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Smashing Energetics: Prey Selection and Feeding Efficiency of the Stomatopod, *Gonodactylus bredini*

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With 5 figures

Abstract

The simplest prey-selection model predicts that predators select prey to maximize energetic benefit and minimize handling time. We tested whether or not energetic indices predict stomatopod preference for prey. The energetic indices included: 1) the ratio of energetic return (mass of prey tissue, M) per unit handling time (feeding duration, T); 2) the ratio of energetic benefit (caloric value of prey tissue, E) to energetic cost (caloric value of energy expended, C); and 3) the ratio of net energetic benefit (caloric value of food minus the caloric value of energy expended, NE) to handling time.

Stomatopods, characterized by highly specialized raptorial feeding appendages, strike and smash the shells of prey such as snails. The prey-capture strike is one of the fastest known animal movements. Stomatopods, presented with snail shells of three size classes (5—6, 8—9, 11—12 mm in length), preferred intermediate and small snails. Oxygen consumption increased an average 2.5-fold above resting rates during feeding and increased linearly with strike frequency. The energetic cost per strike was $1.6 \pm 0.2\ \mu l\ O_2$. Stomatopods obtained more snail tissue from smashing larger snail shells. However, longer handling times were required to open shells of greater size. To obtain snail tissue, stomatopods struck larger shells a greater number of times. Strike frequency (0.72 strikes/min) was independent of shell size. The amount of snail tissue obtained per strike (0.044 mg/strike), M/T, NE/T, and E/C were all independent of snail size. The mean energetic benefit per strike (0.23 calories/strike) was 13-fold greater than the energetic cost per strike (0.017 calories/strike). Energetic cost, energetic benefit and handling time appear not to be the sole variables that explain stomatopod prey selection.

Introduction

The simplest model of optimal diet and prey selection assumes that fitness is linearly related to the net rate of energy intake (Pyke 1984). Consequently, fitness is maximized when the net rate of energy intake is maximized. To test this prey-selection model, the energetic benefit of prey (E), the cost of prey handling (C) and the time spent handling (T) must all be measured. Stomatopods, more

commonly known as mantis shrimps, are appropriate experimental animals for testing this model because: 1) we anticipated a large, measurable energetic cost of prey handling due to its nature, smashing shells; 2) prey handling occurs in discrete units, strikes on the shell; and 3) handling time varies widely from a few min to several h (CALDWELL & DINGLE 1975; CALDWELL et al. 1988).

Stomatopods are characterized by highly specialized second thoracopods or raptorial feeding appendages (KUNZE 1981). Mantis shrimps use these raptorial appendages in a ballistic strike to capture and process prey. The strike is one of the fastest known animal movements, lasting only 4—8 ms (BURROWS 1969). Stomatopods, inhabitants of intertidal and other shallow waters of tropical and subtropical seas, have been divided into two predatory groups, smashers and spearers (CALDWELL & DINGLE 1975). Spearers often feed on soft-bodied prey, such as fish, impaling their victim with a jab of the sharp dactyl spines of the raptorial appendage. Smashers typically prey on hard-bodied prey, such as crabs and snails, striking with a heavily calcified raptorial appendage. We selected one such smashing species, *Gonadactylus bredini*, for the present study.

A common shallow-water denizen, *G. bredini* is found throughout the Caribbean inhabiting cavities in hard substrates and feeding on various crabs, gastropods, and hermit crabs. Stomatopods commonly travel 1—2 m away from their cavities to find prey, with some individuals reported to exceed 4 m (CALDWELL et al. 1988). Individual animals have been observed making 10—12 foraging expeditions per day. In intensively populated areas, predation by *G. bredini* can affect the structure of gastropod and hermit crab populations. *G. bredini*, studied in Panama, significantly reduced populations of the snail *Cerithium* in the prey size range of 2—16 mm (CALDWELL et al. 1988). *Gonadactylus chiragra*, a stomatopod with a similar natural history, preferentially selects snails based on size. CALDWELL & DINGLE (1976) found that *G. chiragra* selects snail sizes to yield the greatest amount of snail tissue per strike. These results suggest that a simple prey selection model may be appropriate. However, no measurement of the energetic cost of smashing has been attempted.

In the present study we examined prey selection in stomatopods and the energetic cost of striking. We measured three energetic indices of prey selection for *G. bredini* feeding on one species of snail which varied in size by 2-fold. These indices included: 1) the ratio of energetic return (mass of prey tissue, M) per unit handling time (feeding duration, T); 2) the ratio of energetic benefit (caloric value of prey tissue, E) to energetic cost (caloric value of energy expended, C); and 3) the ratio of net energetic benefit (caloric value of food minus the caloric value of energy expended, NE) to handling time. We tested whether or not *G. bredini* select prey based on the maximization of one or all three indices.

Methods

Animals

8 stomatopods (*Gonadactylus bredini*) used in this study were collected off the Atlantic coast of Panama in February 1987. The animals weighed 2.51 ± 0.09 g, SE and were 52.1 ± 0.9 mm, SE in length. Stomatopods were housed individually in small plastic containers (ca. 800 ml) at a constant

temperature (25 °C) for two weeks before the experiment. During the experiment animals were housed in clear, extruded cast tubing (inside diameter = 5.7 cm, outside diameter = 6.4 cm, length = 14.5 cm). An opaque tube, 7 cm in length and 2.5 cm in diameter, was glued with silicon sealant 3 cm from an opening to provide a crevice to shelter the stomatopod. To effectively seal the stomatopod in the tube, while not disrupting water flow, fine nylon screen was placed on the ends of tube and secured with rubber bands. Individual tubes were numbered and stored in a large aerated tank (ca. 120 l). Molting or breeding stomatopods were not used. Snails, *Tegula funebralis*, were collected at Pillars Point, San Francisco, California.

Prey Selection

Three snails, one from each size class (i. e. 5—6, 8—9, and 11—12 mm in diameter), were presented simultaneously to stomatopods. Stomatopods and prey were observed continuously for 1 h. Shells were examined after 3 and 12 h to determine if a snail was completely consumed. An observer recorded the first prey size attacked and consumed. An attack was defined as a raptorial strike damaging the shell of the prey. A snail was considered eaten if the ventral portion (i. e. the second whorl) of the shell was pierced or if the shell was completely split open. We defined "preference" based on snail consumption. Stomatopods were fed 3 snails once a day every 3—4 days. All animals were fed snails for 5 trials before data were collected to ensure sufficient experience with the prey.

Oxygen Consumption

Apparatus

A closed system was used to measure oxygen consumption ($\dot{V}_{O_2}$) during rest and feeding. The metabolic chamber was the same size used to house the animals. A peristaltic pump (Cole-Palmer) circulated artificial sea water (s. g. 1.022) through a metabolic chamber and past an oxygen-electrode chamber at 156 ml/min. The volume of the metabolic chamber, probe chamber, and tubing totaled 400 ml. The metabolic chamber was immersed in a water bath (Fisher Thermabath) maintained at 27 °C. Oxygen concentration was measured with an oxygen electrode (Orion model 97—08) interfaced to an ion/gas analyzer (Orion EA 920). O_2 concentration was recorded continuously on a chart recorder (Omega X—Y).

Protocol

Sterilization. Considerable care was taken to maintain control of microbes throughout the experiment. Artificial sea water from a tank source was heated for 2 h at 90 °C after which the specific gravity was checked. Water was stored a maximum of 24 h before use in an experiment. If this time was exceeded, the water was reheated. The electrode chamber, metabolic chamber, and tubing were sterilized for 8 h in distilled water at a constant temperature of 80 °C. After heating, the system was cooled and soaked in a 70 % ethanol solution for 15 min. System components were then thoroughly washed and soaked with water before use.

Each stomatopod was immersed in 200 ml of sterilized sea water for 30 min prior to placement in the metabolic chamber. The sterilized sea water contained an antibiotic solution (1 ml/l) consisting of penicillin (10,000 U/ml) and streptomycin (10 mg/ml, Sigma Chemical Co.).

Black turban snails, *Tegula funebralis*, were sorted into the three size classes, placed into sterilized sea water and stored in a refrigerator at 10 °C for 8 h. At the end of this period dried snails were refrigerated for 1 h. This procedure caused the snails to seal their opercula tightly making them a more realistic prey item. Snails were subsequently quick frozen over dry ice and stored at —10 °C.

Resting oxygen consumption. The sterilized system was placed in a water bath maintained at 27 °C. The O_2 electrode was calibrated in air for 15 min, while the water was aerated vigorously and the temperature of the system equilibrated. Subsequently, the baseline oxygen concentration was monitored for 15 min to ensure the absence of microbial $\dot{V}_{O_2}$. After placing the stomatopod into the chamber and shielding it from visual disturbance, $\dot{V}_{O_2}$ was measured for 4 h. The stomatopod was removed at the end of this period and the water in the metabolic chamber was poured into a sterilized beaker. The water from the beaker was poured back into the chamber and the system resealed. Any subsequent microbial $\dot{V}_{O_2}$ was measured for 40 min. Only trials with a microbial $\dot{V}_{O_2}$ less than 15 % were accepted.

Feeding oxygen consumption. The procedures employed in the measurement of $\dot{V}_{O_2}$ during feeding were similar to those used for the determination of resting $\dot{V}_{O_2}$ except for the addition of a prey item. As a single snail from one of three size classes was introduced into the metabolic chamber, the system was inverted vertically for 6 min. This procedure delays the onset of feeding until the system becomes mixed and stable. A hydrophone, placed next to the metabolic chamber, was used to detect the strike of the stomatopod. An experiment ended when: 1) the animal finished consuming the snail and discarded the shell remains; 2) the animal did not strike the snail for 1 h or; 3) the experiment lasted 7 h. Aerated, sterilized water was added to the system if oxygen concentration decreased below 3.5 ppm ($\approx$ 90 torr, the upper critical P_{O_2} reported for stomatopods by INNES, 1985). Upon terminating the feeding experiment, the stomatopod was removed and microbial $\dot{V}_{O_2}$ was measured. Only trials with a microbial V_{O_2} less than 15 % were accepted.

Data Analysis

Oxygen concentration and strike records were digitized on a tablet (SigmaScan) interfaced with a computer (IBM/AT). Data for the entire project were analyzed using an electronic spreadsheet (Lotus 1-2-3). Unless specified, ANOVA was performed to determine statistical significance.

Energetic Indices

We calculated three energetic indices that can be used to evaluate feeding energetics and as criteria to predict prey selection.

1) *Energy return/handling time.* Prey could be selected on the basis of their energetic return (M) per unit handling time (T), M/T, where M represents the dry mass of prey tissue and T equals the duration of feeding. To obtain an average dry mass of tissue per size class, 30 snails of each size class were sterilized and frozen. After freezing, the snails were wrapped in aluminium foil and desiccated in a small oven at 70 °C for 10 h. After desiccation and careful removal of tissue, size (to the nearest 0.1 mm), shell mass and tissue mass were measured. Dry mass of the snails used in the feeding experiments was estimated from these data. Remains of snails from feeding-metabolism experiments were frozen and then desiccated using the same procedure. The dry mass of the remains was then subtracted from the estimated dry mass to yield the tissue obtained. Handling time (min) was measured from the beginning to the end of a feeding trial.

2) *Energy gained/energy expended.* Energy gained/energy used (E/C) is an efficiency index that includes the actual energetic cost of handling. The ratio compares the energetic benefit of the prey (E) to energetic cost of its handling (C). E represents the caloric value of prey tissue, whereas C is calculated from the calories of energy expended. E was determined from the mass of the prey consumed by using caloric equivalents determined for *Tegula* (1 mg of tissue $\approx$ 5.2 kcal; PAINE 1971). C was calculated from the $V_{O_2 net}$ ($V_{O_2 net} = V_{O_2 feeding} - V_{O_2 rest}$) by assuming 1 l $O_2 \approx$ 4.8 kcal (KING 1957).

3) *Net energy gain/handling time.* The index of net energy gain/handling time (NE/T) includes both the energetic benefit and cost of prey capture along with the time spent in handling. The ratio compares the net energetic benefit (NE) to handling time (T), where NE represents the caloric value of prey minus the caloric value of energy expended (E—C).

Results

Prey Selection

When given a choice of small (5—6 mm), medium (8—9 mm) or large (11—12 mm) prey, stomatopods first attacked prey of medium and large size (Fig. 1, ANOVA, $F_{(2,26)}$ = 12.8, p < 0.001). Within the size range of stomatopods used, body mass had no significant effect on which prey size was selected.

Prey size also had a significant effect on which prey stomatopods preferred to consume (ANOVA, $F_{(2,26)}$ = 15.1, p < 0.001, Fig. 1). Prey of medium size
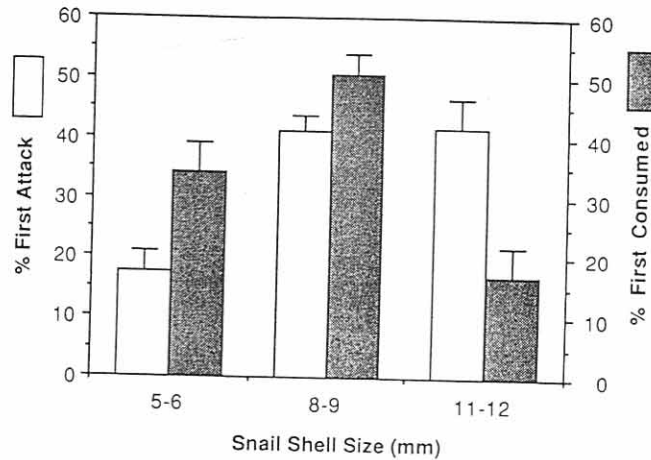
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Fig. 1: Stomatopod prey selection as a function of snail shell length. Stomatopods were presented with a choice of snails from each of three size classes. Open columns: % of prey first attacked; solid columns: % of prey first consumed or finally "preferred". Bars: ± 1 SE

were preferred more frequently than smaller (Scheffé pairwise comparison test, F = 3.6, p < 0.05) or longer (F = 14.0, p < 0.05) prey. Again, body mass of the stomatopod had no significant effect on which prey size was preferred.

Resting Oxygen Consumption

Oxygen consumption of resting stomatopods ($\dot{V}_{O_2rest}$) declined during the initial 2—3 h of monitoring. Mean $\dot{V}_{O_2rest}$ rates were calculated for the last 30 min of the 4-h trials. $\dot{V}_{O_2rest}$ for individuals were obtained by averaging 2—3 trials. Resting stomatopods consumed 0.105 ± 0.005 ml O_2/h, h, SE. $\dot{V}_{O_2rest}$ was within the 95 % confidence interval of resting rates reported for crustaceans of comparable mass (Wolvekamp & Waterman 1960). $\dot{V}_{O_2rest}$ was not a function of body mass over the small range examined.

Feeding Energetics

Animals housed in the metabolic chamber of the respiratory system fed within 10 min of introducing the prey item, frozen *Tegula*. Prey were invariably processed and eaten in the furnished cavity and not in the exposed chamber.

Oxygen consumption versus strike frequency. Oxygen consumption during feeding ($\dot{V}_{O_2feeding}$) increased an average 2.5-fold above $\dot{V}_{O_2rest}$ with a maximum increase of 4.6-fold. Stomatopods striking frequently within a 10-min interval had greater rates of consumption than those striking infrequently; this pattern was observed in each trial. $\dot{V}_{O_2net}$ increased linearly with strike frequency (f, strikes/min; Fig. 2); $\dot{V}_{O_2} = 0.097 f + 0.063$ ($r^2 = 0.28$; p < 0.001).

The increase in $\dot{V}_{O_2feeding}$ depended on snail size as well as strike frequency. Animals eating large snails showed a greater increase in $\dot{V}_{O_2net}$ for a given increase in strike frequency (11—12 mm; $\dot{V}_{O_2net} = 0.117 f + 0.048$; $r^2 = 0.38$) compared to

Fig. 2: Net rate of oxygen consumption ($\dot{V}_{O2net}$) as a function of strike frequency for feeding on small (5—6 mm), medium (8—9 mm) and large (11—12 mm) snails. $\dot{V}_{O2net}$ increased linearly with strike frequency. The y-intercepts represented $\dot{V}_{O2net}$ that is strike independent. $\dot{V}_{O2net}$ and strike frequency were calculated over 10-min intervals
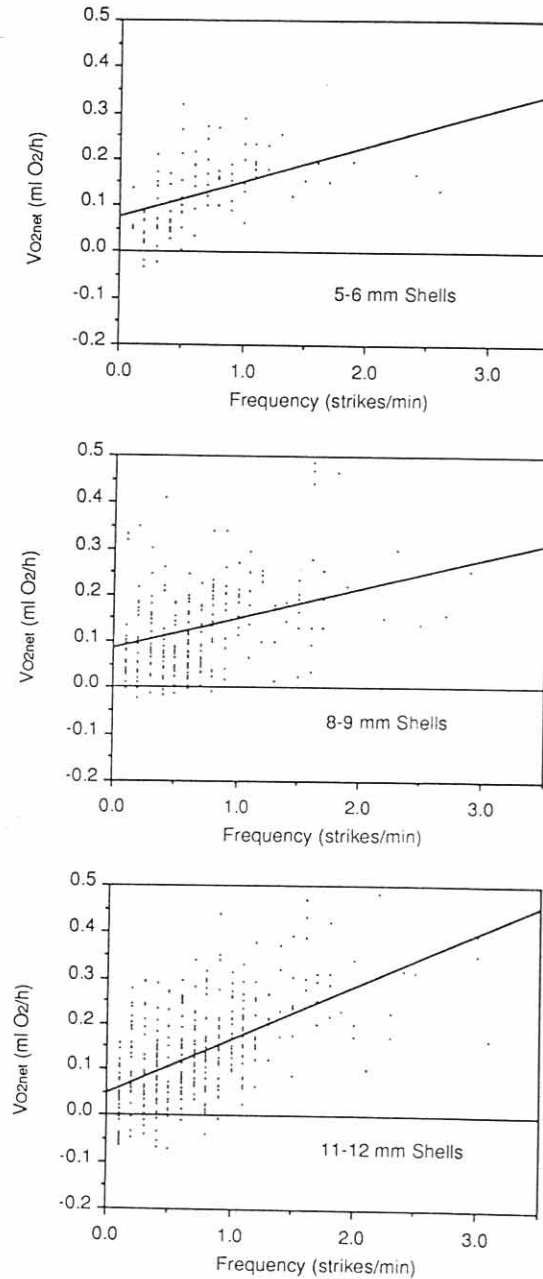
those eating intermediate (8—9 mm; $\dot{V}_{O2net} = 0.064 \, f + 0.086$; $r^2 = 0.13$) and small snails (5—6 mm; $\dot{V}_{O2net} = 0.76 \, f + 0.076$; $r^2 = 0.24$; Fig. 2; test for homogeneity of slopes, $p < 0.001$). The 95 % confidence intervals for the slopes of the $\dot{V}_{O2net}$ versus strike frequency function were: ± 0.026, 0.019 and 0.013 for the small, medium and large shells, respectively.
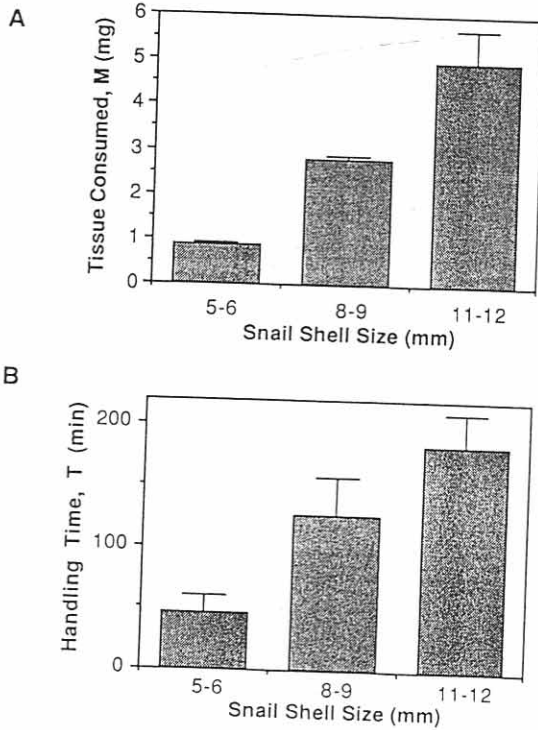
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A

Fig. 3: Benefits and costs of stomatopod prey selection. Stomatopods were presented with a single snail from one size class. A. The amount of snail tissue consumed (M) as a function of snail shell length. B. Handling time (T) required to consume prey as a function of snail shell length

B

Cumulative feeding energetics. Stomatopods obtained more tissue from larger snails (Fig. 3A, $F_{(2,20)}$ = 21.9, p < 0.001), but required proportionally longer handling times to open shells of greater size (Fig. 3B, $F_{(2,20)}$ = 7.8, p < 0.003). To obtain the snail tissue, stomatopods struck larger shells a greater number of times (Fig. 4, $F_{(2,20)}$ = 21.4, p < 0.001). The net amount of oxygen consumed by stomatopods over the entire feeding bout (V_{O2net}) increased in proportion to snail size (Fig. 4, $F_{(2,20)}$ = 17.5, p < 0.001). The average frequency of striking (0.72 ± 0.024 strikes/min, SE) and the amount of snail tissue obtained per strike (0.044 mg/strike) were both independent of snail size.

Fig. 4: Comparison of number of strikes and net oxygen used to consume prey of different size. Open columns: number of strikes required; closed columns: net amount of oxygen consumed (oxygen consumed during feeding — oxygen consumed during rest); bars: ± 1 SE
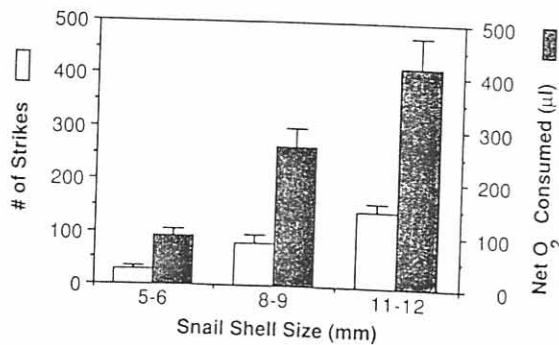
Fig. 5: Prey selection indices as a function of snail shell length. A. Energetic return (M: dry mass of prey tissue) per unit handling time (T). B. Energy gain/ energy used compares energetic benefit of prey (E) to energetic cost of handling (C). E = caloric value of prey tissue, C: calculated from calories of energy expended in handling. C. Net energy gain (NE)/handling time (T); NE: caloric value of prey minus caloric value of energy expended in prey handling (E—C)
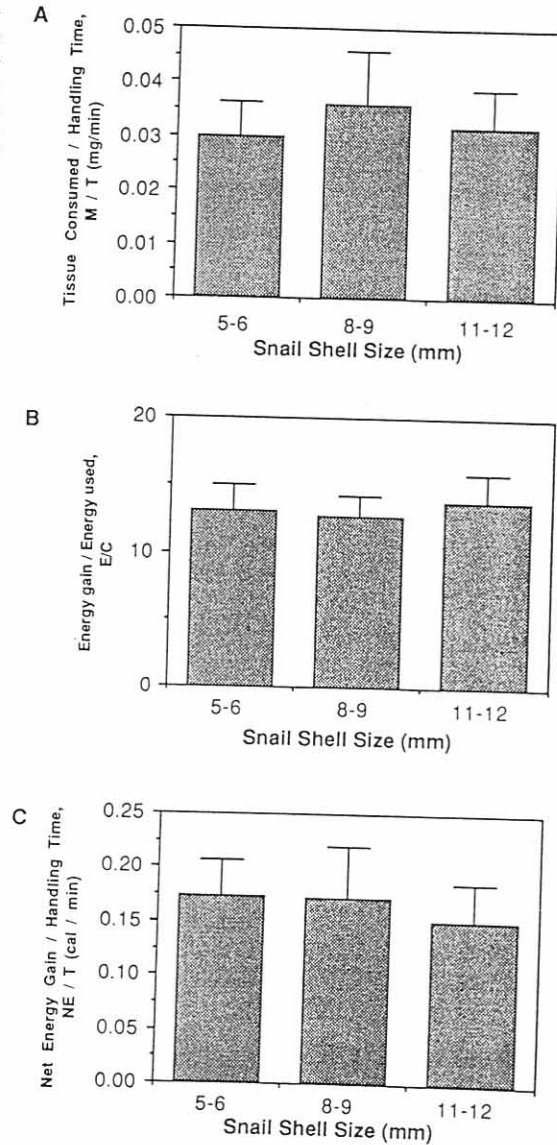
The amount of tissue consumed per unit handling time (M/T) was also independent of snail size (Fig. 5A). The mean energetic benefit per strike (0.23 calories/strike) was 13.2-fold greater than the energetic cost per strike (0.017 calories/strike). The ratio of energetic benefit to energetic cost (E/C) was independent of snail size (Fig. 5B). Likewise, the ratio of net energetic benefit to handling time (NE/T) did not depend on snail size (Fig. 5C).

Discussion

Prey Selection

Stomatopods engaged in selective predation on gastropods (Fig. 1). Other crustaceans show a similar feeding behavior. Crabs have been found to prefer thin-walled snail shells to thick ones (Kitching & Lockwood 1974; Vermeij 1976; Ziipser & Vermeij 1978). When given a choice of prey the stomatopod, G. bredini (52 mm), avoided the largest snails and preferred to consume the intermediate and small sizes (Fig. 1). Caldwell et al. (1988) found similar results for smaller G. bredinii (35—45 mm) in the field. In nature, G. bredini eats an estimated 10 snails per day in the 2—8 mm size class, whereas in the 9—16 mm size class they only consume 1/3 as many snails. Thick-shelled snails larger than 17 mm are rarely selected. A preference for intermediate and small snails is not unique to G. bredini. Although capable of smashing 30 mm shells G. chiragra prefers prey only 1/3 the size (Caldwell & Dingle 1976).

Based on laboratory and field data, G. bredini appear to prey selectively on intermediate and small snail shells. Three alternative explanations may account for the initial attraction and subsequent rejection of larger shells. First, stomatopods might not have been able to smash large shells. However, in feeding experiments where only shells from a single size class were presented, stomatopods were successful in opening the largest shells. Second, our feeding regime could have resulted in satiation. Our data suggest the contrary. Stomatopods could complete consumption of snails from all three size classes. These were presented singly. Moreover, the size range used was based on data from the field and the number of snails presented (i. e. 6 snails per week) was considerably lower than the number consumed in the field during a comparable time. Studies on natural predation indicate that G. bredini of this size class are both capable of attacking a larger prey size range and consuming more prey tissue than offered in the present experiment (Caldwell et al. 1988). A third possibility is that G. bredini preferred intermediate and small snails because larger shells were not recognized. This is highly unlikely and would be a more appropriate argument if small shells were not preferred. The data show that stomatopods recognized the larger shells first, attacked them, and then switched to intermediate and small prey sizes (Fig. 1).

Feeding Oxygen Consumption

Stomatopod $\dot{V}_{O2net}$ increased linearly with strike frequency (Fig. 2). At least two components contributed to the increase. One component was directly proportional to the frequency of striking (i. e. slopes in Fig. 2). This component relates to the cost of striking and perhaps handling that occurs coincident with striking. Oxygen consumption was also elevated during periods when the stomatopod did not strike (i. e. y-intercepts in Fig. 2). The y-intercept represents the cost of handling, manipulating prey and digestion independent of striking. At the mean strike frequency (0.72 strikes/min), strike independent $\dot{V}_{O2}$ (0.063 ml O_2/ h) averaged 26 % of $\dot{V}_{O2feeding}$. The best estimate of the cost per strike can be

calculated by subtracting the y-intercept from $\dot{V}_{O2net}$ and dividing by strike frequency. The cost per strike derived from this calculation was $1.6 \pm 0.2 \, \mu l \, O_2$. The cost per strike accounted for 30 % of $\dot{V}_{O2feeding}$ at the mean strike frequency. The cost per strike at high frequencies was greater for animals smashing large snail shells. This had little effect on the overall energetic cost, however, because high strike frequencies (> 2 strikes/min) occurred so infrequently.

Paced striking in feeding stomatopods appears to be powered primarily by aerobic metabolism. Initial depletion of high-energy phosphate stores, such as arginine phosphate, will be replenished by aerobic metabolism shortly after the strike (FULL, unpubl. data on lactate, ATP, arginine phosphate). BURROWS (1969) discovered that the strike is produced by the co-contraction of flexor and extensor muscles operating a "click" joint. These muscles begin to contract 1 full s before the strike and as a result are not specialized for extraordinarily rapid contraction (BURROWS & HOYLE 1972). Ultrastructurally the muscles appear to be slow twitch fibers (McNEILL et al. 1972). Moreover, $\dot{V}_{O2feeding}$ increased by only 2.5-fold above $\dot{V}_{Orest}$, well below the maximal aerobic capacity of most muscles. INNES (1985) reported a 4.8-fold increase in $\dot{V}_{O2}$ during swimming for the stomatopod, *Heterosquilla tricarinata*. The capacity for oxygen uptake in stomatopods appears to be similar to other crustaceans during activity (McMAHON 1981). Furthermore, stomatopods can sustain a constant strike rate for over 7 h. It is unlikely that feeding could be sustained for this length of time if lactic acid production was significant.

Energetic Indices

Prey selection in *G. bredini* cannot be explained simply by the maximization of energetic indices, M/T, E/C, and NE/T. No significant difference was observed in any of these indices over the range of snail sizes investigated. At least two reasons can be advanced as to why the energetic indices fail to predict stomatopod prey-selection. First, our measurement of the indices may not be equivalent to the theoretical variables required. Second, a simple prey-selection model may be inadequate to explain stomatopod feeding. We will discuss the measurement of each index and subsequently address the inadequacy of the simple model.

Energy return/handling time. In the simplest model prey should be selected on the basis of their energetic return (M) per unit handling time (T). This index has been used to successfully predict prey selection of fish (KISLALIOGLU & GIBSON 1976) and crabs (ELNER & HUGHES 1978). Yet, the model is not without its exceptions. STEIN et al. (1984) did not observe selection in sunfish over the snail size range studied despite a 3-fold variation in M/T.

In the stomatopod, *G. bredini*, both the amount of tissue consumed and handling time varied significantly over the range of snail size we selected (Fig. 3 A, B). However, because both the benefit and cost increased proportionally, their ratio, M/T, did not change as a function of snail size (Fig. 5A). These findings are not unique to *G. bredini*. The M/T ratio in small *G. chiragra* (50 mm in length) also does not change as a function of snail size (CALDWELL, unpubl. data). Therefore, stomatopods should not be able to distinguish among prey based solely on this index.

We believe that our measures of energetic return and handling time faithfully represent the variables required by the model. The actual energetic cost of handling was proportional to handling time, an assumption often made but seldom tested. Energetic return, the mass of prey tissue consumed, could be confounded by variation in assimilation efficiency. However, even though the mass of prey consumed does not necessarily represent assimilated food, it is unlikely that a systematic deviation with snail mass exists. A similar argument may hold for food quality (i. e. specific nutrients).

Energy gained/energy expended. Energy gained (E)/energy used (C) is an index that includes the actual energetic cost of handling. This efficiency ratio compares the energetic benefit of the prey (E) to the energetic cost of its handling (C). SHERRY & McDADE (1982) predicted that prey should be added to the diet of hover-gleaning birds based on the largest E/C ratio. Even though STEIN et al. (1984) also found that the E/C index correctly predicted the selection of snail species by sunfish, the theoretical justification of this index is questionable. Evaluation of handling time should probably be included in foraging models unless a mechanism exists by which an animal can determine net energy balance directly (STEIN et al. 1984).

G. bredini required a greater number of strikes to open larger shells (Fig. 4). The energetic cost of those strikes increased in proportion to shell size. The resulting ratio of energy gained to energy used, E/C, was independent of shell size (Fig. 5B). The energetic cost per strike appeared to be relatively constant at the mean strike frequency. Striking a larger shell costs no more than striking a smaller shell: a larger shell simply required more strikes and a longer time to open.

Questions concerning energy gain (E) in this efficiency index are similar to those pertaining to the M/T index. Again, it is unlikely that a significant systematic deviation with snail mass exists for food quality, assimilated food or the number of calories obtained per unit mass of food. Relatively long handling times (T) required by *G. bredini* to open larger shells gave us an opportunity to measure the energetic cost of handling (E). In many studies the energetic cost of handling takes place within seconds and is undoubtedly confounded by the contribution of both aerobic and anaerobic metabolism.

The actual energetic cost of feeding depends on two measures, $\dot{V}_{O2feeding}$ and $\dot{V}_{O2rest}$. Typically in studies of activity, $\dot{V}_{O2rest}$ is simply subtracted from $\dot{V}_{O2}$ during activity. Resting $\dot{V}_{O2}$ is assumed to remain constant during activity and serves as a "maintenance" cost. This assumption has been difficult to test. Variation in resting metabolism may mask differences in feeding costs. Likewise, feeding costs may be elevated by behavior unrelated to feeding such as escape. We have no reason to believe that either of these complications influenced results in the present study because several $\dot{V}_{O2rest}$ measurements were taken, no energeti-cally expensive, nonfeeding behavior was observed, all trials were randomized and each animal served as its own control.

Net energy gain/handling time. The index of net energy gain (NE)/handling time (T) includes both the energetic benefit and cost of prey capture along with the time spent in handling (PYKE et al. 1977). This index is generally accepted as the most appropriate currency of fitness (see PYKE 1984; PYKE et al. 1977;

MITTELBACH 1981) and has correctly predicted prey selection in the laboratory and field. Once again, however exceptions exist (STEIN et al. 1984).

Given the M/T and E/C indices, no additional measurements are necessary to calculate the NE/T for stomatopod feeding. The above caveats discussed for these two indices apply to the NE/T index as well. In *G. bredini* energetic benefit, the cost of prey capture, and handling time, all increased proportionally with shell size (Figs. 3A, B; 4). As a result, NE/T was independent of snail shell size (Fig. 5C). Again, the hypothesis that stomatopods select snails on the basis of sizes that optimize net energy gain is not supported.

Revisions to the Prey-selection Model

In the present study theoretical predictions of a simple prey-selection model based exclusively on energy and time indices did not coincide with empirical results. We suggest three categories of revisions to the simple model for stomatopod prey selection. Consideration of these additional variables has been discussed in detail by ORIANS (1981) and PYKE (1984). They include: incomplete assessment of energy and time budget; unfamiliarity with the prey resource; and finally, use of variables other than energy and time.

Incomplete assessment of energy and time budget. To test the predictions of foraging models, we assumed that our energy and time budget represented a complete assessment. This assumption can be questioned because our analysis did not include search costs from a central place, the burrow. Searching was not involved in the laboratory experiments. However, recent field observations reveal that *G. bredini* often travel considerable distances to find prey items (CALDWELL et al. 1988). Individuals can forage 1 to 4 m away from their cavities to find prey. Moreover, individuals have been observed making as many as 10—12 foraging expeditions per day. Even though small snails are typically more abundant, stomatopods usually carry only one shell at a time (CALDWELL et al. 1988). The magnitude of searching costs is unknown due to the complications of measuring the energetic cost of walking and swimming under water (HOULIHAN & INNES 1984; INNES 1985). Nevertheless, a greater cost would be incurred by a stomatopod selecting smaller shells, if more foraging expeditions must be under-taken to secure a benefit equivalent to a larger snail. This argument obviously depends on the distance and frequency of snails that differ in size.

Inexperience with prey resource. A second revision to the prey-selection model for *G. bredini* involves the nature of the prey resource. Perhaps, optimal diet is specific to the native gastropod species on which *G. bredini* feeds. In the laboratory, *G. bredini* fed upon the nonnative species of prey, *Tegula*. We attempted to circumvent this problem by giving all animals a minimum of 5 feedings before testing. However, variation in the amount of energetic benefit (i. e. mass of prey) or the strength required to smash shells may have affected prey selection in the laboratory. Prey selection could differ if *G. bredini* assessed snail prey on size and chose this prey based on experience with the native *Cerithium* rather than *Tegula*. It is possible that *Tegula* of a particular shell diameter may be more difficult to open than a comparably sized shell of

Cerithium. Thus, *G. bredini* may have selected *Tegula* at first that were too large and then switched to smaller snails.

Use of variables other than energy and time. The simplest foraging model assumes that net energy gain should be maximized and handling time minimized, all else being equal. Unfortunately all else is seldom equal and other variables that affect fitness need to be considered to improve the model.

One possibility is variation in food quality such as specific ions or metabolites not directly related to energy (i. e. a nutrient constraint). As we mentioned previously, it is possible, though unlikely, that prey quality could vary with snail size and maturity. A second possible variable not evaluated is the amount of food obtained per unit time at any given time period. A stomatopod selecting a large snail is subject to greater variation in metabolite supply due to the long intervals required to open large shells, whereas eating many small snails would provide a more constant resource supply. It is difficult to accept this explanation when long periods of time are considered. Stomatopods can survive for weeks without any energy intake (CALDWELL, unpubl. data). However, temporary depletion of key substrates could impose short-term constraints on behavior. A third variable that may affect fitness involves long-term energy balance and maintenance of function. After many strikes the stomatopod's dactyl shows signs of wear. A worn dactyl increases the likelihood of structural failure. Perhaps large shells increase wear and the probability of failure more so than small shells. A fourth variable that must be considered is competition. Stomatopods venturing on longer search trips may lose their shelter to conspecifics. If the probability of displacement is in some way related to snail size, then prey selection will be affected. A final, important variable that will surely affect fitness is the added risk of predation when large snails are selected. Continuous sound over a long period of time from a single area may aid fish predators in locating stomatopods.

In conclusion, energetic cost, energetic benefit and handling time appear not to be the sole variables determining stomatopod prey selection. Additional variables that affect fitness need to be identified, assessed, and incorporated into the prey selection model.

Acknowledgments

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