

The effect of hunger on drilling behaviour of *Natica tigrina*: An experimental assessment



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ABSTRACT

Drilling predation is one of the unique scenarios where past biotic interactions can be studied quantitatively and used to model behavioural evolution of the involved groups. Although it is recognized that hunger plays an important role in determining the behaviour of terrestrial predatory groups, its specific effect on drilling gastropods is largely unexplored. Muricids have been shown to demonstrate change in prey preference and foraging behaviour when starved. Such behaviour is yet to be tested for naticid gastropods.

In an experiment with live naticid gastropods, *Natica tigrina* and their bivalve prey *Cardium* sp., we evaluated the effect of hunger on the following aspects of predation: 1. Drilling frequency, 2. Size selectivity, and 3. Site selectivity. Comparing gastropods between satiated controlled group and starved experimental group we demonstrated a positive effect of hunger on drilling frequency. Using different stages of hunger, we found that hunger plays an important role in dictating prey size-selectivity. While hunger increases drilling frequency, it reduces the degree of prey size selectivity. Hunger is not found to initiate edge-drilling or incomplete drilling in *N. tigrina*. It has been postulated that prey selection by gastropods are correctly modelled by cost–benefit analysis; but the standard cost–benefit analysis does not account for hunger. However, our study demonstrates the relative importance of hunger in guiding drilling behaviour in naticids and hence it should be incorporated in future cost–benefit models. As hunger is often related to nutrient depleted conditions, these modifications in behaviour could be used to explain the spatial variation in drilling pattern by naticid gastropods.

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1. Introduction

Predator–prey interaction plays a vital role in structuring the community and population of the prey (Fairweather et al., 1984; Sih et al., 1985; Hughes, 1988; Hines et al., 1990; Peterson, 1990; Kvittek et al., 1992). Therefore, ecologists and palaeontologists are keen to study the long term record of predation and its possible effect on evolution. Drilling predation is important in that aspect where predatory gastropods drill the hard shell of their prey to consume soft tissue inside and leave a durable record of predation behind. Although the earliest drill holes date back to late Precambrian (Bengtson and Zhao, 1992) and several others are reported from Paleozoic (Sheehan and Lesperance, 1978; Smith et al., 1985) and Mesozoic (Kowalewski et al., 1998; Bardhan et al., 2012), the identity of pre-Cretaceous drilling predators are not clearly established. The two gastropod families primarily responsible for modern drilling predation, naticids and muricids, did not appear before Cretaceous (Sohl, 1969; Kabat, 1990). To model the behaviour of these Cenozoic predatory gastropods, researchers have conducted several neontological experiments with extant species of muricids and naticids (Chattopadhyay et al., 2014a).

Previous neontological experiments on drilling predation examined various aspects of drilling behaviour including predation intensity, selectivity, rate of drilling and consumption etc. Kitchel et al., (1981) which correctly predicted the selectivity shown by naticid gastropods using a cost–benefit analysis. This was later modified to accommodate time of consumption by Chattopadhyay and Baumiller (2009) for muricid gastropods. In another study, Casey and Chattopadhyay (2007) explored the effect of clumping in mussels as a defence strategy against drilling predation of muricid gastropods. Although incomplete drill holes are often interpreted as failed predation events and its frequency is considered a proxy of prey-effectiveness, Chattopadhyay and Baumiller (2007) demonstrated that the frequency of incomplete drill holes by muricid gastropods change with mortality threat caused by secondary predator. A similar pattern is demonstrated by Hutchings and Herbert (2013) where incomplete drilling frequency is shown to be dependent on conspecific competition among naticid gastropods (but see Visaggi et al., 2013). Competition among predatory snails leads to enhanced site-selectivity and often produces edge-drilling (Dietl and Herbert, 2005; Chattopadhyay et al., 2014b). Dietl et al. (2004) showed that enhanced competition leads to modification in drilling behaviour of muricid gastropods. One important reason behind enhanced competition is resource limitation and such low nutrient availability often subjects the population to hunger. It is recognized that

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hunger plays an important role in determining the behaviour of other predatory groups (Ware, 1972; Pastorok, 1980; Molles and Pietruszka, 1987) including muricid drillers (Hughes and Dunkin, 1984a; Perry, 1987; Vadas et al., 1994), its specific effect on Naticid drilling behaviour is yet unexplored. In our experiment with extant naticid gastropods we tried to evaluate the effect of hunger on the behaviour of drilling gastropods.

In an experiment with live naticid gastropods, *Natica tigrina* and their bivalve prey *Cardium* sp., we evaluated the effect of hunger on the following aspects of drilling predation:

1. Drilling frequency: In order to compensate for the nutrient deprived state, a hungry gastropod is expected to increase its energy intake by increasing the drilling frequency. As a result, we might expect to see an increase in drilling frequency with hunger.
2. Size selectivity: It is observed that prey selection by gastropods can be predicted correctly by cost–benefit models (Kitchell et al., 1981). This model also predicts selection of an optimal prey-size for every predator to ensure the highest energy gain. As energy requirement increases with hunger, we expect to see a lack in size selectivity with hunger.
3. Site selectivity: It has been argued that edge drilling is practiced in extreme conditions (reference). We can expect to see such behaviour during starvation.

2. Materials and methods

The specimens examined in this study were collected from a tidal flat situated along the Odisha coast at Chandipur, India (21°27'27.01" N, 87°03'25.09"E). Two major naticid genera, *Polinices* and *Natica* dominate this tidal flat (Mondal et al., 2010). The two species *N. tigrina* and *Cardium* sp. (Fig. 1) are commonly found to be together in their natural habitat and the *Natica* preferentially preys upon the *Cardium* (Chattopadhyay et al., 2014a).

2.1. Specimens

We collected 200 live individuals of *N. tigrina* and around 2000 individuals of *Cardium* sp. from the tidal flat of Chandipur between May–July, 2014. All the specimens were brought to the experimental facility in plastic containers (0.5 m × 0.5 m × 0.5 m) along with the sea water and sediments. Later, they were transferred to the experimental chambers (Fig. 2). We used the specimens of *N. tigrina* that belong to the most abundant size class (shell height: 2–2.5 cm). The bivalves were subdivided into three size classes based on their antero-posterior length: small (<6 mm), medium (6–9 mm) and large (>9 mm).

2.2. Experimental setup

For this experiment we used the synthetic salt water aquarium housed in Ecological Field Station, IISER Kolkata. It is comprised of

multiple glass tanks (1.2 m × 0.5 m × 0.5 m) with re-circulating synthetic salt water. In order to understand their normal food intake, we observed the feeding habit of 10 gastropods after bringing them to the experimental facility from the field. We provided 10 bivalves to each of them and monitored their drilling activity for 4 days. We found that none of the gastropods consumed more than 1 bivalve prey in a span of one day. Hence 1 bivalve prey per gastropod per day is used as sufficient diet for the rest of the experiment. In the first couple of runs of the experiment it was observed that for a gastropod to become hungry it takes at least 2 days of starvation. Therefore gastropods suffering less than 2 days of starvation were considered as the controlled group during the experiment. The bivalves used for this experiment were all alive as detected from their closed shell. Apart from the permanent glass partitions, we created temporary confinements using plastic bottles (diameter: 8 cm, height: 15 cm) with netted tops (Fig. 2) that were used during the experiments. We created 20 equidistant holes on the wall of each bottled chamber to ensure circulation. As *Natica* drill their prey underneath the substrate 10 cm thick layer of coral sand was kept in each bottled chamber to ensure the normal drilling activity of the predator (Visaggi et al., 2013). We also maintained a near constant chemical composition (pH, salinity) and temperature (24 °C–25 °C) of this system.

2.3. Experimental design

We selected 36 healthy (mobile) gastropods and placed each of them in separate bottled chambers. Controlled group consisted of 12 chambers and the rest, 24 chambers, were treated as experimental group. The gastropods of the controlled group were not hungry as they were provided with prey initially. The gastropods in the experimental group were kept hungry for a period of at least 2 days. We created four subsequent stages of hunger (corresponding to 2, 3, 4 and 5 days) and 6 bottled chambers were assigned for each stage. A total of 6 bivalves, 2 of each size class, were provided in each chamber on a specific day as required by the particular stage of hunger. For example, a gastropod in hunger stage-3 is provided with 6 bivalves after the third day of starvation. We observed each chamber for signs of drilling at an interval of 12 h for a period of 2 days after introducing the prey. Two days after providing the bivalve the experiment was terminated for individual gastropods. The sequence of attack, number and size of drilled bivalves were documented for each chamber. Each drill hole was also characterized by its position (near the umbo or away from it) and completeness.

2.4. Analysis

Bivalve shells with complete drill holes and without soft tissue inside are considered as signatures of successful attack and drilling frequency is calculated by dividing the number of complete drill holes by the total number of bivalves provided. The position of the drill hole is estimated visually and broadly categorized into umbonal- and edge-drilling. The drill holes that did not penetrate the shell completely (incomplete drill holes) are considered signatures of failed attack. All statistical analyses (t-test, correlation table and Chi-square test) were performed in PAST 2.12 (Hammer et al., 2001).

3. Results

In our experiment, 36 gastropods attacked a total of 133 out of 216 bivalves. We found a total of 130 complete (DF = 0.6, Table 1) and 3 incomplete drill holes. All the drill holes are located near the umbo. We did not find any edge drilling. None of the bivalves died because of the natural causes other than drilling predation during this experiment.

We found an appreciable difference in drilling frequency between controlled and experimental groups (Fig. 3a). The drilling frequency significantly changes after the first two days of hunger (t-test,

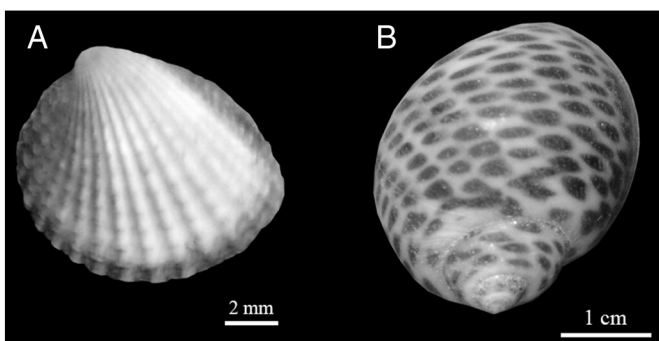


Fig. 1. Specimens used for the experiment. A) *Natica tigrina*. B) *Cardium* sp.



Fig. 2. Experimental setup showing the saltwater aquarium containing twelve bottled chambers with netted tops.

$t = -12.876$, $p < 0.01$). Our data of drilling frequency shows a strong positive correlation with hunger ($r = 0.94$, $p \ll 0.01$, Fig. 3b).

The proportion of all complete drill holes is highest in the medium size class (45.4%) followed by the large (30%) and small size classes (24.6%). Also, the drilling frequency was highest in the medium-sized bivalves (Fig. 4), making the medium size the preferred one (Fig. 4 & Table 1). However this preference changes with hunger. There is a strong negative correlation between the proportion of drilled medium-sized bivalves and hunger (Spearman's $\rho = -0.74$, $p < 0.01$, Fig. 5).

4. Discussion

Hunger is considered a trigger that leads to various behavioural modifications in organisms (Molles and Pietruszka, 1987). Arber et al. (1995) found that hunger has a significant effect on shoaling behaviour of small fresh water fishes. Hunger level also influences predatory reception of visual and vibratory signal of prey in the case of wolf spider, *Schizocosa ocreata* (Persons et al., 2001). Runge (1980) reported a significant effect of hunger on the feeding behaviour of zooplankton *Calanus pacificus*. Ware (1972) demonstrated that the rate of predation increases with an increase in hunger for rainbow trout. Prey selection is shown to be inversely proportional to the degree of hunger for glassworm larvae, *Chaoborus* (Pastorok, 1980). Work has also been done to understand different behaviours of hungry predatory snails, mostly muricids. Perry (1987) studied the foraging behaviour of muricid predator *Acanthina spirata* preying upon barnacles; he demonstrated that under starvation, drillers attack *Chthamalus fissus*, a less preferred prey in normal times. In an experiment with live dog whelk *Nucella lapillus*, Vadas et al. (1994) showed that the starved individuals take greater risk than satiated individuals during foraging. Using the same species Hughes and Dunkin (1984b) observed that the foraging path of the predator is controlled by the state of hunger. As muricids and naticids have different predatory behaviours, rates and success (Tull and Böhning-Gaese, 1993), the effect of hunger might not be identical among these groups. Our study demonstrates the role of hunger in naticid drilling predator–prey system.

Drilling frequency has been considered a measure of success of the predator (Leighton, 2001; Leighton, 2003). However, recent studies identified factors other than predatory traits that can affect drilling frequencies. Response to a secondary predator often plays a crucial role in modifying drilling frequency (Chattopadhyay and Baumiller, 2007, 2010). Level of competition is also documented to affect drilling frequency (Hutchings and Herbert, 2013). Other than biological influences, taphonomic biases can also alter drilling frequency (Lever et al., 1961; Roy et al., 1994; Harper et al., 1998; Klompmaker, 2009; Klompmaker et al., 2013; Chattopadhyay et al., 2013; but see Hagstrom, 1996; Kelley, 2008; Zuschin and Stanton, 2001). Our present study demonstrates the positive influence of hunger on drilling frequency. Hence caution should be taken in interpreting the record of drilling frequencies to model predator–prey interactions.

Previous studies documented a strong effect of hunger on foraging behaviour where increased hunger in predators diminishes prey-selectivity (Pastorok, 1980; Rechten et al., 1983; Bence and Murdoch, 1986; Michelli, 1995). Our experimental data shows a similar pattern. When the prey is available, *N. tigrina* preferentially selected medium-sized bivalve prey. However, such selectivity decreases with increased hunger level. Generally prey size selection is predicted by cost–benefit models (Kitchell et al., 1981; DeAngelis et al., 1985) and the same has been practiced for Recent and fossil assemblages (Kelley, 1988; Kelley, 1989; Chattopadhyay and Dutta, 2013). Nonetheless, the conventional cost–benefit model fails to accommodate the role of hunger.

Generally predators show a preferential drilling site to maximize the energy gain from an attack (Kitchell et al., 1981). In a competitive environment the gastropods often show a preference for the edge of a shell as the drilling site (Dietl et al., 2004; Dietl and Herbert, 2005; Chattopadhyay et al., 2014b). As competition and starvation may often be related, it is important to evaluate the direct role of hunger on edge drilling. Our experiment shows that all the gastropods made umbonal drilling on the prey during their hungry stage when they were kept in separation; no edge drilling is observed. This experimental finding is not different from the drilled specimens collected from the same field locality with conspicuous absence of edge drilling; this confirms that *N. tigrina* rarely engages itself in edge drilling even during highly stressed condition.

Table 1

Table summarizing successful attacks at various stages of hunger. Days of starvation indicate the various hunger stages with controlled group consisting of gastropods which were hungry for less than 2 days. The total number of bivalves of a particular size class given to the gastropods of a particular hunger stage is given in brackets.

Size of bivalve	Days of starvation					Total	Drilling frequency	Proportion of all drill holes (%)
	Controlled group		Experimental group					
	<2	2	3	4	5			
Large	2 (24)	6 (12)	10 (12)	10 (12)	11 (12)	39 (72)	0.54	30
Medium	17 (24)	11 (12)	10 (12)	10 (12)	11 (12)	59 (72)	0.82	45
Small	3 (24)	6 (12)	5 (12)	9 (12)	9 (12)	32 (72)	0.44	25
Total	22	23	25	29	31	130		
Drilling frequency	0.31	0.64	0.69	0.81	0.86	0.6		

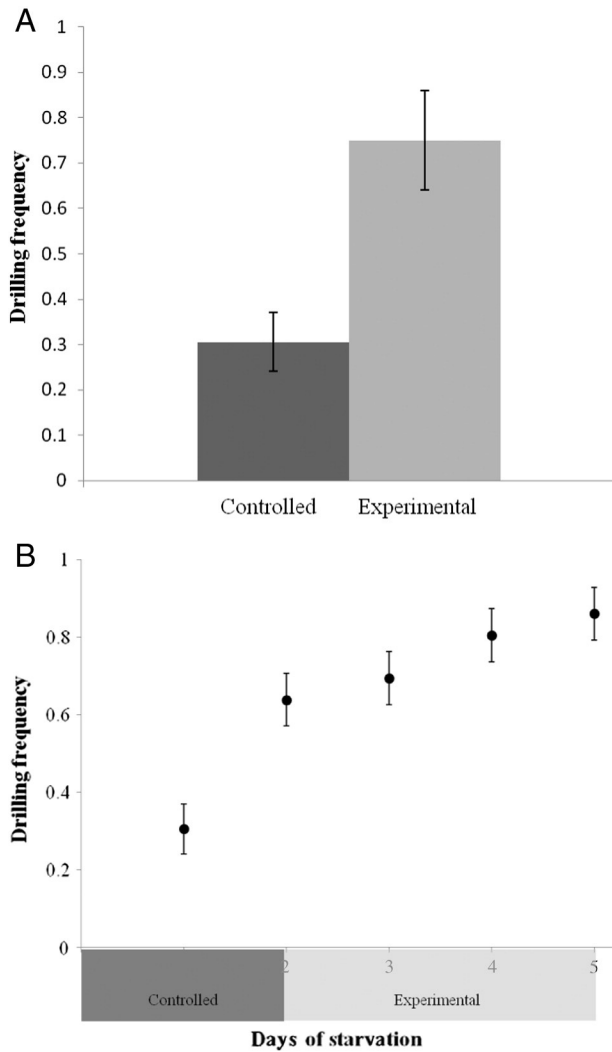


Fig. 3. a) Plot showing the drilling frequency in controlled group and in experimental group. The black bar represents the controlled group and the grey bar represents the experimental group. b) Plot showing the relationship between drilling frequency and the number of days the gastropod was starved. The error bar represents the standard deviation in drilling frequency.

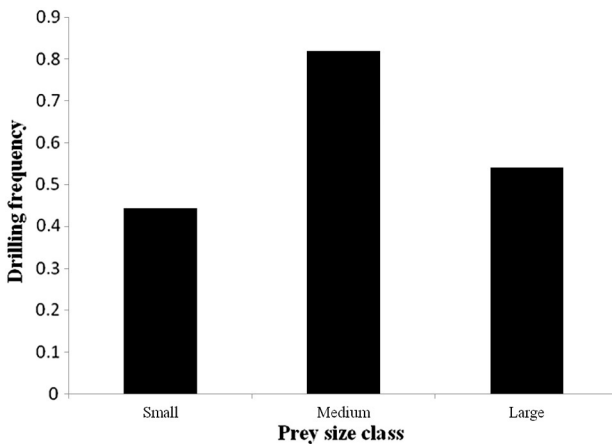


Fig. 4. Plot showing the preferred size class of the prey as selected by the predator. The black bars represent the drilling frequency of the smaller, medium and large size classed bivalves.

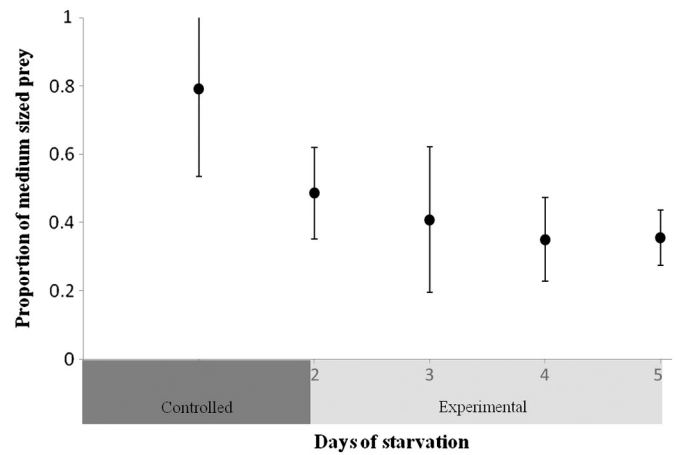


Fig. 5. Plot showing the difference in proportion of medium sized bivalves drilled by the gastropods in different stages of hunger. The error bar represents the standard deviation in the proportion.

5. Implication

Various aspects of predatory behaviour of gastropods have been modelled by a cost–benefit analysis. However, people have raised concern regarding the assumptions of standard cost–benefit model (Anderson et al., 1991; Leighton, 2001b; Chattopadhyay and Baumiller, 2007). Our study, yet, demonstrates another important factor in guiding drilling behaviour, namely hunger, that has not been directly considered in the standard cost–benefit analysis. A possible modification in the standard cost–benefit model to incorporate effects of stress should be an important area for future research.

As hunger is related to prey availability, which in turn varies spatially, hunger induced drilling behaviour could be important to understand the spatial variation in drilling frequency of naticid gastropods. All of the studies including the current one, evaluating the effect of hunger on drilling gastropods are conducted in laboratory setup. It would be important to validate the claims in natural settings in order to evaluate the role of hunger in explaining the spatial variation in drilling patterns. However this effect is unlikely to play a major role in fossil assemblages that are time averaged.

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