Drilling under threat: An experimental assessment of the drilling behavior of *Nucella lamellosa* in the presence of a predator

Devapiya Chattopadhyay*, Tomasz K. Baumiller

*Museum of Paleontology, University of Michigan, 1109 Geddes Road Ann Arbor, MI 48109-1079, USA*

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**Abstract**

Using the drilling muricid, *Nucella lamellosa* (Gmelin 1791) and its prey, the mussel *Mytilus trossulus* (Gould 1850), the impact of a secondary predator, the crab *Cancer gracilis*, on drilling was investigated experimentally. The frequency of incomplete holes was compared under two conditions: (1) when the gastropod’s natural predator, *C. gracilis*, was present and (2) when it was absent. The results indicate that the presence of a secondary predator can affect drilling activity, leading to a significant increase in the frequency of incomplete drill holes. The introduction of a secondary predator can also decrease the overall drilling frequency. The size distributions of completely and incompletely drilled mussels suggest that in the presence of the secondary predator the decision by the gastropod to either abandon or continue drilling its prey might be influenced by how much time it has already invested into drilling or the size of the prey item. These results are important for the ecological and evolutionary implications of incomplete drill holes frequencies, especially with regard for their use as proxies for evolutionary prey improvement.

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**Keywords:** *Cancer gracilis*; Drilling predation; Gastropod; *Mytilus trossulus*; Secondary predator

1. **Introduction**

In modern marine environments, predation is a significant agent of mortality. However, evidence of predation in fossils is generally rare, primarily because most predators destroy the prey or leave no traces on any preservable hard parts of the victim. Drilling predation of shelled marine invertebrates by muricid and naticid gastropods represents one of the very rare instances that allow biotic interactions to be evaluated quantitatively in the Recent and in the geologic record. Not surprisingly, drill holes have been used as an important source of information on the nature of biotic interactions and to explore the ecological and evolutionary roles of such interactions (Vermeij, 1987; Kelley and Hansen, 1993; Dietl and Herbert, 2002a,b). For example, the frequency of drill holes has been used to estimate predation intensity (Taylor, 1970; Stanton and Nelson, 1980; Vermeij et al., 1980; Vermeij and Dudley, 1982; Kabat and Kohn, 1986) while frequencies of incomplete drill holes have been used as a measure of failed predation events (but see Kowalewski, 2004) and thus is an indicator of prey-effectiveness (Kelley and Hansen, 2001). In this context, incomplete drill holes are thought to result when a predator abandons its prey because it failed to overcome the prey’s defenses. However, prey abandonment could occur for reasons that have little to
do with the effectiveness of the prey vis-a-vis the predator, for example when the driller is physically interrupted by an external agent such as its own predator, hence referred to as “secondary predator” (Kelley and Hansen, 2003). In fact, behavior of snails may be affected even by the presence of a secondary predator or the mere evidence of its predatory activities. Of course, the probability of being interrupted by a secondary predator may be a function of prey-effectiveness such as when the prey is thicker-shelled, requiring more drilling time and thus increasing the probability of interruption.

An example of the effect of secondary predators has been reported for the Recent mud snail *Nassarius obsoletus* by Atema and Burd (1975). These authors demonstrated that whereas normally the snails scavenge crushed mussels and snails, they departed rapidly when placed in the vicinity of crushed conspecifics. In other studies, it has been shown that snails responded negatively to the presence of crushed conspecifics, but that their escape response was diminished by hunger (Stenzler and Atema, 1977; Morton and Chan, 1999).

If the mere presence of a secondary predator or of its activities can threaten the driller and cause abandonment, the frequency of incomplete drill holes could vary as a function of the presence of secondary predators rather than prey-effectiveness. Even the threat of a secondary predator might affect drilling frequency and thus have consequences for interpreting predation intensity.

The present study was designed to assess the effect of threat of a secondary predator on the drilling behavior of a muricid gastropod, including its effect on incomplete drill hole frequency and overall drilling frequency.

2. Materials

The experiments were conducted at Friday Harbor Laboratory (San Juan Island, Washington, USA). Specimens of the gastropod *Nucella lamellosa* and the mussel *Mytilus trossulus* were collected from nearby False Bay. False Bay is a semicircular bay on the west side of San Juan Island (Fig. 1) with a substrate of fine sand and mud

![Fig. 1. Location map of False Bay in San Juan Island, WA, USA.](image-url)
surrounded by a rocky shoreline. The island has a tidal range of about 4 m enough to cause near total exposure of False Bay at low tide and total immersion at high tide. Both species were collected from rocks and tide pools in the SSE side of the mouth of the bay. *N. lamellosa* are particularly abundant at False Bay, whereas mussels are quite rare. *N. lamellosa* probably prey primarily on barnacles but it has bee shown that mussels are also part of their diet (Kowalewski, 2004) and, while collecting live specimens, six drilled mussels were recovered from this locality. The crab, *Cancer gracilis*, collected during a dredge trip, was selected as a secondary predator; *C. gracilis* is relatively common in False Bay and live specimens of *N. lamellosa* collected for the experiments often possessed repair scars, suggesting that they were frequently attacked by durophages such as *C. gracilis* in their natural habitat (mean temperature 20 °C and salinity 27‰).

After collection, the gastropods were placed in a flow-through sea water table and left without food for a minimum of one week. There was no attempt of cannibalistic drilling observed when the snails were in the sea table. The mussels and crabs were kept in two separate sea water tables until needed. All water tables had a constant flow of seawater.

2.1. Experimental design

To study the effect of the presence of the crab on gastropod drilling behavior, two sea tables with identical dimensions (127 cm × 66 cm × 20 cm), water levels and with a steady and continuous flow of sea water were used. Each sea table contained 100 individuals of *M. trossulus*, from which barnacles, limpets and other epibionts had been removed by careful scraping with a blunt knife to reduce the effect of epibionts or encrusters on susceptibility to predation. Mussels damaged during this procedure or that were heavily encrusted were not used in the experiment.

A total of 200 specimens of *N. lamellosa* were divided into two groups of 100 individuals each. Each individual was marked using a black grease pencil so that their behavior could be monitored.

In both sea tables, roughly 1/6 of the area on the upstream side was separated from the rest by a plastic mesh that allowed free flow of water. In that enclosed upstream area of one sea table (“experimental table”), one crab was introduced twice daily, at 12 h intervals for 30 min. At the same time, 2 crushed *N. lamellosa* were also placed on the upstream side of the mesh in the experimental table. The other sea table (“control table”), without the crab and the crushed snails, served as a baseline for the experiment. In the initial phase of the experiment we tried introducing the crab and the crushed snails separately. There was no significant difference between the effects. We observed that the combined effect was much stronger. So we decided to introduce them together.

Experiments in both tables were started simultaneously by random introduction of 100 predatory gastropods at densities approximately corresponding to natural densities which were allowed to hunt freely. The mussels were separated from each other to prevent clumping, as clumping behavior has been shown to inhibit predators that need to orient their prey during attacks (e.g. Bertness and Grosholz 1985; Cote and Jelnikar, 1999). Whenever a gastropod latched onto a mussel, both predator and prey were isolated by using a meshed plastic cage. We wanted to monitor the effect of the presence of secondary predator on the snail’s drilling behavior. After latching onto a mussel if they were not separated from the rest of the snails, most frequently they were disturbed by other snails. In that case it would have been really difficult to recognize whether the effect

![Fig. 2. In the left, a shell of *Mytilus trossulus* with incomplete drill hole produced by *Nucella lamellosa* in the experimental sea table. In the right, a close up view of the incomplete drill hole.](image-url)
was a result of the disturbance caused by a conspecific or a secondary predator. Use of the plastic cage solved the problem. Secondly, although we marked the snails, during the drilling sometimes they orient themselves in such a way that it is impossible to see their marking. So it was much easier to identify them once and mark their cage with the same number. That way every time when taking a reading, we did not have to look for the mark on the snail. Time from latching through consumption and release was used as an estimate of handling, drilling and feeding time. The tanks were monitored every 3 h during daylight hours (6 A.M.–9:30 P.M.). Detailed observations of the snails and mussels were also made just prior to the introduction of the crab and 30 min after it had been introduced. There was no observation made at night (9:30 P.M.–6 A.M.). The only data that might have been affected by the lack of observations at night would be for drilling time. When estimating drilling time, we considered the factor and calculated the maximum or minimum estimate. Temperature and salinity in both sea tables were monitored throughout the duration of the experiments (mean temperature 16 °C±3 °C and salinity 29 ‰±1 ‰).

When a mussel was killed or abandoned with an incomplete drill hole present (Fig. 2), it was removed from the sea table and replaced by one of similar size. If the mussel retained considerable soft tissue, the specimen was preserved in alcohol (99%). Otherwise the mussel was washed and dried.

Table 1
Table summarizing all the results of predatory attacks in two sea tables

<table>
<thead>
<tr>
<th>Events</th>
<th>Control sea table</th>
<th>Experimental sea table</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Crab present</td>
<td>Crab absent</td>
</tr>
<tr>
<td>Successful attack</td>
<td>Drilled (complete)</td>
<td>78</td>
</tr>
<tr>
<td></td>
<td>Undrilled (dead)</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Abandoned (dead)</td>
<td>0</td>
</tr>
<tr>
<td>Failed attack</td>
<td>Incompletely drilled</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Abandoned (alive)</td>
<td>8</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Events</th>
<th>Control sea table</th>
<th>Experimental sea table</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Crab present</td>
<td>Crab absent</td>
</tr>
<tr>
<td>Successful attack</td>
<td>Drilled (complete)</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Undrilled (dead)</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Abandoned (dead)</td>
<td>2</td>
</tr>
<tr>
<td>Failed attack</td>
<td>Incompletely drilled</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Abandoned (alive)</td>
<td>38</td>
</tr>
</tbody>
</table>

Fig. 3. a) Frequency of different results of attacks in two sea tables by the drilling predator *Nucella lamellosa*. Results are presented up to one decimal place. The black bar represents the control sea table and the white bar represents experimental sea table. The first three results (drilled, undrilled (dead), abandoned (dead)) are considered as successful attacks. The last two results (incompletely drilled, abandoned (live)) are considered failed attacks. b) Sketch showing the sequence of abandoning a prey. Time elapsed between A and C is approximately 15 min. In this case the snail did not leave any predation mark on the mussel.
3. Results

3.1. Impact on overall drilling frequency

Snails in the two sea tables attacked a total of 181 out of 324 individuals of *M. trossulus* (Table 1). Fatal attacks, where the snail killed and consumed (fully or partially) the soft parts inside the mussel, were considered successful. Success rates were significantly different in the two tables. In the experimental table, 26% of the attacks were successful (24 dead mussels), whereas in the control table 89% of the attacks were successful (79 dead mussels) \((p \ll 0.05)\). Of all the successful attacks, 97% involved drilling: one dead Mytilus from the control table and three from the experimental table were found without a drill hole. The shells of the four victims without drill holes were gaping. The one from the control table had no soft tissue left, whereas the three mussels from the experimental table had some soft tissue inside, as the snails abandoned them when the crab was introduced. Since no edge drill holes or other damage to the shells was detected, it would be impossible to identify them as victims of successful predation without having observed the attacks. Although in the experimental table successful attacks without drilling were more common, the difference between the tables was not statistically significant.

During unsuccessful attacks, the snail either abandoned the prey, leaving behind an incomplete drill hole, or left no visible trace. In 53% of the attacks in the experimental table, snails abandoned their prey leaving no trace, while in the control table only 9% of the attacks resulted in abandoned prey without any trace (Fig. 3a and b). This difference is statistically significant \((G=91.4, p \ll 0.05, \text{Likelihood-ratio test})\).

In the experimental table, the success rate of attacks depended on the presence of the crab and crushed conspecifics: in their presence, in 89% of cases \((n=63)\) the prey was abandoned; in their absence, abandonment occurred in 43% of cases \((n=30)\) \((G=21.2, p \ll 0.05, \text{Likelihood-ratio test})\) (Fig. 4).

3.2. Impact on frequency of incomplete drill holes

The frequency of incomplete drill holes in the experimental table \((21.5\%)\) was significantly higher than in the control table \((1.1\%; G=23.6, p \ll 0.05, \text{Likelihood-ratio test})\). Only one incompletely drilled mussel was recovered from the control table, and it was exceptionally big and thick \((\text{length}=46.27 \text{ mm}, \text{thickness}=1.42 \text{ mm}; \text{for the mussels in the control table, mean length}=27.68 \pm 7.17 \text{ mm and mean thickness}=0.66 \pm 0.22 \text{ mm})\). In the experimental table, two shells with one complete and one incomplete drill hole were found (Fig. 5a). In each instance a single snail produced both holes and was observed to relocate when the crab was introduced; presumably, the incomplete hole was produced initially, prior to disturbance and the complete hole subsequently. This suggests that these snails lack the ability to reoccupy the same spot when perturbed (c.f. Kelley and Hansen, 2003).

In the control table, one mussel had two complete drill holes, one on each valve (Fig. 5b). Two separate individuals were observed attacking this mussel and drilling simultaneously.

3.3. Time and/or size dependence of the incomplete drill holes

The median size of mussels with incomplete drill holes is 26.08 mm whereas the median size of completely drilled mussels is 28.63 mm, but this difference is not statistically significant \((W=222, p=0.52, \text{Wilcoxon rank test})\). The lack of statistical significance might suggest that there is nothing of interest in this result, but this is not the case. The statistical test assumes that the median sizes of completely and incompletely drilled mussels should be the same \((\text{Ho: median}_{\text{complete}}=\text{median}_{\text{incomplete}})\), whereas one ought to expect them to differ: the median size of the incompletely drilled mussels should be larger than that of the completely drilled mussels because smaller mussels have thinner shells and are presumably easier to handle, and on average it should take less time to drill a complete hole in a smaller mussel \((\text{Ho: median}_{\text{complete}}<\text{median}_{\text{incomplete}}})\).
The observed pattern is qualitatively opposite to this prediction, but to assess it quantitatively, a computer simulation was developed.

The variables used in the simulation were chosen such that the number and size of mussels and the number of complete and incomplete drill holes were similar to those in the actual experiments. In the computer simulation, 45 mussels were “attacked” and occupied by snails instantaneously at time $t=0$. The drilling rate was obtained from regressing drilling time on mussel size for individuals that had been drilled to completion in the experimental table (sea table 2) (Fig. 6).

At each time increment, each snail could continue drilling its prey, consume its prey if it had penetrated the shell (complete drill hole), or abandon its prey with a probability, $P_r$ (abandon). The probability of abandoning the prey was held constant in each time increment; it was calculated based on the observed proportions of incomplete (20/45) mussels in the experimental table. In each time increment, a tally was kept of mussels that had been penetrated and these were placed in a category “completely drilled”; abandoned mussels could not be re-occupied and were placed into a category “incompletely drilled.” Each simulation was run for 200 time increments, equivalent to 200 h. Given those parameters, at the end of each simulation approximately 20 mussels were incompletely drilled while 25 had complete drill holes, just as in the actual experimental observations. The distributions of sizes in each of the two categories as well as the median of each distribution were determined (Fig. 7). A metric, MEDDIF, the difference in median size between “completely drilled” and “incompletely drilled” was calculated; by repeating the simulation 1000 times, a frequency distribution of the MEDDIF metric was obtained.

As the simulation results illustrate (Fig. 8), the mode of the frequency distribution of MEDDIF, the differences
in the median sizes of completely and incompletely drilled mussels, is negative (−2.3 mm), in other words, the median size of completely drilled mussels is smaller than that of incompletely drilled mussels. These results are in contrast to the experimentally observed difference in median sizes of complete and incomplete mussels which was positive (2.5 mm). A comparison between the observed difference to the results of the simulation, indicates that the two are significantly different at \( p < 0.05 \) (in more than 900 simulations, the difference in median size was smaller than the observed difference in median size). This confirms our qualitative predictions and indicates that the observed differences in median sizes of completely and incompletely drilled mussels are significantly different from the null expectation, perhaps implying something about the behavior of snails.

What other mechanism could explain the slightly larger median size of completely drilled mussels? One possibility is that snails do not abandon their prey with constant probability when disturbed. For example, if a snail had already invested significant time, and thus energy, into drilling its prey, it would be less likely to abandon the prey when disturbed, than if it had invested little time into drilling its prey. Because it takes more time to penetrate a larger, thicker mussel, on average a snail occupying a larger mussel has occupied it longer than a snail occupying a smaller mussel and, if the probability of abandoning the prey decreases as a function of the time of occupation, smaller prey would be more likely to be abandoned. Thus larger prey would be preferentially drilled to completion. The same pattern would result if snails somehow recognized the size of their prey and were less likely to abandon larger than smaller prey. Henceforth, the former scenario will be referred to as “time dependent” and the latter as “size dependent”.

To explore the “time dependent” and “size dependent” scenarios described above, the computer simulations used previously were modified by adjusting the probability of abandoning prey, \( Pr(\text{abandon}) \). In the time dependent scenario, the snail’s tenacity increases with time, i.e., the probability of abandonment drops with time. This was simulated by decreasing the probability of abandonment in each of the time increments by a factor of \( 20/t \), where \( t \), time, ranges from 1 to 200. The results of 1000 simulations are summarized by the solid line in the same figure (Fig. 9). Note that the distribution has now shifted towards an increase in median size of the complete drill holes, and thus a decrease in the median size of the incomplete drill holes. Although the mode of this distribution is around 0, the experimentally observed difference of 2.5 is not statistically distinguishable from the distribution.

Finally, the simulation approach was used to evaluate the size dependence scenario. In this case, the probability of abandonment was time independent but varied as a function of the size of the prey (mussel), such that \( Pr(\text{abandon}) \) was proportional to the reciprocal of size (1/size), in other words, snails held onto larger mussels with greater tenacity. Fig. 10 illustrates the results of 1000 simulations. Again, the dashed line represents results of the null model (time and size independence) whereas the solid line, results of the size dependent model.
dependent model. The latter shows a shift in the distribution of the difference in the median sizes of completely drilled and incompletely drilled mussels towards the experimentally observed value of 2.5.

The simulations confirm that the experimentally observed sizes of completely and incompletely drilled mussels are indicative of snails possessing a complex predatory behavior. This behavior might be influenced by the size of their prey or by the time they have already invested into obtaining a meal. Neither the results nor the simulations allow discriminating between these options, but these hypotheses are testable with future experiments or observations.

4. Discussion

In reconstructing the record of drilling predation from fossils, paleontologists commonly rely on data on drilling frequencies. Although different techniques exist for calculating predation intensity using drilling frequency data (Kelley and Hansen, 2003), the basic assumption is that the drilling frequency is an indicator of the relative performance of predator and prey, performance that is a reflection of their intrinsic properties. But as this study clearly shows, extrinsic ecological factors might be extremely important in affecting drilling frequencies. In this study, N. lamellosa drilling frequencies were significantly lower in the presence of a secondary predator (24% vs 66%), in spite of the fact that the intrinsic properties of the predators and prey remained constant.

While in any given situation it might be difficult to evaluate the magnitude of the impact of secondary predators on drilling frequencies, this study suggests that when evidence of the presence of such secondary predators, either direct or indirect (shell breakage caused by crab claws, for example), exists, the recorded drilling frequencies might be lower than they would have been otherwise.

As for incomplete drill holes, these have been widely used to estimate the frequency of unsuccessful predatory events, both in recent (Vermeij et al., 1989; Dietl, 2000) and fossil faunas (Vermeij, 1987, 2002; Kowalewski, 2002; Kelley and Hansen, 2003, 2006). The observations by Kowalewski (2004) on muricids, suggest that incomplete drill holes may overestimate the frequency of failed attacks because in some instances incompletely drilled prey were, in fact, killed. However, as this study demonstrates, incomplete drill hole frequencies might sometimes underestimate unsuccessful predatory attacks since an incomplete hole was produced in only 29% of the failed attacks in the experimental table; in 71% of cases, failed attacks left no mark on the prey.

The frequency of incomplete drill holes has often been used as an indicator of “prey-effectiveness” which is defined as the ratio of incomplete to complete attempted drill holes (complete + incomplete) (Vermeij, 1987). Increase in the frequency of incomplete drill holes has been interpreted as evidence of effective resistance against drilling predation. The metric of prey-effectiveness has also been used to document the dynamics of the escalation between drillers and their victims (In Vermeij, 1987, p. 311). Using this metric with data from the present study would suggest a 22-fold difference in “prey-effectiveness” between the control (1% of total attack) and experimental (22% of total attack) tables, but given that the prey and drilling predators in both sea tables came from the same populations, the difference is not a measure of adaptive differences in resistance against drilling predators, but rather a consequence of the presence of a secondary predator. It also represents an example of one of the two main emergent effects that is a risk reduction caused by predator–predator interaction (Sih et al., 1998).

The incomplete drill hole data clearly suggest more complex behavior by predatory snails than simple abandonment of prey when a secondary predator is introduced. As shown through simulations, in the presence of a secondary predator the decision by the snail to either abandon or continue drilling its prey might be “time dependent” or “size dependent”. Although it is difficult to distinguish between these two scenarios, the “size dependent” scenario assumes that the snail has the ability to assess the size of its prey. Since such an ability should also be expressed by the snail while foraging, snails should select their prey based on size (“optimum foraging strategy”, Krebs, 1977). If there is no appreciable size difference between attacked and non-attacked prey, “size dependence” can be eliminated as a plausible scenario. Unfortunately, the methods employed in this study do not allow for a test of such size selectivity.

Other results of this study with potential impact on the use of drill hole frequency data for estimating predation intensity relate to facultative predatory behavior. In this study, 13% of the prey were killed by N. lamellosa without drilling in the experimental table and only 2% in the control table, although the differences are not statistically significant. Such facultative predatory behavior has been observed among many drilling predators including naticids (Vermeij, 1980; Ansell and Morton, 1987; Kabat, 1990; Kelley and Hansen, 2003), octopods (Steer and Semmens, 2003) and muricids (Taylor et al., 1980; Kent, 1981; Moran, 1985; Gutiérrez and Gallardo, 1999; Vermeij and Carlson, 2000); in some instances,
more than 10% of the prey were killed without drilling (Vermeij, 1980:330). The exact cause of death of the prey in these examples is unclear. In some instances it has been suggested that it may represent unsuccessful attempts to drill (Kowalewski, 2004). For example, in aquarium experiments, Ansell and Morton (1987) observed the naticid Glossaulas didyma consuming some of its prey without drilling a complete hole; apparently, prey were suffocated during the initial phases of drilling. In the present study, however, the lack of associated incomplete drill holes makes it difficult to assess whether drilling was even attempted. Perhaps death resulted from prey having experienced prolonged contact with the attacker (e.g. prey anesthesia by secretions from the hypobranchial gland; Moran, 1985; Taylor and Morton, 1996). Regardless of the exact cause of death or nature of predatory behavior, the killing of prey by drilling predators without drilling may be a relatively frequent phenomenon (Vermeij and Carlson, 2000), suggesting that drill hole frequencies might often be an underestimate of the intensity of interactions between drilling predators and their prey.

5. Conclusions

Drill holes in the shells of invertebrates represent one of the most unambiguous signatures of predator–prey interactions and have been commonly used by neontologists and paleontologists to explore ecological and evolutionary questions. While complete holes are by far the more common, frequency of incomplete holes is also informative and has often been invoked as a proxy for prey-effectiveness. Incomplete holes may be produced in several ways; here the impact of a secondary predator on incomplete drilling was investigated experimentally. Using the drilling muricid, N. lamellosa (Gmelin, 1791) and its prey, the mussel M. trossulus (Gould 1850), the frequency of incomplete holes was compared under two conditions: (1) when the gastropod’s natural predator, the crab C. gracilis, was present and (2) when it was absent. The presence of a secondary predator affected drilling activity, resulting in a significant increase in the frequency of incomplete drill holes. In the presence of a secondary predator, the overall drilling frequency also decreased. The decision by the gastropod to either abandon or continue drilling its prey when a secondary predator is present might be influenced by how much time it has already invested into drilling its prey, as shown by computer simulations. These results might have important consequences for the ecological and evolutionary implications of incomplete drill hole frequencies, for example, for their use in evaluating the evolutionary improvement of prey. Our future research will be directed to evaluating these effects using data from the Recent and fossil record.

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