the pharyngeal area, and crushed the shells. Prey rejection occurred infrequently for *Physa* and *Helisoma* but was more common for *Oxytrema*. *Oxytrema* were rejected apparently because they were difficult to crush. Rejection usually followed vigorous crushing attempts (reflected in the movement of the gill covers) by sunfish. For snails not rejected, we could determine the moment a snail was crushed because pieces of shell would be ejected. After crushing, sunfish continued to manipulate the snail in the pharyngeal area. Usually this ma-

nipulation was coupled with movement of the gill covers. Near the end of handling, sunfish stopped this manipulation (we interpreted this as swallowing the snail tissue) and then ejected a large proportion of the shell. This pause also may be associated with grasping the soft parts before spitting out the shell. In mollusc-feeding catostomids, Eastman (1977) postulates that holding the prey (between the chewing pad and the pharyngeal teeth) in the posterior pharynx is a necessary procedure during this "spitting" maneuver to prevent loss of soft tissue. Redear sunfish were efficient in separating the shell from snails they consumed, eliminating \approx 85% of the shell (Table 1). No differences in amount of shell ingested among genera or sizes of snails were apparent.

SELECTIVE PREDATION

Certain shell features of gastropods, including ornamentation, shell thickness, and low spires, have been interpreted as antipredation devices (Kitching and Lockwood 1974, Vermeij 1974, 1976, Heller 1976, Vermeij and Covich 1978). In piscine predators, development of pharyngeal teeth has been linked with crushing and manipulating rigid prey organisms (Vasnetsov 1939, Liem 1973, Liem and Osse 1975, Eastman 1977). Apparently, shell strength and form have influenced development and evolution of the morphology of predators (Zipser and Vermeij 1978, Vermeij 1979a).

In turn, predators choose prey based on shell strength and form. In experiments with crab predators in marine environments, workers (Kitching and Lockwood 1974, Vermeij 1976) have found that snails with thin shells were eaten, whereas those with thick shells were not. In freshwater environments, Vermeij and Covich (1978) postulate that shell form and strength of snails is related strongly to resistance to predation. In those fish species that crush molluscs before ingestion, shell strength would seem to be an important parameter

upon which prey choice should depend. Ivlev (1961) found that carp (*Cyprinus carpio*) chose individuals of *Dreissena polymorpha* with thinner shells over those with heavier shells in laboratory experiments. In a field analysis of food selectivity by carp in Skadar Lake, Yugoslavia, Stein et al. (1975) found that carp preferred molluscs that were thin shelled and possessed some appropriate size and shape. Presumably, thin-shelled gastropods were chosen because they were easier to handle (crush) compared to thick-shelled organisms. Workers have either quantified shell strength, by measuring crushing resistance of shell material (Currey 1975, 1976) or of the complete shell (Vermeij and Currey 1980), or they have documented selective predation (Ivlev 1961, Stein et al. 1975, Kitching 1976). Rarely have both quantities been measured in a single study. In this section we evaluate selective predation by sunfish on snails and the importance of shell strength in influencing selection.

Methods

To determine crushing resistance of these molluscs, we assembled the following equipment. A pancake load cell (Sensotec Incorporated, Columbus, Ohio) with a capacity of 0–440 N was mounted on an Enco Arbor bench press with a capacity of 4400 N. As protection from forces >440 N, we placed the load cell in a machined well across which was laid a flat steel bar that was flush with the load button of the transducer. This bar functioned both as a surface for crushing individual molluscs and a mechanical stop. Output from the transducer was amplified and fed into a Leeds & Northrup chart recorder and calibrated for 0–255 N full-scale deflection.

For estimates of critical loading, snails were measured to the nearest 0.1 mm with dial calipers and individually crushed by slowly and steadily increasing pressure on the animal. Crushing resistance was read directly off the chart paper. Ten animals per 1-mm size-class were crushed. Based on our observations, redear sunfish oriented snails of all three species between their pharyngeal plates so as to crush them across their minimal dimension. Thus, we oriented snails similarly for crushing: *Physa* and *Oxytrema* with their apertures facing down, *Helisoma* on their sides. Preliminary dissection of the internal jaw muscles and pharyngeal apparatus of redear sunfish suggests that these animals possess little ability to manipulate food items once these items are positioned between the pharyngeal plates (G. Dalrymple, Department of Biological Sciences, Florida International University, Miami, *personal communication*). Only vertical movement of the pharyngeal teeth appears possible. Consequently, our press with simple vertical pressure compares well with the operation of the crushing apparatus of redear sunfish.

To evaluate the influence of shell strength on selective predation, we provided redear sunfish with choices

(in separate experiments, all run at 20°C) between two genera or among three genera of snails. To determine if the conclusions generated from these experiments held within a genus, we also ran single-genus size-selection experiments. In all experiments, redear sunfish were separated into five size-classes based on total length: 130–139, 150–159, 180–189, 200–209, and 210–219 mm. Snails were measured along the longest shell dimension (see Fig. 1) and separated into four size-classes that spanned their length range: 6.0–6.9, 8.0–8.9, 10.0–10.9, and 12.0–12.9 mm. Throughout this paper, we identify these length-classes of predator and prey by the lowest value in each range.

For two-genus experiments, we placed 10 individuals of each genus from each of the four size-classes with a redear sunfish (130, 150, 180, 200 mm, total length). For three-genus experiments, five individuals of each genus from each of the four size-classes were placed with redear sunfish. For size-selection experiments, 20 individuals of *Physa* and *Helisoma* (*Oxytrema* was not tested) within each of the four size-classes were placed with sunfish (150, 180, 210 mm, total length). By providing a total of 60–80 snails in a 30 × 60 cm aquarium, we can assume that search time would not be a factor contributing to selection of prey by sunfish. Experiments ended after sunfish had consumed 20–50% of any size within any genus; at this time, remaining snails were retrieved, counted, and measured. For this amount of predation to occur, sunfish typically (in 90% of 141 experiments) were permitted access to snails for 10–45 min. Exposure times up to 120 min sometimes were necessary for the 130-mm size class of predators. Considering all size-classes offered across all selective predation experiments, redear sunfish consumed >60% of any one size-class only 5% of the time. With sunfish eating so few snails during an experiment, the problem with depletion of specific sizes with a subsequent switch to other, more abundant sizes was avoided. Before each experiment, sunfish were satiated with just the snail genera and range of sizes to be tested (to prevent conditioning effects from biasing predator selectivity), then starved for 2 h before snails were introduced. With only 2 h of starvation at 20°, redear sunfish should be at a low level of hunger, and as such, should be quite selective in their choice of prey (as is the case for most predators, see Pyke et al. 1977). Unless otherwise noted, measures of central tendency and variance were medians and 95% confidence limits calculated using Walsh averages (Hollander and Wolfe 1973:33).

Results and discussion

Crushing resistance increased with size within each genus. In comparisons among genera, the crushing data were \log_{10} transformed to account for differences in variance among genera, and then compared using ANOVA. *Physa* were most easily crushed, followed by *Helisoma*, then *Oxytrema* ($P < .005$, Fig. 2). For 10-

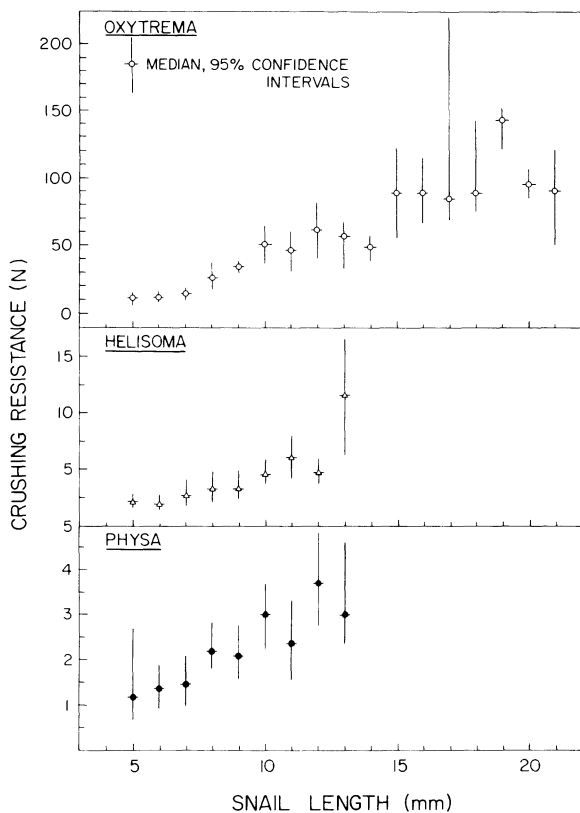


FIG. 2. Crushing resistance, measured with a pancake load cell, as a function of snail size for three genera of snails: *Oxytrema*, *Helisoma*, and *Physa*. 10 animals were crushed per 1-mm size-class. Note differences in vertical scale among the three genera.

mm individuals, crushing resistances were 3, 4, and 52 N, respectively. These differences in crushing resistance were associated with snail genera and not with differences, such as calcium concentration, among snail habitats (see Hunter and Lull 1977 for a review). Crushing resistance did not differ between the two species of *Helisoma*, *H. anceps* and *H. trivolvis* ($P > .05$, two-way ANOVA), so we felt justified in using these species without distinguishing between them in selection experiments.

For nearly all size-classes of redear sunfish, snails in the two-genus comparisons were chosen according to the order: *Physa*, *Helisoma*, and *Oxytrema* (Fig. 3). Although we did not observe the actual predation acts or attempts within each experiment, we believe the results of the selection experiments accurately reflect prey choice by the predator. These results were not just a consequence of sunfish attempting to eat all snails and spitting out those it could not crush. Observations during the course of this work suggested, instead, that redear sunfish rarely rejected a prey once the prey had been grasped. When predation sequence on *Helisoma* was monitored, sunfish consumed the snails they picked

up 98% of the time ($N = 496$ snails eaten). Hence, we believe that thin-shelled *Physa* were chosen preferentially over thick-shelled *Helisoma* and *Oxytrema* without the predator attempting to crush each prey. Specific size-classes (6, 8, 10, or 12 mm) within any genus were not selected by redear sunfish ($P > .05$, Kruskal-Wallis Multiple Comparisons, $N = 77$ experiments). Although differences between *Physa* and *Helisoma* were not as pronounced as in the two-genus comparisons, the three-genus choice tests yielded the same order of preference by sunfish: *Physa*, *Helisoma*, and *Oxytrema* (Fig. 4). As in the two-genus tests, no differences were apparent among sizes of snails eaten ($P > .05$, Kruskal-Wallis Multiple Comparisons, $N = 17$ experiments). In single-genus experiments with a choice among four sizes of snails, redear sunfish rarely chose any one size of snail (see Fig. 12, A panels). Number of *Physa* eaten by 150- or 210-mm sunfish did not differ among snail sizes (Friedman rank sums, $P > .42$, Hollander and Wolfe 1973:138). For 180-mm predators, 12-mm snails were selected over 6- or 8-mm ones (Friedman rank sums, $P < .05$); no other differences were apparent. Number of *Helisoma* eaten by 180- or 210-mm sunfish did not differ among sizes (Friedman rank sums, $P > .05$). For 150-mm predators, 6-mm *Helisoma* were preferred over 10- and 12-mm ones (Friedman rank sums, $P < .05$). Based on 141 separate size-selection experiments (Figs. 3, 4, and 12) in which one, two, or three genera were offered to four size-classes of sunfish, we conclude that this fish predator exhibits little selectivity for specific snail sizes.

As indicated above, snail choice among genera was correlated with crushing resistance: *Physa* (3 N), *Helisoma* (4 N), and *Oxytrema* (52 N). Because redear sunfish crush snails before ingestion, crushing resistance may limit prey exploitation. In contrast, choice among sizes within a genus was not governed by crushing resistance; redear sunfish did not choose the smallest (with lowest shell strength) individuals in these experiments.

OPTIMAL FORAGING: COST/BENEFIT AND ENERGY/TIME RATIOS

To explain redear sunfish choice among genera as well as the lack of preference among sizes, we used an optimal foraging construct operationally described by Werner (1974). This framework provides testable hypotheses regarding prey selectivity by predators. From the predictions of this model (and others, see Pyke et al. 1977 for a review), predators should consume prey with minimal handling time/energy return (time C/B) ratios. (For a full discussion of prey handling see Sherry and McDade 1982.) To evaluate this prediction, we measured handling time as costs and dry mass of snails as benefits to determine if redear sunfish were optimal foragers.

To assess the usefulness of another construct: energy gained per unit time handling (E/T), we quantified both

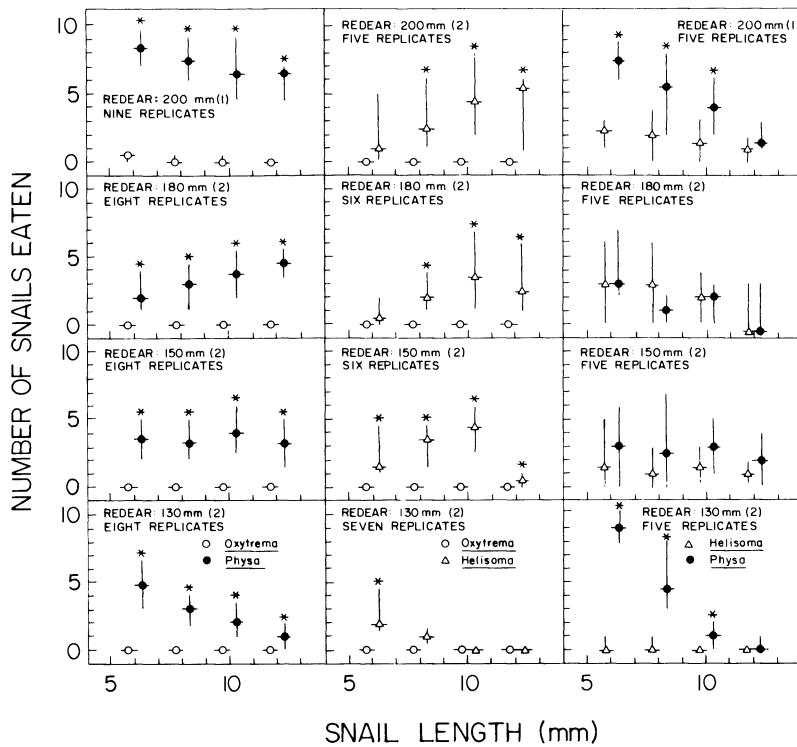


FIG. 3. Number of *Physa*, *Helisoma*, and *Oxytremata* eaten (median and 95% confidence limits) by reदार sunfish (130, 150, 180, and 200 mm, total length). Sunfish could choose between two genera of snails each with 10 prey individuals in each of four size-classes. Numbers in parentheses after fish size represent number of individual fish tested. Asterisks (*) indicate significant differences between genera within a size-class ($P < .05$, Kruskal-Wallis test).

energetic cost of handling and energetic value of prey. First, though time spent in handling should reflect the energetic cost of handling, no a priori reason exists why a linear relationship between time spent handling and energetic outlay should exist. Thus, to assess energy expended in handling, we measured oxygen consumption by sunfish eating snails over a range of handling times. Second, the dry mass of a prey organism should reflect its energetic content. However, energy per unit mass could change with prey size (owing to sexual maturation or some other physiological change) and thus modify predictions of optimal prey size or type. To account for this possibility, we measured energy per unit mass of prey across a range of prey sizes via bomb calorimetry to generate measures of E/T .

Finally, we calculated an energetic C/B ratio (Sherry and McDade 1982) that is simply energetic costs of handling a particular prey divided by the energetic benefit provided by that prey (energetic C/B).

Methods

The time C/B ratio.—After starving sunfish for 12 h at 20°C, we used a stopwatch to measure their handling times for snails. Handling began with prey capture and ended when the predator swallowed the snail. *Physa* and *Helisoma* rarely were rejected once they were grasped by the sunfish; in contrast, *Oxytremata* often

was spit out. For measures of handling time, we used just the amount of time spent in successfully crushing an individual. Thus, estimates for *Physa* and *Helisoma* should reflect actual time spent in consumption, whereas estimates for *Oxytremata* were somewhat conservative, given that rejections were not included. Dry mass was estimated by first killing snails in boiling water, then dissolving the shell with 25% HCl (7 mol/L). When CO_2 evolution from shell dissolution ceased after ≈ 5 min, the tissue remaining was rinsed in distilled water, dried at 80° for 48 h, and weighed to the nearest milligram. We stratified our samples to weigh 10 snails per millimetre length-class.

The energy per time ratio.—Here, optimal prey are those with a maximal ratio of net energetic value of the prey (calculated as prey energy content [in joules] minus the energetic cost of handling [in joules]) per unit handling time (in seconds) for that prey. To determine the amount of energy expended during handling by reदार sunfish 161 to 205 mm (72–170 g, wet mass), we measured their oxygen consumption rates before, during, and after feeding on a particular length-class of snail. Five sunfish were held and tested at an experimental temperature of 20°. After starvation for 48 h, fish were placed individually into a 5-L, aerated experiment tank within a 20° water bath, and allowed to acclimate for 15 min. After acclimation, a plexiglass

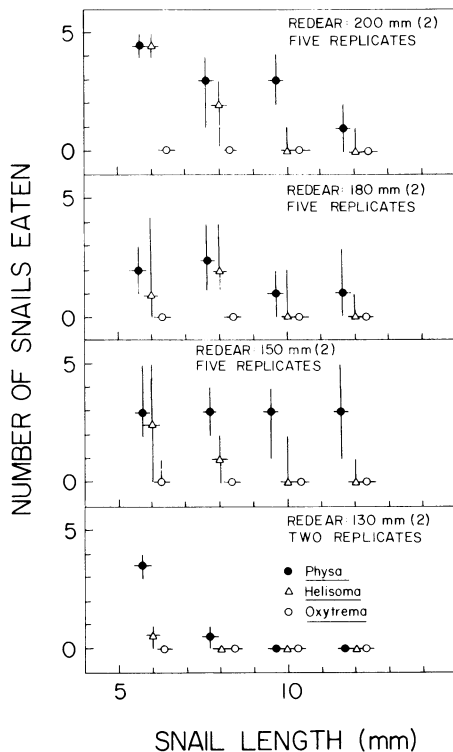


FIG. 4. Number of *Physa*, *Helisoma*, and *Oxytrema* eaten (median and 95% confidence limits) by redear sunfish (130, 150, 180, and 200 mm, total length). Sunfish could choose among three genera of snails, each with 5 prey individuals in each of four size-classes. Numbers in parentheses after fish size represent number of individual fish tested.

top was sealed with stopcock grease onto the tank; an oxygen probe from a Beckman model 0260 oxygen analyzer was placed into the water through a hole in the plexiglas. A magnetic stirrer provided continuous water movement within the tank. Snails were fed to fish through a second hold in the plexiglas top. Because the experiment tank was only 22 cm in diameter and sunfish generally waited at the hole for snails to be dropped, oxygen consumption measurements reflected feeding costs and were not compounded by searching and swimming costs. Output from the oxygen analyzer was monitored continuously with a chart recorder. Records of oxygen consumption were digitized with a Hewlett-Packard 9825B computer and a 9874A digitizer to determine metabolic rate. Prefeeding, feeding, and postfeeding periods were all between 20 and 40 min. Comparisons among slopes from these three periods were determined by testing for homogeneity of slope with $\alpha = .05$ (Sokal and Rohlf 1969:448). In addition to feeding experiments, we also ran two types of controls to evaluate whether we actually were measuring energetic cost of snail consumption. In one set of controls, no snails were fed to sunfish. In a second set, we fed just two to five 8-mm *Physa* (typically, 50–

75 8-mm snails were eaten in an experiment) to determine if any changes in metabolic rate might derive from the excitement at the onset of feeding by redear sunfish (i.e., as separate from the actual metabolic cost of handling and crushing snail prey).

Metabolic rate was first standardized by dividing by the wet mass of redear sunfish in grams (as in Brett 1964), then multiplying by 100 g to produce estimates of oxygen consumption of a "standard" 100-g fish. Because prefeeding metabolic rates varied from experiment to experiment, the increase in metabolic rate (MR) from prefeeding to feeding was used to obtain the energetic cost of handling a particular snail. Oxygen concentration in milligrams per litre was converted to millilitres per litre by dividing by the molecular mass of O_2 (32 mg/mmol) and multiplying by the constant 22.4 mL/mmol. The increase in metabolic rate ($\mu L \cdot L^{-1} \cdot \min^{-1}$) was converted to energy expended per minute per 100-g fish, using an oxyenergetic conversion factor of 20 J/mL (originally expressed as 4.8 calories per millilitre of oxygen in Brett [1973]). During feeding, energy expended ($\text{joules} \cdot \min^{-1} \cdot 100 \text{ g}^{-1}$) = [feeding MR ($\text{mL} \cdot \min^{-1} \cdot 100 \text{ g}^{-1}$) minus prefeeding MR] · [conversion factor (20 J/mL)]; all volumes refer to oxygen. Energy expended per snail during feeding equaled:

$$\frac{(\text{joules} \cdot \min^{-1} \cdot 100 \text{ g}^{-1})(\text{min})}{\text{mean number of snails eaten}}$$

To determine energy content of snails, *Physa integra* and *Helisoma anceps* were collected from sites on the Scioto River and its tributaries, Franklin County, Ohio, USA. Snails were held in standing water aquaria at 19°–21° with algae and lettuce provided ad libitum for as long as 1 d. Individuals were separated into 1-mm length-classes (5–12 mm). Shells were dissolved in 25% HCl and the tissue was rinsed with distilled water and dried for 48 h at 80°. Dried tissue from each size-class was ground with a mortar and pestle and pressed into 6.2-mm diameter pellets (about 80 mg each) with a Parr pellet press. Energy content (joules per gram dry mass) was determined by burning samples in a semimicro oxygen bomb, 22 mL, (Parr, Model 1107) used in conjunction with an adiabatic calorimeter jacket (Parr, Model 1221). For our work, the jacket was used non-adiabatically. This calorimeter jacket was designed to be used with a 360-mL oxygen bomb; thus the procedure for use of the semimicro bomb was modified slightly. Instead of the required amount of water for the semimicro bomb calorimeter, we used 1500 mL of distilled water in the jacket bucket holding the bomb. Otherwise, the instructions (Parr, Manual 144) for operating the semimicro bomb calorimeter and for taking temperature readings were followed. The calorimeter was calibrated ($\bar{x} = 2331 \pm 2 \text{ J}^\circ\text{C}$), using ≈ 0.1 -g benzoic acid pellets, before any energy determinations were made. At least three samples were burned for each size

class, except for 6-mm *Helisoma*, for which only two samples were burned.

The energetic C/B ratio.—With this construct, optimal prey are those with the minimal ratio of the energetic cost of handling (J) per unit of prey energetic content (J). The two parameters necessary for calculating this construct were measured as described in the previous section.

Results and discussion

The time C/B ratio.—Handling time increased exponentially with snail length for all three genera of snails, with *Physa* handled most quickly, *Helisoma* intermediate, and *Oxytrema* least quickly (Fig. 5). Slopes and intercepts followed the order: *Physa*, *Helisoma*, and *Oxytrema*. Slopes for *Helisoma* and *Oxytrema* did not differ (test for homogeneity of slope, $P = .58$) but both were significantly greater than the slope for *Physa* (test for homogeneity of slope, $P < .05$). Handling time was a function of crushing resistance; as crushing resistance increased, handling time also increased, regardless of snail type (Fig. 6). Dry mass of snail tissue increased as a power function of shell size within all three genera (Fig. 7). *Helisoma* provided the most dry mass per millimetre of snail length, with *Physa* intermediate; *Oxytrema* provided the least amount of dry tissue per shell length. By dividing handling time by dry mass of snails, we generated cost/benefit ratios as suggested by Werner (1974). Theoretically, we should be able to predict prey selection

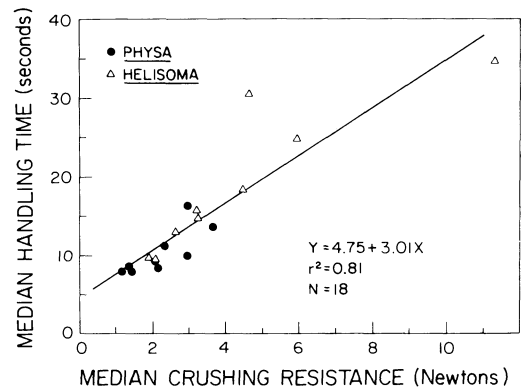


FIG. 6. Median handling time (time from prey capture to complete ingestion) by 180-mm redear sunfish for three genera of snails plotted against median crushing resistance (from Fig. 2) of similar-sized snails. N is the number of points in the regression.

by redear sunfish based on sunfish adding snail genera and sizes to their diet in ascending order of cost/benefit. From calculations of these ratios (Table 2), we would predict the order of selection to be first, selection against *Oxytrema* (greatest difference in C/B); second, selection among sizes within a genus; and finally, weakest selection between *Physa* and *Helisoma* (smallest differences in C/B). In selection experiments, redear sunfish showed selection first against *Oxytrema*, followed by weaker selection between *Physa* and *Helisoma*, and

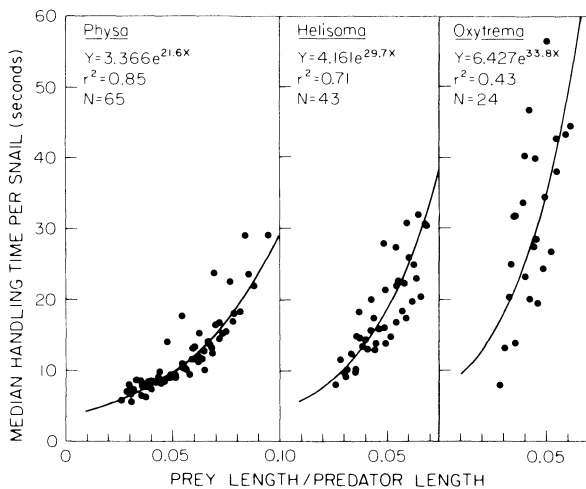


FIG. 5. Median handling time (time from prey capture to complete ingestion) by redear sunfish for three genera of snails as a function of prey length divided by predator length. For all genera, prey length ranged from 5 to 12 mm and predator lengths from 130 to 220 mm. N represents the number of median handling times calculated for each unique combination of individual fish- and snail-length class; sample sizes for the calculation of individual medians were never < 6 and more than 85% were > 10 for *Physa* and *Helisoma*. For *Oxytrema*, each median was based on 1–6 handling times.

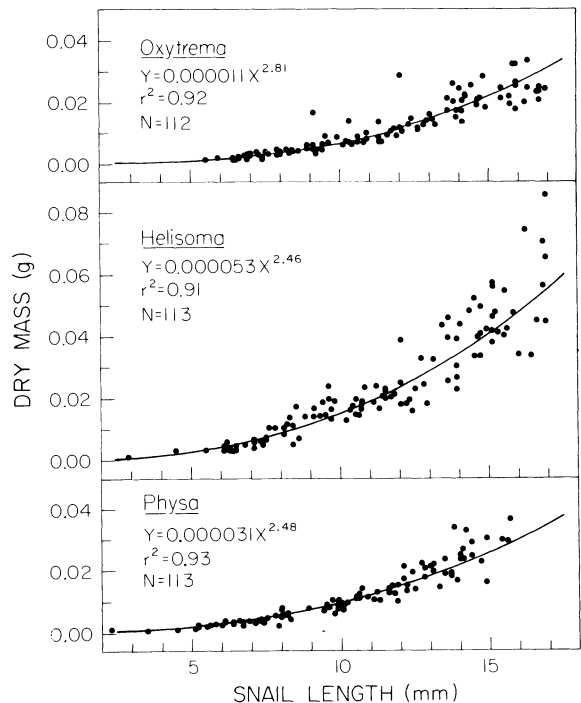


FIG. 7. Dry body mass (without the shell) of three genera of snails as a function of snail (shell) length.

TABLE 2. Median handling times (H_i , in seconds) and two constructs used in predicting optimal prey size and type for 180-mm redear sunfish preying on four size classes of snails. H_i/M = time cost/benefit ratio, where handling time was divided by prey dry mass. E/T = energy gained per unit time, where E = energetic value of the prey (J) minus energetic cost of handling that prey (J) divided by handling time for that prey (s). Dash indicates no data available. Note that the energetic C/B ratio was constant for all sizes of snails at 9.2 mJ/J for *Physa* and 12.6 mJ/J for *Helisoma* (see text).

Genus	Prey size											
	6 mm			8 mm			10 mm			12 mm		
	H_i (s)	H_i/M (s/mg)	E/T (J/s)	H_i (s)	H_i/M (s/mg)	E/T (J/s)	H_i (s)	H_i/M (s/mg)	E/T (J/s)	H_i (s)	H_i/M (s/mg)	E/T (J/s)
<i>Physa</i>	8.6	2.76	7.48	8.4	1.38	12.01	10.0	0.96	16.43	13.7	0.66	20.30
<i>Helisoma</i>	9.7	2.30	7.60	15.7	1.39	11.11	17.8	1.04	13.85	30.5	1.28	15.61
<i>Oxytrema</i>	31.6	15.05	—	28.4	6.45	—	—	—	—	—	—	—

no consistent selection among sizes within genera. Thus, predictions from time C/B were consistent with the strong selection against *Oxytrema*, but not with the order of strength of selection shown between the other two genera and the size-classes.

The energy per time ratio.—For all 50 experiments during which redear sunfish were fed different sizes of either *Physa* or *Helisoma* ad libitum, we found significant increases in metabolic rate based on oxygen consumption (Fig. 8, test for homogeneity of slope, $P < .05$). To determine whether these differences were strictly related to feeding, we measured oxygen consumption through time without feeding snails to the predator (Fig. 8A). In these 10 experiments, we designated the first 20 min as prefeeding, the next 20 min as a simulated feeding period, and the last 20 min as a simulated postfeeding period. Simulated feeding metabolic rate did not increase significantly in four trials and declined significantly in the remaining six (test for homogeneity of slope, $P < .05$). Average percent change in slope for all experiments was -20.6% . We believe this decline occurred as the sunfish, after being transferred to the test container, became more acclimated to the confined environs, resulting in a continually declining metabolic rate (Fig. 8A). In a second control, we attempted to evaluate the importance of excitement as a result of feeding, by feeding two to five 5–8 mm *Physa* during the first 2 min of the feeding period (Fig. 8B). In six of eight trials, metabolic rate did not change (test for homogeneity of slope, $P > .15$); in the remaining two, metabolic rate changed significantly, increasing in one and decreasing in another. Overall, metabolic rates increased $\approx 3\%$ from the prefeeding period to feeding period (only 2–5 snails were fed). From these two sets of controls, we suggest that the excitement of feeding by redear sunfish in our experiments may well account for a 20% increase in metabolic rate.

Metabolic rates declined during the simulated feeding period (when no snails were fed); in addition, metabolic rates changed only slightly during feeding when sunfish were fed just a few snails. Consequently, we conclude that the large increases in metabolic rate dur-

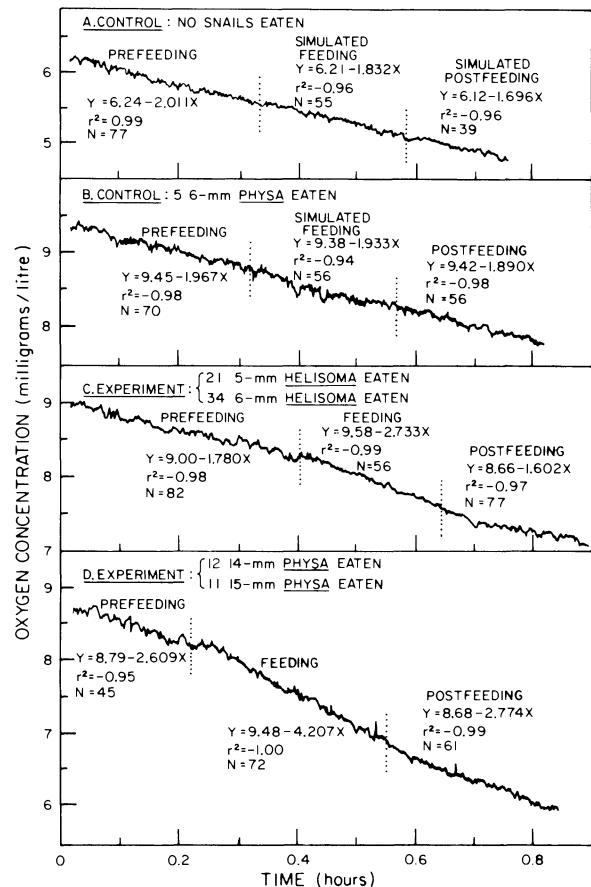


FIG. 8. Chart recorder output of oxygen consumption by individual redear sunfish over time. Each panel represents an independent experiment, with a different fish. Records were analyzed with a Hewlett-Packard digitizer, which recorded ≈ 4 values/min from each period; linear regression techniques were then used to generate equations for the lines denoting oxygen consumption during prefeeding, feeding, and postfeeding periods. For each segment of the line in all panels, N represents the number of data points upon which the regression values were based. (A) No snails fed; feeding and postfeeding periods were artificially designated to serve as controls. (B) Only five 6-mm *Physa* were fed in the first 2 min of the feeding period to serve as a control. (C) Small *Helisoma* were fed ad libitum during the feeding period. (D) Large *Physa* were fed ad libitum during the feeding period.

ing intensive snail feeding must result from crushing and handling these snails, rather than from any experimental artifact or feeding excitement per se. Thus, we expect our estimates of the metabolic cost of handling snail prey to approximate realistic energetic expenditures by redear sunfish (Fig. 8C and D).

Basing calculations of energetic costs on oxygen consumption is only appropriate if respiration is aerobic, not anaerobic. Using lactic acid concentration in muscle tissue as an indicator of anaerobic respiration, Burton (1970) found bluegills at 20° respiring aerobically at environmental oxygen levels greater than about 2.3 mg/L (5.3 kPa partial pressure), and anaerobically at lower oxygen levels. Oxygen concentrations in our experiments were never < 5.0 mg/L, so anaerobic respiration as a result of hypoxia probably did not occur. Possible anaerobic costs of muscle activity in feeding have not been examined (Heath et al. 1980, Jobling 1981). Brett (1964) suggests that activity beyond a certain active metabolic rate (respiration rate at the maximum swimming speed that could be maintained for 60 min) could produce an oxygen debt. The maximum rate of oxygen consumption in our feeding experiments was only 59% of the active rate determined for pumpkinseed (*Lepomis gibbosus*) by Brett and Sutherland (1965). Based on these arguments, we believe that our estimates of the metabolic cost of crushing and handling a snail by redear sunfish using measures of oxygen consumption are not confounded by anaerobic metabolism.

Much like handling time, the energetic cost of crushing both *Physa* and *Helisoma* increased as a power function of the prey/predator length ratio (Fig. 9). In these comparisons, small sizes of *Helisoma* were substantially more expensive to handle than *Physa* (compare intercepts, Fig. 9). And even though rates of in-

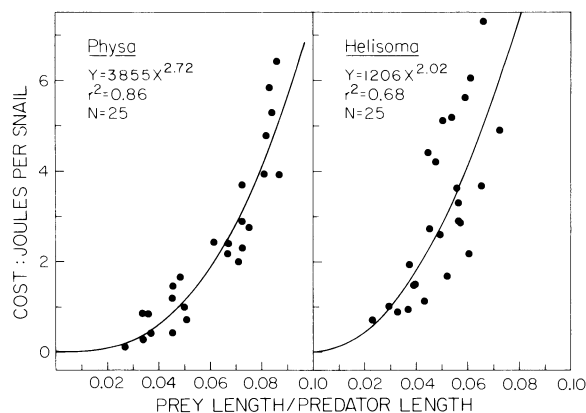


FIG. 9. Energetic cost of handling individual *Physa* and *Helisoma* by redear sunfish as a function of prey length divided by predator length. Energetic costs were estimated from oxygen-consumption experiments ($N = 25$ experiments). For both genera, prey lengths ranged from 5 to 12 mm and predator lengths from 130 to 220 mm.

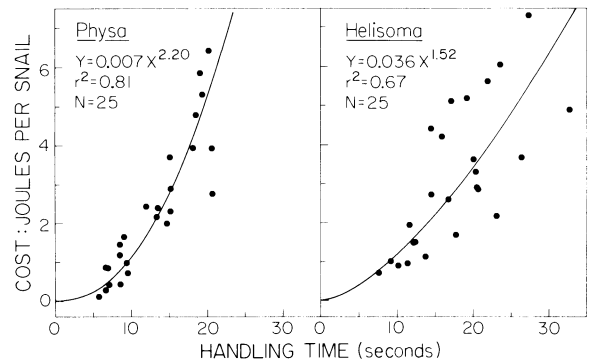


FIG. 10. Relationship between energetic costs of handling (J/snail, Fig. 9) and handling time (Fig. 5) for redear sunfish eating *Physa* and *Helisoma* of different sizes. Snail sizes increase as costs increase. N represents the number of oxygen-consumption experiments completed.

crease for *Physa* exceeded those for *Helisoma* (test for homogeneity of slope, $P < .05$), *Physa* never were more costly to consume than *Helisoma*, regardless of prey/predator length ratios.

To examine the relationship between handling time in seconds and handling energy in joules, we plotted energy as a function of time (Fig. 10). As handling time increased, so did the energetic cost of handling, though the exact relationship between these two variables is unclear. We fitted these data with a power function rather than a linear one for two reasons. First, though coefficients of determination were exactly the same for *Physa* ($r^2 = .81$), values for *Helisoma* were improved substantially by the use of a power curve ($r^2 = .48_L$ [linear fit], $r^2 = .67_P$ [power fit]). And both curves fitted the data equally well (F test for linearity, $F = .58_L, .70_P$ for *Physa*; $F = 2.88_L, 2.89_P$ for *Helisoma*). We used the power curve because it better represented the functional relationship between these two variables. The line for the linear fit crossed the abscissa at a handling time of 5 s for *Physa* and 4 s for *Helisoma*, implying that handling times of this magnitude had zero (or negative) energetic costs associated with them. From these arguments, we conclude that the relationship between handling time and handling energy would be best expressed as a power function, suggesting that handling time may overestimate somewhat the energetic costs of handling small snails and underestimate these costs for large snails.

Significant differences in energy content per dry mass of snail were not apparent among length-classes of *Physa* (ANOVA, $P > .20$) with one exception; the mean value for the 5-mm length-class was significantly higher than that for the 12-mm class (Table 3, ANOVA, Scheffé pairwise comparison test, $P < .05$). No significant differences existed among length-classes of *Helisoma* ($P > .20$). Thus, dry mass accurately reflects energetic content in these snails. For the purpose of generating overall C/B ratios, we used the grand mean for all

TABLE 3. Joules of energy per milligram dry mass of tissue (no shell included) within each size-class of *Physa* and *Helisoma*, estimated by bomb calorimetry. Data are $\bar{x} \pm \text{SD}$.

Length class (mm)	<i>Physa</i>	<i>Helisoma</i>
5	21.20 \pm 0.30	...*
6	20.60 \pm 0.26	...†
7	19.72 \pm 0.14	19.38 \pm 0.23
8	20.40 \pm 0.65	19.72 \pm 0.67
9	19.48 \pm 0.81	19.69 \pm 0.62
10	19.00 \pm 0.81	19.56 \pm 0.25
11	19.17 \pm 0.20	19.89 \pm 0.18
12	18.81 \pm 1.24	20.71 \pm 1.20
Grand mean	19.77 \pm 1.01	19.86 \pm 0.74

* No 5-mm *Helisoma* were available.

† The two burns for 6-mm *Helisoma* appeared incomplete.

length-classes of *Physa* (19.77 J/mg dry mass) and *Helisoma* (19.86 J/mg dry mass).

With these data, we were able to calculate net energy gained per unit time for each genus and size of snail tested by first subtracting the energetic cost of handling (see Fig. 9) from the energetic value of the prey (see Table 3), then dividing this result by handling time (see Fig. 5). As with the time C/B , we should be able to predict prey selection by sunfish based on these predators adding snail genera and sizes to their diet in descending order of E/T . From the E/T ratios plotted in Fig. 11A, we would predict no selection of *Physa* over *Helisoma* (test for homogeneity of slope, $P = .16$), though actual E/T values for *Physa* were usually higher than those for *Helisoma* (Table 2). Hence, perhaps one could argue that E/T accurately predicted the weak species selection of *Physa* over *Helisoma* in two- and three-genus selection experiments. However, E/T values for *Physa* were much larger than for *Helisoma* for snail lengths of 10 and 12 mm. Yet in our selection experiments we did not find stronger selection for *Physa* in these size-classes (see Figs. 3 and 4). Across sizes within any genus, we find that E/T values predicted that large size-classes should be preferred over small size-classes in any choice tests (ANOVA, $P < .05$, Fig. 11A). Yet redear sunfish did not consistently choose any snail size within single-genus experiments. Hence, we conclude that the ratio of energy gained per unit handling time provides results inconsistent with our selection experiments, predicting no selection between *Physa* and *Helisoma* when weak preference occurred, and strong selection among size-classes when no size preference was observed.

With these same data, we also were able to calculate an energetic C/B by dividing metabolic costs of handling (see Fig. 9) by prey energy content (see Table 3). As with other constructs, we should be able to predict prey selection by sunfish based on these predators adding snail genera and sizes to their diet in ascending order of the energetic C/B . From the energetic C/B

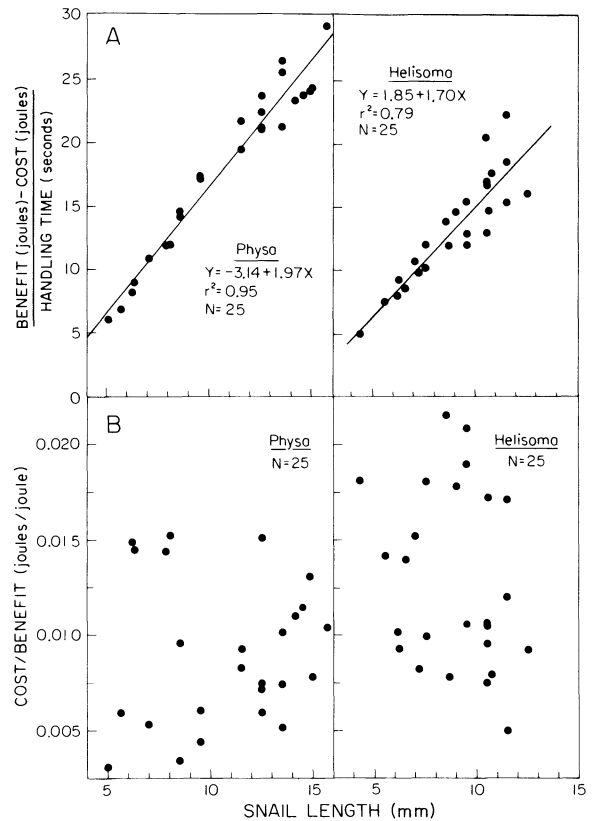


FIG. 11. (A) Energetic benefit (from Table 3) minus energetic cost (from oxygen-consumption experiments) divided by handling time (from Fig. 5) or E/T , as a function of snail length, for redear sunfish eating *Physa* and *Helisoma*. (B) Energetic cost of handling (from oxygen-consumption experiments)/benefit (from Table 3) ratios, as a function of snail length, for redear sunfish eating *Physa* and *Helisoma*. Individual points in all panels were derived directly from individual experiments estimating metabolic rate during feeding for sunfish; these values were not generated from the equations in Fig. 9. In each panel of A and B, N represents the number of oxygen-consumption experiments completed.

ratios (J/J) plotted in Fig. 11B, we would predict selection for *Physa* over *Helisoma* (9.2 vs. 12.6 mJ/J, ANCOVA, $P < .05$) though the absolute differences between genera were small for this ratio, and no selection among sizes within either *Physa* (ANOVA, $P = .34$) or *Helisoma* (ANOVA, $P = .87$). This agrees with the results of the size-selection experiments in which *Physa* were either chosen or equally preferred when compared to *Helisoma*, and in which there was no consistent selection among sizes within either genus.

To demonstrate the different predictions generated by the time C/B , E/T , and the energetic C/B , we plotted all ratios plus the results from our size-selection experiments in Fig. 12. Time C/B decreased by nearly 300% as snail size increased, providing a prediction that largest snails should be chosen. E/T values increased by nearly 600% (from 5 to 30 J/s) for 210-mm

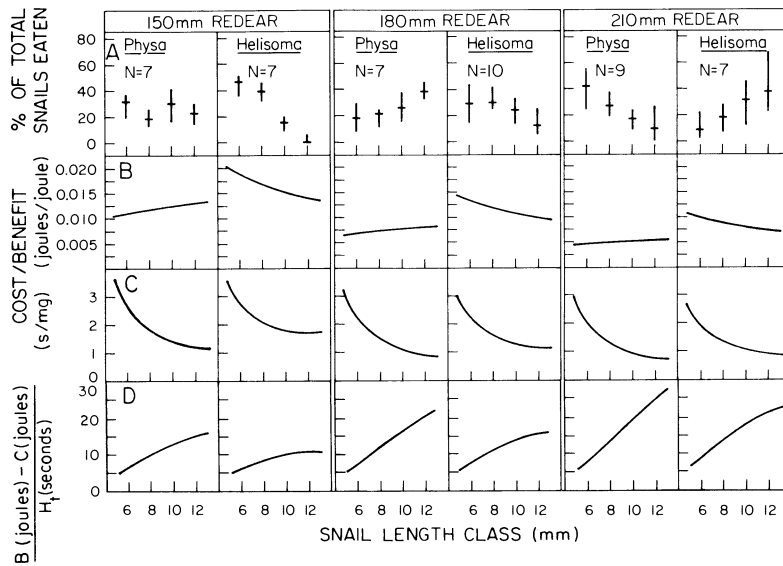


FIG. 12. A Panels: Percent (median and 95% confidence limits) of the number of *Physa* and *Helisoma* within four length-classes eaten by redeer sunfish. Sunfish could choose among four (either *Physa* or *Helisoma*, $N = 20$ per length-class) classes with equal numbers of snails in each class. At least two sunfish individuals were represented within any one length-class of predator, and N represents the total number of experiments completed for each combination of snail genus and fish size. B Panels: Energetic cost/benefit ratios for redeer sunfish eating different genera and sizes of snails. Estimates of energetic cost of handling (values generated from the equations given in Fig. 9) were divided by the energy content of snails (Table 3). C Panels: Time cost/benefit ratios for redeer sunfish eating different genera and sizes of snails. Handling time (s) per dry mass (mg) of snails (s/mg) derive from estimates of handling time (Fig. 5) and dry mass of prey (Fig. 7). D Panels: Energy per unit time (E/T) ratios for redeer sunfish eating different genera and sizes of snails. E/T estimates were calculated by subtracting the energetic cost of handling (values generated from the equations given in Fig. 9) from the energetic content of snails (Table 3) and dividing the result by handling time (values generated from the equations given in Fig. 5).

sunfish eating *Physa*, suggesting that largest snails should be preferentially chosen. In contrast, the energetic C/B changed little (<50%) over the size-range tested, predicting little, if any size selectivity, a result consistent with the outcome of our size-selection experiments. Surprisingly, differences between 1 and 3 s/mg in the case of the time C/B and between 5 and 30 J/s in E/T were not sufficient to cause selection. Only the energetic C/B successfully predicted the lack of size selectivity within any genus and the weak selection for *Physa* over *Helisoma* in two-genus choice experiments.

CONCLUSIONS

Although time C/B was not a good predictor of snail selection by redeer sunfish, it was used successfully by Kislalioglu and Gibson (1976) to predict prey selection by 15-spined sticklebacks (*Spinachia spinachia*). They found sticklebacks in the field to be eating the size ranges of prey predicted as optimal from time C/B . In that system, for any one size fish at a particular hunger level, H_i/M varied as much as 30 s/mg over the sizes of prey eaten, whereas redeer sunfish feeding on snails had H_i/M that varied only from 1 to 3 s/mg. Werner (1974) also found H_i/M to vary by as much as 30 s/mg for bluegill feeding on *Daphnia* and fish fry. As differences in H_i/M between prey become large, discrimi-

nation by predators probably becomes easier. In addition, the advantage gained by distinguishing between these prey increases, relative to those prey with small differences in H_i/M . So although we see a 300% difference in H_i/M across snail sizes in our system, the absolute magnitude of the difference is not great enough to allow, or possibly to necessitate, selection. However, Gillen et al. (1981) documented a similar range of H_i/M (0-3 s/mg) and found an esocid predator selecting the optimal sizes of bluegills and minnows (*Notropis* spp. and *Pimephales promelas*). As suggested by Orians (1981), theoretical predictions of optimal diet may not be borne out by experiments because predators (1) have incomplete knowledge of the prey resource, (2) use currencies other than energy for diet choice, and (3) possess imperfect perceptual abilities. In our experiments run in confined aquaria, we believe that the predator did have complete knowledge of the prey present. In terms of currency, redeer sunfish appeared to be using energy rather than time as a measure of handling costs. If only time C/B data were available, we might have concluded that sunfish, by not choosing prey with minimal C/B , could not perceive the measured differences among sizes of prey. However, based on energetic considerations, differences among snail sizes were perhaps too small to generate sufficient se-

lection pressure to improve perceptual abilities. Given that certain fish predators can choose prey consistent with time C/B (Kislalioglu and Gibson 1976, Stein 1977, Gillen et al. 1981), we can either conclude that these predators differ in their discriminating abilities or that time is the currency upon which prey choice decisions are made. And until we are aware of the capabilities of a particular predator, in terms of perceptual abilities and relevant currency, we cannot predict accurately prey choice based on C/B approaches.

Because E/T and energetic C/B provide measures of actual costs and benefits to the predator, we might expect them to have greater general utility in predicting diet selection than H/M . Yet E/T measures provided predictions in direct contrast to the results from our selection experiments. The energetic C/B ratio seemed to provide predictions consistent with our experiments, but the general utility of this construct still remains in doubt. Might predators actually add prey to their diet based on a joules expended to joules return ratio? Certainly, a ratio that incorporates both the net energetic value of a prey and the time required for handling would seem most appropriate (and is justified in the theoretical literature, see Pyke et al. 1977). Yet sunfish did not choose prey based on this ratio. Hence, as above, we have no standards against which we can judge the discriminating abilities of fish predators. Without these standards, and given that differences in E/T of 600% were not sufficient to generate selectivity, these constructs are of little predictive value. Questions such as which prey will be chosen cannot be answered with simple estimates of cost per benefit or energy per time per prey type, because investigators do not know the discriminatory abilities of their predators (nor the currency upon which they are making decisions, see Orians 1981). Whether based on time or energy, C/B or E/T values alone, without empirical results from selection experiments, provide little insight into the intensity of prey selection by predators.

ACKNOWLEDGMENTS

We thank L. Greenwald for his help and guidance during the metabolic studies. C. W. Sechnick and C. Schlichting provided technical support. C. H. Boggs, K. M. Brown, P. Cochran, A. P. Covich, R. W. Elnor, G. G. Mittelbach, E. Rankin, and J. A. Rice provided careful, constructive reviews of an early draft of this manuscript; we appreciate the statistical help and expertise of S. Klosiewski. This research was supported by the National Science Foundation, DEB 77-16167.

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