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Comparison of Penetration Costs and Ingestion Speeds among Muricid Gastropods with Different Foraging Strategies

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Abstract. Penetration costs and ingestion speeds were compared among three sympatric muricid gastropods, *Morula musiva*, *Cronia margariticola*, and *Ergalatax contractus*, in relation to their preferences for drilling predation or kleptoparasitism. Scraping volume per unit shell thickness, which was used as an index of penetration cost, followed the order: *E. contractus* > *C. margariticola* > *M. musiva*. The ranking of the penetration costs of these muricids is consistent with each animal's inclination for drilling predation as previously reported. Ingestion speed of *E. contractus* and *C. margariticola* was significantly faster than that of *M. musiva*. For *E. contractus* and *C. margariticola*, which are kleptoparasitic more frequently than *M. musiva*, their faster ingestion speed would be advantageous in acquiring food by the kleptoparasitic strategy, which usually requires scrambling among other muricids. Proboscis diameter of *E. contractus* and *C. margariticola* was significantly larger than that of *M. musiva*. Proboscis morphology may mediate the trade-off relationship between drilling predation and kleptoparasitism, since a muricid acquires faster ingesting ability by thickening its proboscis, but, on the other hand, a greater penetration cost might be inevitable because of the need to make a larger hole for its insertion.

INTRODUCTION

Foraging processes often differ among animals that utilize the same food resource. These differences are found in, e.g., prey detection cues, attacking methods, and foraging group size. Morphological and behavioral characteristics related to foraging activity are considered to have evolved in relation to the process of prey handling, and are expected to be different among these animals. For example, prey detection cues differ among some carabid and staphylinid insects, and species that employ visual cues have a high degree of diurnal activity compared to species using olfaction cues (Wheater, 1989). Canine tooth morphology, which relates to its bending strength, differs among carnivorous mammal families and reflects various species' foraging behavior, e.g., deep killing bite by felids or shallow slashing bite by canids (Van Valkenburgh, 1987). Frigatebirds and skuas, which are considered specialized kleptoparasites (food stealing), have evolved structural adaptations to enhance their success in food plundering, such as unwebbed feet, large wings, and small body mass compared to their related, non-kleptoparasitic species (Brockmann & Barnard, 1979; Furness, 1987). Vultures, which often feed in groups, develop vigilance and threat behavior against same-guild consumers (Prior & Weatherhead, 1991). Some authors have pointed out that competitive scrambling may promote the evolution of specific foraging speeds (Shaw et al., 1995; Parker, 2000).

Differences in foraging processes for the same food are also found in marine carnivorous mollusks. For example, both direct predation and kleptoparasitism are reported in muricid gastropods. Most muricids can drill calcareous seashells and insert their proboscis to ingest the flesh of the prey, but some species also kleptoparasitize other muricids by displacing them from drilled holes (Hughes & Dunkin, 1984) or by ''pilifering'' with insertion of their proboscis into the valve-aperture of prey mussels that have been drilled by other muricids (Morgan, 1972). Pilfering was often observed in feeding aggregations, that is, swarms of muricids around a prey item (Brown & Alexander, 1994). Thus, some morphological and behavioral characteristics associated with foraging activity are expected to differ among these muricids. However, there are few comparative studies of such characteristics in muricids. In the present study, I compare the characteristics of three sympatric muricid species, *Morula musiva* (Kiener, 1834), *Cronia margariticola* (Broderip, 1833), and *Ergalatax contractus* (Reeve, 1846), which have different foraging strategies for the same food resource, at the rocky intertidal seashore of Shirahama, Wakayama, in the south-western part of Honshu, Japan.

A previous study (Ishida, 2001) revealed foraging strategy and interactions between these three muricid gastropods in the field as follows. Most *M. musiva* prey upon the mussel *Hormomya mutabilis* (Gould, 1861) by dril-

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ling (see also Abe, 1989). *Cronia margariticola* initiates predation by drilling or by the ''gape insertion method'' (ingestion by inserting its proboscis into the mussel valve aperture with or without valve edge drilling, see Menzel & Nichy, 1958; Rovero et al., 1999a, b), but often kleptoparasitizes prey by either pilfering the flesh from the valve aperture or by dislodging the initiator. Most *E. contractus* acquire mussel flesh by pilfering, although they have the ability to use penetration. The differences in preferences for drilling predation (*M. musiva* > *C. margariticola* > *E. contractus*) and that for pilfering (*E. contractus* > *C. margariticola* > *M. musiva*) were also supported by the results of laboratory experiments (Ishida, 2001). When a muricid preys upon mussels, few muricids initially cluster around it because the odors of prey flesh have not leaked out (Carriker & Van Zandt, 1972). As prey flesh is ingested, the flesh odors leak out, and then some muricids cluster around the prey. The valves of mussel, especially when attacked by the gape insertion method, are liable to be open, and other clustered muricids simultaneously insert their proboscis between mussel valves to pilfer (Ishida, 2001). Thus, drilling predators can secure a reasonable amount of flesh, whereas pilfering feeders must scramble to compete for flesh with others. Those muricids that can ingest faster will potentially obtain more flesh under such scrambling conditions.

In view of these observations, I propose two hypotheses to explain the difference in the characteristics of the three muricids: (1) the penetration cost (defined here as the scraping volume per unit penetration) is higher for *E. contractus* than for *C. margariticola,* and higher in *C. margariticola* than in *M. musiva,* and is negatively correlated with their preference for the drilling strategy; (2) ingestion speed is faster in *E. contractus* than in *C. margariticola,* and faster in *C. margariticola* than in *M. musiva,* as an adaptation to the pilfering feeding strategy. I use laboratory experiments to measure and compare the former two characteristics among the three muricids. Furthermore, I discuss the possibility that the proboscis diameter mediates the trade-off relationship between the strategies because of the contradiction of lower penetration cost and faster ingestion speed.

MATERIALS AND METHODS

Materials Collection Site

All laboratory experiments were carried out at the Seto Marine Biological Laboratory of Kyoto University (SMBL), Wakayama, in the southwest of the main island of Japan 33°41′N, 135°21′E), during May–August 1999 and May–August 2000. Experimental muricids and mussels were collected from the intertidal seashore near the SMBL. Each individual muricid was used only one.

Scraping Volume Measurement

To collect samples of muricid drill holes for measuring scraping volume, each experimental muricid was kept in a plastic aquarium under running seawater (temperature fluctuation was within 0.2°C during each replication, and the range was 20–30°C during the experiment), and was provided with a mussel, *H. mutabilis* (10–25 mm in shell length). After the completion of predation, shell thickness was measured at four points along the edge of drilled holes using a micrometer with a precision of 10 μm. Specimens in which the mean thickness at the drilled site was thicker than 220 μm and thinner than 340 μm were employed for the analysis, to eliminate the effect of thickness difference on the comparison of scraping volume. When muricids drilled at an extremely bent area of mussel shells resulting in an abnormal hole shape, or when they attacked mussels by inserting their proboscis between valve-apertures without shell penetration, I removed that data from the analysis. I obtained 27 replicates of *M. musiva* (12.8–23.6 mm in shell height), 13 of *C. margariticola* (17.1–24.9 mm), and 14 of *E. contractus* (16.7–23.3 mm). To estimate the scraping volume, I assumed that the dimension was a frustum. The volume of a frustum, $V(\text{mm}^3)$ is defined as follows:

$$V = D/3(A + B + \sqrt{AB})$$

where D = height of frustum (i.e., shell thickness, mm), A and B = top and bottom section area (i.e., external and internal drill hole area, mm^2), respectively. Therefore I used $(A + B + \sqrt{AB})$ as an index of scraping volume. Both hole areas were measured by an image analyzing program (NIH image 1.62) from the drill hole pictures that were taken with a digital camera attached to a binocular microscope (final resolution was 1 mm = ca. 340 pixels).

To eliminate the size effect among different species on the comparison of scraping volume, I introduced the dry weight of the muricid's soft body as a covariate. I broke and removed the shells from experimental muricids, dried each soft body for 40 hr at 60°C, and weighed it with an electronic balance with a precision of 1 μg.

I assumed the regression function to compared the scraping volume of the species as follows:

$$\ln(A + B + \sqrt{AB}) = a_0 + a_1 \ln W$$

where W = muricid dry weight (g), a_i (i = 0,1) = coefficients. I compared the scraping volume index with ANCOVA, as the independent variable was a covariate.

Ingestion Speed Measurement

To measure ingestion speed, I provided each muricid with a flesh-exposed *H. mutabilis* mussel (10–20 mm in shell length), the valves of which had been opened by cutting its adductor muscle with a razor. Seawater temperature condition was the same as in the drill hole sam-

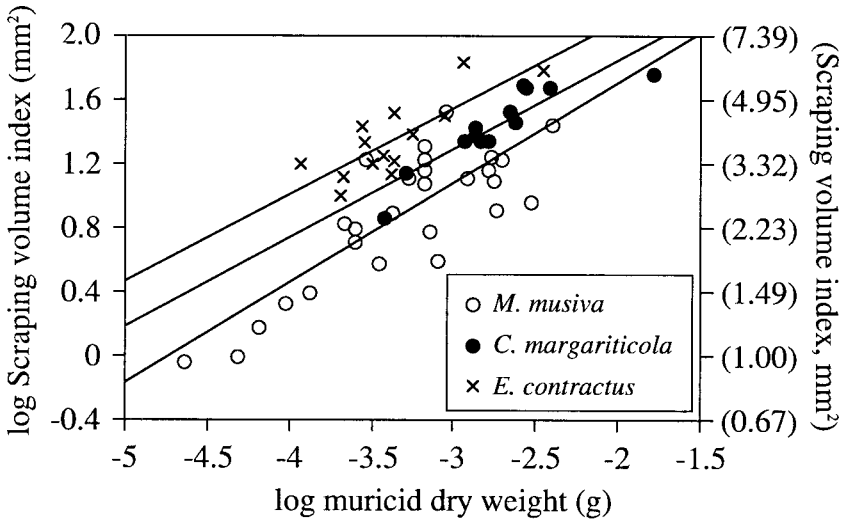

Figure 1. Relationship between log (scraping volume index) on log (muricid dry weight) for *Morula musiva, Cronia margariticola,* and *Ergalatax contractus.* Regression lines are shown with solid lines. Untransformed values of the index are shown in parentheses on the right axis. Each coefficient is shown in Table 1.

ple collection experiments. I then directly observed the muricids' feeding behavior to measure the period from the start of ingesting flesh to its completion. I defined the ingestion speed as dry weight of ingested mussel flesh per unit time. Mussel flesh dry weight was obtained from mussel shell length by the equation: $W_m = 0.016 \times L^{2.67}$, where W_m = flesh dry weight (μg) and L = shell length (mm). Coefficients were derived from 19 mussles (shell length 11.2–24.7 mm) dried for 40 hr at 60°C (n = 19, $R^2 = 0.87$). I obtained 57 replicates of *M. musiva* (12.1–23.2 mm in shell height), 57 of *C. margariticola* (13.5–29.1 mm), and 59 of *E. contractus* (12.3–23.8 mm). I used the following multiple-regression function to compare the ingestion speeds of the species.

$$\ln S = b_0 + b_1 \ln W + b_2 \ln T$$

where S = ingestion speed (μg/min), W = muricid dry weight (g), T = mean seawater temperature (°C) and b_i (i = 0,1,2) = coefficients. Then I employed ANCOVA, as these independent variables were covariates.

Table 1

Parameter values of the regressions of log (scraping volume index) on log (muricid dry weight) ($\ln A + B + \sqrt{AB} = a_0 + a_1 \ln W$). n, sample size; R^2, coefficient of determination. Asterisks affixed to each F value denote the P value: ** $P < 0.001$; *** $P < 0.0001$.

Scraping volume index	n	a_0	a_1	R^2	F
M. musiva	27	2.96	0.63	0.677	52.44***
C. margariticola	13	2.96	0.55	0.800	44.13***
E. contractus	14	3.17	0.54	0.645	21.85**

Proboscis Diameter Measurement

Similar weighed muricids fixed with 8% seawater formalin were dissected and their retracted probosces were exposed. Proboscis diameter (at 1 mm distance from the end) was measured from the proboscis pictures with the same system as measuring drill hole area. Six individuals for each of the three species were examined.

RESULTS

Scraping Volume

Regression of scraping volume index ($A + B + \sqrt{AB}$) on muricid dry weight was significant for all three muricids (Figure 1 and Table 1: linear regression analysis with log-transformed dependent and independent variables). Results of ANCOVA indicated that scraping volume index was significantly different among the three muricids (Table 2a; interaction effect rejected, $P > 0.8$). Multiple comparison testing with the Bonferroni correction (threshold for significance: $P = 0.0167$) indicated that the scraping volume index of *E. contractus* was significantly larger than that of *C. margariticola,* and that of *C. margariticola* was larger than that of *M. musiva* (Table 2b; all interaction effects rejected, $P > 0.6$). These results suggest that the scraping volume per unit shell thickness of *E. contractus* (1.87 mm^3) was ca. 1.8 times and that of *C. margariticola* (1.28 mm^3) was ca. 1.3 times larger than that of *M. musiva* (1.02 mm^3) of equal dry weight (0.05 g).

Table 2

Results of ANCOVA for log (scraping volume index), with log (muricid dry weight) as covariate. (a) Comparison among three species; (b) multiple comparison. The threshold for significance of the multiple comparison was $P = 0.0167$ with the Bonferroni correction.

(a)

	DF	SS	MS	F	*P*
Species	2	2.28	1.14	29.14	< 0.0001
ln(muricid dry weight, g)	1	4.25	4.25	108.93	< 0.0001
Residual	50	1.95	0.039		

(b)

Multiple comparison	DF	F	*P*
Mm vs. *Cm*	1, 37	6.47	0.0153
Cm vs. *Ec*	1, 24	13.92	0.0010
Ec vs. *Mm*	1, 38	47.66	< 0.0001

Ingestion Speed

Significant positive correlations between ingestion speed and both muricid dry weight and mean seawater temperature were detected in each muricid (Table 3: multiple regression analysis with log-transformed dependent and independent variables). The results of the ANCOVA indicate that ingestion speed was significantly different among the three muricids (Table 4a; all interaction effects rejected, $p > 0.05$). Multiple comparison testing with the Bonferroni correction (threshold for significance: $P = 0.0167$) indicates that the ingestion speed of *M. musiva* was significantly slower than that of either *C. margariticola* or *E. contractus*, and that of *C. margariticola* tended to be slower than that of *E. contractus* although the *P*-value ($P = 0.086$) exceeded the significance level (Table 4b; all interaction effects rejected, $P > 0.05$). Ingestion speed of *E. contractus* (0.21 μg/min) and *C. margariticola* (ca. 0.16 μg/min) was ca. 5.0 times faster than that of *M. musiva* (0.037 μg/min) of equal body weight (0.05 g), in 25°C seawater. Even the smallest *C. margariticola* or *E. contractus* (ca. 12–13 mm in shell height; 0.1 μg/min) ingested ca. 2.0 times faster than the largest *M. musiva* (ca. 23 mm in shell height; 0.05 μg/min).

Proboscis Diameter

The proboscis of *M. musiva* was significantly thinner than that of either *C. margariticola* or *E. contractus* of equal weight, and no significant difference was detected between the last two with the present sample size (Table 5: Kruskal-Wallis test, $H = 11.9$, $P = 0.0026$; Dunn-test: *Mm* vs. *Cm*: $Q = 2.54$, $P < 0.05$; *Cm* vs. *Ec*: $Q = 0.75$, $P > 0.5$; *Ec* vs. *Mm*: $Q = 3.30$, $P < 0.005$).

DISCUSSION

Scraping volume index, that is, internal and external hole area, of *E. contractus* was significantly larger than that of *C. margariticola*, and that of *C. margariticola* was larger than that of *M. musiva*. Carriker & Van Zandt (1972) observed that a muricid (*Urosalpinx cinerea follyensis*) continued enlarging a borehole until it was large enough to admit the proboscis, while repeatedly trying to force the proboscis into the hole. Therefore, the hole area would be essentially determined by the thickness of the proboscis to be inserted. Actually, *C. margariticola* and *E. contractus* have thicker probosces than *M. musiva.*

Ingestion speed significantly differed between muricids. *Cronia margariticola* and *E. contractus*, which

Table 3

Parameter values of the multiple regressions of log (ingesting speed) on log (muricid dry weight) and log (mean seawater temperature) ($\ln S = b_0 + b_1 \ln W + b_2 \ln T$). n, sample size; R^2, coefficient of determination. Asterisks affixed to each F value denote the *P* value: *** $P < 0.0001$.

	n	b_0	b_1	b_2	R^2	F
M. musiva	57	−18.87	0.51	5.31	0.502	27.23***
C. margariticola	57	−17.73	0.80	5.69	0.418	19.40***
E. contractus	59	−8.20	0.56	2.58	0.351	15.17***

Table 4

Results of ANCOVA for log (ingesting speed), with log (muricid dry weight) and log (mean seawater temperature) as covariates. (a) Comparison among three species; (b) multiple comparison. The threshold for significance of the multiple comparison was $P = 0.0167$ with the Bonferroni correction.

(a)

	DF	SS	MS	F	*P*
Species	2	93.08	46.54	153.26	< 0.0001
ln(muricid dry weight, g)	1	12.78	12.78	42.08	< 0.0001
ln(mean seawater temp, °C)	1	25.08	25.08	82.57	< 0.0001
Residual	168	51.02	0.30		

(b)

Multiple comparison	DF	F	p
Mm vs. *Cm*	1, 110	158.24	< 0.0001
Cm vs. *Ec*	1, 112	2.99	0.086
Ec vs. *Mm*	1, 112	214.57	< 0.0001

adopt a kleptoparasitic strategy by pilfering from mussel valve apertures and scramble for prey with other muricids, ingested flesh considerably faster than *M. musiva*. One of the important characteristics to enable faster ingestion may be a thick proboscis, which is present in *C. margariticola* and *E. contractus.*

The shell penetration process of muricids consists of chemical dissolution and radular rasping. Greater scraping volume in penetration would consume more physiological energy (e.g., secretion of chemicals, radular movement, and secretion). Assuming that such inclusive costs per muricid dry weight are comparable among species, *E. contractus* needs more energy for shell penetration than does *C. margariticola,* which in turn uses more energy than *M. musiva*. This may explain the differences in the preference for their drilling predation strategy, which has been observed in the field and the laboratory (Ishida, 2001). *Morula musiva* would use only 60–80% of the penetration cost incurred by *E. contractus* and *C. margariticola* when preying upon mussels of the same size. On the other hand, faster ingestion will be more advantageous in acquiring food under scrambling conditions. If the three muricids were to ingest the same mussel simultaneously, the expected gain of *M. musiva* will be certainly less than 50% of that of *C. margariticola* and *E. contractus.* Thus, even if an exploitable resource is available for *M. musiva,* it may have to compensate food acquisition by drilling predation when it coexists with the other two species. These results may explain partly the differences in relative frequency of pilfering, especially between *M. musiva* and the other two species in the field (Ishida, 2001).

If a muricid has a thicker proboscis that seems to enable faster ingestion, it has to make a larger hole to insert its proboscis for drilling predation. Therefore, the ability to ingest quickly may be at the expense of a greater penetration cost. Thus, a trade-off relationship is expected between drilling predation and pilfering kleptoparasitism in the muricid. To test for this trade-off, we need to evaluate the actual cost of penetration. If penetration accounted for a relatively small part of the total cost of foraging, the increase in penetration cost with increased proboscis thickness may not affect the muricid's dependence on a drilling predation strategy.

For a more robust evaluation of penetration cost in these muricids, we will need to collect information about the functional and morphological parameters of drilling organs (e.g., accessory boring organ or radula) that would also determine the drill hole size. In addition, I did not examine the time cost of penetration which previous stud-

Table 5

Mean proboscis diameter of three muricids. Lowercase letters (a, b) affixed to the diameter values represent the result of a post-hoc test (see text).

Species	n	Shell height (mm)	Muricid dry weight (mean ± 1SD, g)	Proboscis diameter (mean ± 1SD mm)
M. musiva	6	18.5–19.7	0.054 ± 0.010	0.97 ± 0.09 a
C. margariticola	6	19.0–19.4	0.064 ± 0.016	1.52 ± 0.16 b
E. contractus	6	19.9–22.5	0.053 ± 0.014	1.69 ± 0.20 b

ies employed to discuss the muricids' foraging ecology especially in the intertidal environment (Hughes & Dunkin, 1984; Abe, 1989; Serra et al., 1997). To test the trade-off hypothesis carefully, the penetration time for each muricid must be determined. For example, radular size and stroke would need to be examined not only to determine penetration efficiency but also ingestion speed—a larger and longer radular ribbon may be able to shorten both the penetration and ingestion processes. Even a thicker proboscis may reduce the time required for drilling. The muricid proboscis itself also plays a role in the penetration process, e.g., by absorbing fragments of rasped shell from the borehole or possibly delivering enzymes to hydrolyze the prey shell (Carriker, 1981). A thicker proboscis may reinforce these functions.

The present study examines two possible characteristics affecting the foraging strategy of muricids; there may be other important factors. Ishida (2001) showed that *E. contractus* responded to mussel flesh quicker than *M. musiva* in the laboratory. Thus, the ability to detect olfactory cues emitted from potential exploitable prey may differ among the three muricids. Furthermore, the ability to crawl quickly to reach the prey would be advantageous for a pilfering strategy. More investigation and integration of these factors are needed to further understand the behavioral ecology of the foraging muricid.

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