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# The bigger they are the better they taste: size predicts predation risk and anti-predator behavior in giant clams

G. C. Johnson, M. T. Karajah, K. Mayo, T. C. Armenta & D. T. Blumstein

Department of Ecology and Evolutionary Biology, University of California Los Angeles, Los Angeles, CA, USA

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**Correspondence**
Daniel. T. Blumstein, Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive South, Los Angeles, CA 90095-1606, USA. Email: marmots@ucla.edu

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## Abstract

The decision to hide from predators and the time allocated to hiding are economic decisions that integrate the benefits of escaping a predator and the costs of reduced resource acquisition. Body size is a factor that influences many antipredator decisions. Giant clams, *Tridacna maxima*, depend on photosynthesis as their main source of energy; thus, retracting their mantle into their shell inhibits energy acquisition and ultimately growth. We experimentally encouraged 95 individual clams to hide by touching them and found that after accounting for variation explained by observer, larger clams remained closed longer. When we looked at the response of these 95 clams to a total of four consecutive experimentally induced closings over about 10 min, we found that larger clams on average hid longer and that clams had individually consistent hiding times and generally habituated to repeated experiments. We then focused on a subset of 30 clams and continued this experiment every other day over 6 days for a total of four sessions. Over this longer duration, clams consistently habituated to repeated disturbance, but the effect of size disappeared. We also found that larger clams were bitten by predators more often than smaller clams. Large clams pay an immediate cost to hiding from benign stimuli and apparently learn to modify their behavior to repeated benign experiences.

## Introduction

Predation is a strong selective force that has generated a diverse set of behavioral adaptations (Lima & Dill, 1990; Caro, 2005). Prey frequently engages in a variety of escape behaviors to avoid predation when the benefits of escape outweigh its costs (Cooper & Blumstein, 2015). Hiding in a refuge is one such form of escape where the decision of how long to hide is based on balancing the benefits of predator avoidance against several potential costs (Martín, López & Cooper, 2003). These costs may include reduced foraging time (Dill & Fraser, 1997), lost mating opportunities (Cooper, 1999), greater risk of territorial intrusion (Elwood & Appel, 1998), and physiological costs arising from suboptimal conditions inside refuges (Wolf & Kramer, 1987). A potential indicator of an animal's perception of predatory threat can thus be measured by quantifying hiding time (Cooper & Blumstein, 2015; Martín & López, 2015). Formally, hiding time is the elapsed time between entry into a refuge and emergence from the refuge (Cooper & Blumstein, 2015; Martín & López, 2015).

Shelled species, such as hermit crabs and clams, have a built-in refuge and respond to perceived threats by closing or retreating into their shell (Scarratt & Godin, 1992; Soo & Todd, 2014). Giant clams, specifically *Tridacna maxima*, are a suitable species to study hiding behavior because they retract their mantle and close their shell when threatened and hiding time is easily observed (Todd, Lee & Chou, 2009). Furthermore, giant clams have a symbiotic relationship with photosynthetic dinoflagellates, zooxanthellae (Kawaguti, 1950). These zooxanthellae provide the clam with its main source of energy (Klumpp, Bayne & Hawkins, 1992); thus, while closed, clams cannot photosynthesize and are therefore directly reducing energy intake (Soo & Todd, 2014). For giant clams, safety from predators comes directly at the expense of growth – the fundamental life-history tradeoff that all animals face (Stearns, 1976). This is even more important in the predator-rich marine environment because rapid growth is selected since being larger is correlated with reduced predation risk (Sogard, 1997).

Energetic constraints (Schmidt-Nielsen, 1984) and predation risk (Preisser & Orrock, 2012) vary with body size and should therefore explain variation in antipredator behavior. For clams, the mantle becomes proportionally smaller as size increases (Griffiths & Klumpp, 1996), and thus we would predict larger clams to emerge sooner to photosynthesize. Larger clams also have thicker mantles and therefore require higher light intensity to penetrate the mantle to undergo photosynthesis (Fisher, Fitt & Trench, 1985) and this too would predict that larger clams would emerge sooner to photosynthesize. However, large individuals may be more profitable to predators and therefore may be targeted by predators (Koga *et al.*, 2001). In this case, we expect larger clams to hide longer. Finally, larger clams may have more energy stores and therefore may be able to afford to hide longer than smaller clams.

Although hiding offers safety, escape behavior is energetically costly and animals should habituate to repeated exposure to non-threatening stimuli. We know that body size explains interspecific variation in habituation. Samia *et al.* (2015) found that larger bird species reduce flight initiation distance more than small bird species in populations around humans compared to populations that do not occur near humans. These findings suggest that larger species may be under more pressure to tolerate non-lethal intrusions, perhaps because the energetic cost of fleeing is higher with increased mass. We do not know if intraspecific variation in body size explains variation in habituation; however, if the same logic applies, we predict that it is more costly for larger individuals to respond to benign disturbances and that these large individuals will therefore habituate more quickly to repeated disturbances.

To test these predictions, we repeatedly probed giant clams on two time scales and asked: (1) whether hiding time increases or decreases with body size, (2) if individuals are consistent in their hiding time response, (3) whether large individuals habituate to benign stimuli faster than small individuals and (4) do larger clams experience increased predation?

## Materials and methods

### Data collection

Between 21 January and 9 February 2016, from 07:30 to 11:30 h and 13:30 to 17:30 h, we studied hiding time of giant clams in two Marine Protected Areas along two fringing reefs in Mo'orea, French Polynesia. We tested $N = 70$ clams in Gump Reef, Cooks Bay (17°29′25.0″S, 149°49′33.1″W) and $N = 25$ clams in between Motu Fareone and Motu Tiahura Islands (17°29′21.0″S, 149°54′56.3″W). Gump Reef is dominated by sandy areas and highly eroded coral covered in algal turf and various macroalgal species (Fong & Fong, 2014). Les Motus Islands has a more pristine reef with live coral cover and sandy substrate (Wilson, 2009). Clams occurred at 0.5–1.1 m deep and were studied in 29.5–30.5°C water. To study the effect of clam size, we measured maximum shell diameter (range: 3–30 cm).

For the first experiment, 95 clams were tested over a period of 4 days. Seventy clams were tested in Gump Reef, while 25 were tested in the channel reef between Les Motus Islands. Each observer ($N = 3$) experimentally disturbed an average of 7.8 clams per day. Clams respond to predators by retracting their mantle. Based on pilot observations, clams do not respond to snorkelers when they are >1–2 m away; thus, each observer stopped at a distance of 1–2 m away to standardize treatment. The snorkeler then approached a targeted clam with a white 2 m long, 1.9 cm diameter, PVC pipe and pushed the pole toward the clam until it tapped the external shell once. We were careful to tap each clam with the same force, as well as push the pipe toward the animal at the same constant rate. Hiding time was measured to the nearest second using a stopwatch. We defined hiding time as the interval between when the clam fully closed and when the mantle reemerged and returned to a relaxed state (not tensing or closing its shell). After recording each hiding time, we waited 2 min before performing the next trial. This was done four consecutive times for 95 individual clams. Overall, most clams remained closed for <30 s. After testing, each individual clam was marked by nailing flagging tape into adjacent coral bommies (ensuring that the tape did not disturb the clams) to avoid accidental retesting.

In a second experiment, we tested 30 of the 70 clams marked on the Gump Reef. Over the course of 7 days, these 30 clams were tested every other day, resulting in four sessions. We recorded hiding time using the method previously described. This repeated exposure to a benign stimulus was used to test for both consistent individual differences as well as longer term changes in anti-predator behavior (Biro & Adriaenssens, 2013).

Predators regularly take bites out of clam mantles (Eckman, 2014). In order to quantify the number of bites, we photographed each of the 95 clams in the first experimental set using a FujiFilm FinePix XP80 waterproof digital camera (FUJIFILM Corporation, Tokyo, Japan). Each photograph was taken immediately after testing each individual in order to ensure it did not have an effect on the clam's behavior. From the photographs, we counted the total number of bites in each clam's mantle. Over the course of our repeated observations conducted over 11 days, we saw bites begin to heal; these were obvious by their color difference. In addition, it is important to note that although both scars and 'fresh' bites were observed on clam mantles, we only counted the 'fresh' bites.

### What explains variation in initial hiding time?

To explain the overall variation in hiding time for all 95 clams, we fitted a general linear model (GLM) in JGR using the Deducer interface (Fellows, 2012) in R version 3.2.3 (R Core Team, 2015). In the GLM, we included clam size and observer as predictor variables to control for these effects, while the outcome variable was how long a clam hid the very first time it was tapped. We calculated the relative importance of each of these variables using the relaimpo package in R (Groemping, 2007). Hiding time was $\log_{10}$ transformed to achieve data normality. We tested the assumptions of the GLM by examining residuals. Residuals were normal and there was no reason to exclude outliers.

### Do individual clams respond to threats in consistent ways?

Using the lme4 package in R (Bates *et al.*, 2015), we fitted a series of mixed effects models to explain variation in $\log_{10}$ hiding time in order to assess behavioral repeatability. We assessed short-term consistent individual variation on the full, 1-day dataset ($N = 95$) and longer term repeatability on the subset of individuals that were tested for 4 days ($N = 30$). To evaluate within clam repeatability, we first created a null model where individual was set as a random intercept. Second, because we expected clam size and observer to influence hiding time, we created a mixed model with individual as a random variable and these fixed effects for the 1-day dataset. For the 4-day dataset ($N = 30$), we created a similar mixed model and added the fixed effect of day.

## Do clams habituate to benign stimuli on short or longer term time scales?

We then created a mixed model with a random intercept for individual and random slope for trial for both the 1- and 4-day datasets. Here, the random slope allows us to evaluate two predictions: whether individuals habituate to probing across trials and whether large clams habituate more quickly to the perceived threat than small clams. We evaluated these models using a likelihood ratio test and then compared the best of these three models to a linear model, without the random effect of individual, to evaluate whether individuals significantly differed in their hiding time response from each other for both datasets. We tested the assumptions of these mixed models by examining residuals. Residuals were normal and there was no reason to exclude outliers.

## Is clam size a predictor of attacks?

Finally, to assess whether large clams are more susceptible to predation than small clams, we correlated size with the number of bites taken out of the mantle. Residuals were normal and there was no reason to exclude outliers.

# Results

In the full dataset of giant clams ($N = 95$), our GLM significantly predicted $\log_{10}$ hiding time. After controlling for variation explained by observer (relative importance 0.78), we found that clam size (relative importance = 0.22) was significantly and positively associated with hiding time (estimate = $0.010 \pm 0.004$ SEM), $P = 0.021$, Fig. 1). This model significantly ($P = 0.001$) explained 14.2% of the variation in clam hiding time. To ensure the largest clam was not driving the relationship between size and hiding time, we removed this potential outlier (size >30 cm) and re-fitted the GLM. Results were similar: observer (relative importance 0.72), claim size (relative importance 0.28; estimate = $0.013 \pm 0.005$ SEM, $P = 0.010$).

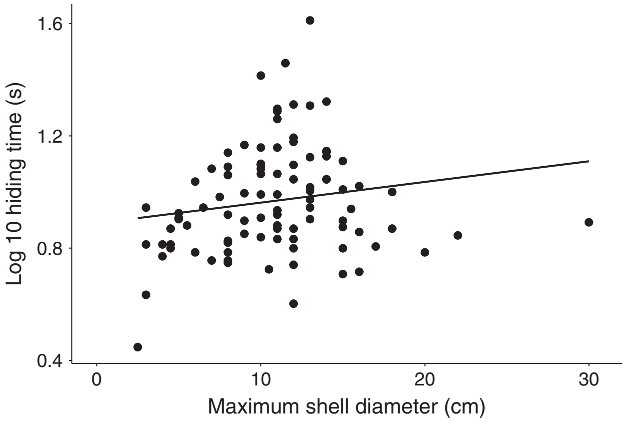

**Figure 1** The relationship between a giant clam's maximum shell diameter and initial hiding time (in seconds, $\log_{10}$ transformed). The regression line shows that as clam size increased, so does initial hiding time, after controlling for the effects of observer and trial.

For our four trial-1 day experiment, the model that best explained hiding time in clams was the random intercept-random slope model (Table 1a). This mixed model included clam size (estimate = $0.0123 \pm 0.003$ SEM, $P = 0.0001$), observer (obs1: estimate = $-0.252 \pm 0.031$ SEM, $P = 2.67e^{-12}$; obs2: estimate = $-0.067 \pm 0.034$ SEM, $P = 0.049$), and trial (estimate = $-0.016 \pm 0.005$ SEM, $P = 0.005$) as fixed effects, while allowing individuals to also have random slopes for trial. After controlling for all covariates, clam size was positively associated with hiding time. Furthermore, the correlation between the random intercept and random slope of trial in this analysis was $-0.72$. This highly negative correlation shows clams that initially hide longer have steeper trial slopes (i.e. they habituate more quickly to the stimulus than clams with lower initial hiding times) (Fig. 2). To estimate the repeatability of hiding time within individuals after controlling for all fixed effects, we calculated adjusted repeatability (Nakagawa & Schielzeth, 2010; function provided by J. N. Audet, pers. comm.). Currently, it is not possible in this program to calculate adjusted repeatability for models with more than one random effect. Thus, we calculated the adjusted repeatability for the random intercept + fixed effects model (Table 1a) and found that 61.4% of the variation in hiding time is explained by between-subject variation.

In our 4-day experiment, the linear mixed effects model with random intercept + fixed effects best explained clam variation in hiding time (Table 1b; Fig. 3). This model included the

**Table 1** Models fitted to explain variation in giant clam hiding time (a) over four successive trials in 1 day, and (b) over four successive trials presented every other day for a total of 4 days (16 trials). Best-fit models are in bold

| (a) Description | Model | AIC |
|---|---|---|
| Random intercept | Log$_{10}$HT ~ (1 \| clam) | −432.7 |
| Random intercept + fixed effects | Log$_{10}$HT ~ size + observer + trial + (1 \| clam) | −485.0 |
| Random intercept + random slope | **Log$_{10}$HT ~ size + observer + trial + (1 + trial \| clam)** | **−496.0**[a,b] |
| Linear model | Log$_{10}$HT ~ size + observer + trial | −321.7 |
| (b) Description | Model | AIC |
| Random intercept | Log$_{10}$HT ~ (1 \| clam) | −656.7 |
| Random intercept + fixed effects | **Log$_{10}$HT ~ size + observer + trial + (1 \| clam)** | **−728.1**[c,d] |
| Random intercepts + random slope | Log$_{10}$HT ~ size + observer + trial + (1 + trial \| clam) | −724.8 |
| Linear model | Log$_{10}$HT ~ size + observer + trial | −572.1 |

[a] Comparison to basic random intercept + fixed effects model $P = 3.27e^{-14}$.

[b] Comparison to basic linear model $P < 2.2e^{-16}$.

[c] Comparison to basic random intercept model $P = 2.36e^{-16}$.

[d] Comparison to basic linear model $P = 1.439e^{-11}$.

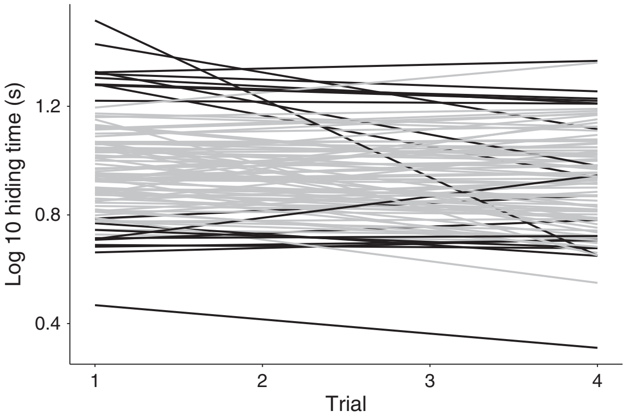

**Figure 2** The relationship between four successive trials in 1 day on giant clam hiding times ($\log_{10}$ transformed). To illustrate differential habituation to repeated testing, the 10 clams with the highest and lowest initial hiding times are shown in black, while all others are in grey. Clams with high initial hiding times have highly negative slopes while those with low initial hiding times have less negative and sometimes positive slopes.

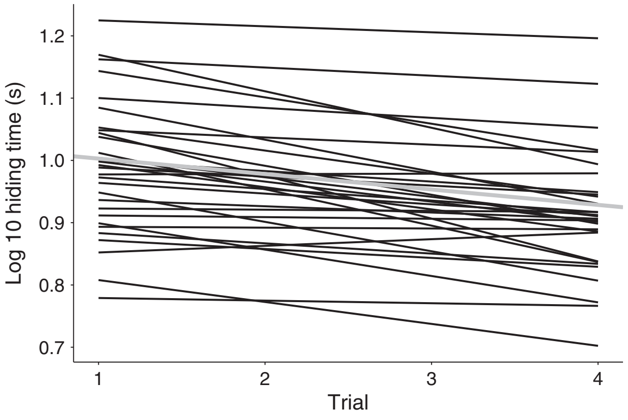

**Figure 3** The relationship between trial and hiding time when four successive trials were presented every other day for 4 days on 30 clams. Black lines indicate an individual's response by trial, averaged across the 4 days. The thick gray line illustrates population level mean response, and the negative slope indicates a general habituation to the stimulus.

random intercept of individual and fixed effects of size (estimate = 0.003 ± 0.004 SEM, $P = 0.395$), observer (obs1: estimate = −0.098 ± 0.014 SEM, $P = 2.93\text{e}^{-11}$; obs2: estimate = −0.095 ± 0.018 SEM, $P = 2.67\text{e}^{-7}$), and trial (estimate = −0.025 ± 0.004, $P = 9.07\text{e}^{-9}$). Adding the fixed effect of day to the model did not significantly improve model fit. Because the random slope of trial was not included in the best model for this dataset, we found that individual clams do not differ in how they respond to probing in the longer term. We calculated the adjusted repeatability for this model as before, and found that 41% of the variation in hiding time is explained by between-clam differences.

Finally, we found that the number of bites seen on the mantle, measured once on the 95 clams, was positively and significantly associated with clam maximum shell diameter (Pearson's $r = 0.27$, $P = 0.010$, Fig. 4). Again, to ensure that the large clam was not driving this relationship, we removed it and reran analysis. The results were very similar (Pearson's $r = 0.23$, $P = 0.028$).

## Discussion

As predicted, we found that size influenced giant clam hiding time following an experimental disturbance. When studied once, or across four trials within a single day, larger clams hid significantly longer than smaller clams. These single day results reject the three hypotheses that predict a decrease in hiding time as size increases, but are consistent with the hypothesis that because larger clams are more attractive to predators, they are more frequently targeted as prey, and must close their shell for longer periods to prevent attacks. This suggests that the cost of predation may outweigh the energetic costs of remaining closed. Interestingly, when studied over 4 days, the effect of size disappears as does the variation in degree of habituation, since the random slope is no longer included in the best model. Figure 3 shows that with more sampling, all individuals show similar patterns of habituation. Initially, size matters, but ultimately benign repeated experimental tests drive all clams to habituate.

Large clams are more profitable prey and, because they are also sessile, predators that detect a larger clam may benefit by waiting for it to open. Additionally, larger clams have more abundant energy stores, and therefore can afford to hide for longer. Consequently, it would be in the best interest of the clam to stay closed for longer and wait out an attack rather than to reopen sooner. There also may be selection on hiding time. If clams that tend to stay hidden for longer are more likely to survive recurring predatory threats, this would result in a higher proportion of large clams that are more cautious and have higher mean hiding times.

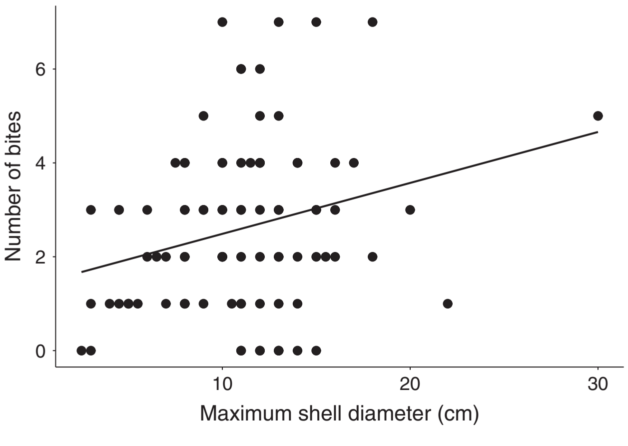

**Figure 4** The relationship between the maximum shell diameter and the number of bites detected on giant clam mantles. Larger clams received more bites by predators.

An alternative hypothesis is that smaller (and therefore younger) clams are under strong selective pressure to grow fast. Blumstein & Pelletier (2005) found that for yellow-bellied marmots *Marmota flaviventris*, the value of food is greater for young because they need to gain sufficient body mass to survive their first hibernation. This same logic can be applied to small clams. In an aquatic environment, larger individuals, on average, are safer (Sogard, 1997). Smaller clams may have reduced growth if they hide longer following disturbance compared to larger clams. Thus, there may be selection for small, young clams to be relatively bold and re-emerge sooner. Hence, the relative cost of hiding is higher for smaller clams, resulting in shorter hiding times.

The addition of clam identity consistently explained variation in clam hiding time. Clam's responses to probing differed significantly from one another and these individual differences were consistent over multiple days. A possible explanation for individual variation in clam hiding time could be due to relative conspicuousness. Crypsis and visible polymorphism are established defense mechanisms to avoid detection by visual predators (Endler, 1978). In fact, a study using plaster models of Australian rock dragons found that 'bright' models were attacked significantly more often than 'dull' models suggesting that differential conspicuousness translates to differential predation risk in the wild (Stuart-Fox *et al.*, 2003). Giant clams range from brilliantly colored to relatively dull, and it is possible that brightness increases predation risk, resulting in longer hiding times, as seen in male rock lizards (Cabido *et al.*, 2008).

Clams may also have to learn to respond to predation risk appropriately and both our 1- and 4-day results suggest that they do. Trial significantly and negatively predicted hiding time in our best-fit models for both of these datasets, suggesting that after repeated disturbance, clams habituate to the benign stimulus and emerge sooner. In addition, the highly negative correlation between an individual's random intercept and random slope across trial suggests that clams that begin with higher hiding times habituated more quickly to the benign stimulus than clams with shorter hiding times. This may reflect the hypothesis that young animals generally have to learn to respond in optimal ways to risk (Martín & López, 2015). For instance, young vervet monkeys, *Chlorocebus pygerythrus*, initially emit alarm calls to a wide variety of species, including non-predators. As they get older, monkeys apparently learn to differentiate between benign and harmful stimuli (Cheney & Seyfarth, 1990), but such habituation is rarely studied experimentally in the field.

Size is undoubtedly correlated with age, but we believe that it was the size, not the age that modulated clam behavior. This is because the clams we studied were under constant attack. Like other studies (Ozog, 2009; Eckman, 2014), we found that fish regularly bit clams' mantles and we observed these injuries healing over the duration of our study and new bites appearing. Importantly, healing was fast and since we only recorded 'fresh' bites on the first 95 clams studied, there is no possibility of healing and thus, our results reflect larger clams having a greater attractiveness to predators.

Unlike the natural damage inflicted by predators, our experimental stimulation was benign. If it is costly for clams to close every time they are attacked, there might be strong selection on clams to learn the difference between benign and damaging threats. While constant threats may maintain consistent hiding times, the fact that we also observed consistent habituation profiles suggests that large clams were under the strongest selection to habituate to benign threats. This finding is consistent with an emerging theme in the escape behavior literature that has begun to show that individuals or species that pay the greatest costs to escaping from benign threats have the most to benefit from habituation (Samia *et al.*, 2015).

Our results highlight novel insights into the escape behavior of sessile organisms. Most animals flee to a refuge, but many are able to choose their refugia and change to another if attacks persist. An intermediate situation occurs when animals have protective structures, such as shells, but are also able to actively move to safer refuges in their habitat (Martín & López, 2015). Such individuals may decrease their hiding time and switch to active fleeing earlier when predators are present (Mima, Wada & Goshima, 2003). However, there is little known about hiding behavior in species that are predominantly sessile. Species such as polychaete tubeworms, caddis-fly larvae and mollusks can only take refuge in the protective structure surrounding their bodies (Martín & López, 2015). Similarly, the only form of escape behavior for a giant clam is to hide within its shell. Sessile organisms offer a predator the opportunity to simply wait for the prey to re-emerge from hiding, resulting in different predator–prey interactions than those seen in mobile prey.

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