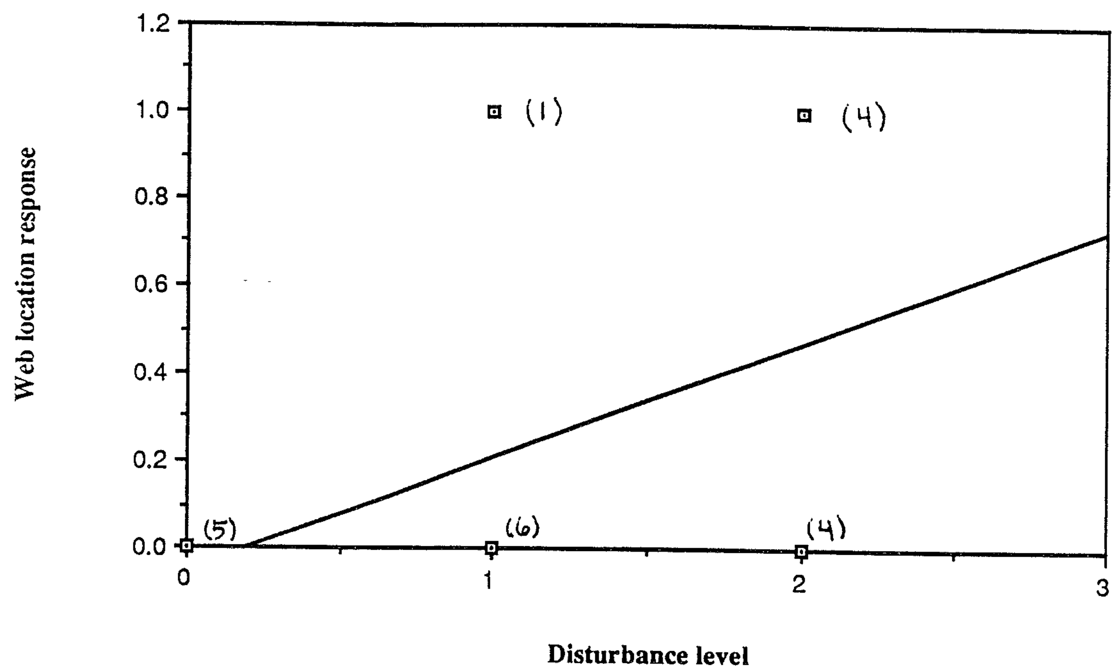
Figure 1 The positive correlation between level of web disturbance and web relocation response in the Golden Orb spider (r=0.487, n=20, p<0.05). The web disturbance was ranked as follows; 0=control, 1=partial web destruction, 2=total web destruction. The web relocation response was ranked as follows; 0=spider remained, 1=spider relocated. Numbers in parenthesis indicate the number of data points represented by each dot. Line slope=0.254.



PREDATOR AVOIDANCE IN HERMIT CRABS (PAGURIDAE)

Abby Bergholtz, Dan Gavin, Vijay Vaswani, and Todd Young

Abstract (A.B.)

We investigated the responses of variously sized groups (1 to 26) of hermit crabs (Paguridae) to simulated threats of predation. We found that for solitary crabs, shell size was positively correlated with time to emergence from shell following a disturbance. However, time to emergence varied more for larger crabs than for smaller crabs. We also found that feeding groups were significantly more likely to flee from a continuous disturbance than solitary crabs, but the percent of crabs leaving within 60 seconds was not correlated with group size.

Introduction (T.Y.)

Hermit crabs (Paguridae) live on and near beaches. They forage individually, but aggregate in shaded areas and feed together - since food is a patchy resource. They are very slow travelers and use empty gastropod shells to protect their fleshy abdomens. We observed that when approached, hermit crabs sense a threat, and retreat completely into their shells. Potential predators on hermits may be raccoons and birds. A predator would be more likely to approach a larger crab and invest more time waiting for its emergence, than a smaller crab due to the size of the potential meal. While it is possible that very small predators may prefer small crabs as prey, we were unable to identify a potential predator that would be so small. We also observed that when a constant threat (simulated by continual motion over the crab) is present for a group of crabs, they retreat into their shells, and then scatter. If a predator attacked a group of crabs that had been feeding, the threat per individual crab would be less than if a predator attacked a solitary crab. This is partially due to a handling time associated with eating each crab. If there is a group of crabs, then it is more advantageous to each individual to run, rather than to remain as a "sitting duck". A solitary crab is the single focus of the attack and its best defense is in its shell. Therefore, besides being forced to feed together due to patchy food, grouping may be beneficial to individual safety.

From these observations and lines of scientific reasoning, we put forth three hypotheses. Our first, dubbed "Predation Pressure"; is that after a sudden shock disturbance, a large crab will be more cautious and remain longer in its shell before re-emergence than a small crab. The second hypothesis, dubbed "Singling Out"; is that during a continuous threat of predation, individual crabs feeding in a group will emerge from their shells and move away from the predator faster than a solitary crab will under a similar threat. Branching from group theory, is that if the group is larger, then the threat there would be per individual is less than if the group were smaller. Following this reasoning, the third hypothesis is that, when placed under a continuous threat of predation, individuals in larger groups of crabs will emerge from their shells and scatter faster than individuals in smaller groups.

Methods (A.B.)

We conducted our study on 23 January 1991, from 8:30 am to 12:00 pm and from 4:00 pm to 5:45 pm. The site of the study was the beach, approximately 400 meters South of the airstrip at Sirena Biological Station, Corcovado National Park, Costa Rica. To test our predation pressure hypothesis (see Introduction) each pair of our 4-person group found and tested solitary hermit crabs. We defined solitary crabs as those with the nearest neighbor greater than one meter away. To simulate a threatening disturbance, we tossed an 11 x 9cm rock to within 20cm of each of 75 focal crabs, and recorded the length of time each crab remained in its shell after the disturbance. We also measured the length and width of each crab's shell.

To test the singling out hypothesis and hypothesis #3, we used 16 aggregations of feeding crabs. An aggregation was defined as a group of two or more crabs within a 20 x $20cm^2$ area. To simulate a disturbance, two people ran up to the crabs, dropped a wire circle (radius = 15cm) around them, marched in place, and waved their arms. The circle of wire was used as an aid in measuring dispersal; it was not also part of the disturbance. We then counted the number of crabs leaving the area enclosed by the wire circle, at 10-second intervals for one minute. We also recorded the total number of crabs in each initial aggregation. The same procedure was performed on 18 solitary crabs. All crabs used to test the second hypothesis were of medium size.

Results (D.G.)

We used the average of shell width and shell length as an index of crab size. Testing the predation pressure hypothesis, we found a significant correlation between crab size and time to emergence after a disturbance ($r^2 = 0.18$ $n = 75$, $p < 0.01$). However, there was a much greater variation in time to emergence for crab sizes greater than 9mm (S.D. = 9.8) than for small shell sizes (S.D. = 4.3) (Figure 1). We tested the singlary out hypothesis by comparing feeding groups and solitary individuals the percentage of crabs leaving a 15cm radius within 60 seconds of constant disturbances between. Individuals

feeding in groups were more likely to flee from disturbance than solitary individuals (Mann Whitney U = 240, n = 18, $n_2 = 16$, $p < .007$, Table 1).

The third hypothesis, that individuals in larger groups flee before individuals in smaller groups was tested using the data collected to test the singling out hypothesis. There was no correlation between feeding group size and percentage of crabs that left a 15cm radius within 60 seconds ($r^2 = .03$, $n = 16$, $p > 0.05$).

Discussion (V.V.)

Our first hypothesis ("Predation Pressure") states that after an instantaneous disturbance, a larger crab would remain longer in its shell before re-emergence than a smaller crab. Our results supported this hypothesis: larger crabs had longer re-emergence times than smaller crabs (Fig. 1).

Larger crabs would be preferred prey for most predators, and so have a greater predation risk. As a predator may invest more time in waiting for large prey to re-emerge, the large crabs should wait longer before re-emergence.

As well as differences in predation risk, it is possible that large and small crabs also differ in experience. The larger (and presumably older) crabs may have more experience of predation attempts and therefore be more cautious. Most of the small crabs have a short re-emergence time (Fig. 1), consistent with relative lack of experience. The large crabs, in contrast, have a high variance in re-emergence times (which may account for the low r^2 value). It is possible that some have learned about the dangers of predation while others have not.

Our second hypothesis, ("Singling Out") states that during a continuous threat of predation, individual crabs in a feeding group re-emerge from their shells and move away from the predator faster than a solitary crab under a similar threat. Our results supported this hypothesis.

We observed that when a solitary crab was subjected to simulated predator threat (approach by an observer) it would immediately retreat into its shell. On continuous threat of predation (stamping of our feed and waving of arms above the shell), 83% of the solitary crabs remained in their shells for their entire 60 second test (Table 1).

This response (dubbed the "nobody home" response) can be explained as follows. A hermit crab is a relatively slow-moving organism, and has little chance of out-running a predator once discovered. Rather than attempting a futile escape and thereby attracting more attention to itself, the crab freezes and withdraws into its shell increasing the chance that the predator will treat the shell as if it were empty ("nobody home"). The 3 solitary crabs that did re-emerge from their shells and move away from the simulated constant predation threat all did so in the latter part of the test minute. However, in a natural predation attempt, the crabs may not re-emerge if handled by the predator.

The crabs in feeding groups immediately retreated into their shells upon approach of the simulated predator. Under continuous predation threat, individual crabs in the groups gradually re-emerged and moved away from the group. During the test minute, 63% of the crabs scattered from the original feeding site. In contrast to most social animals, which aggregate as a defense mechanism against predation, the hermit crabs left the group under predation threat.

Possibly the aggregation of feeding crabs attracts predators. For the individual crab, it would then be advantageous to disperse away from the group, if the group does not in itself confer protection. If there were no dispersal, the predator could easily prey on each individual. Since the predator's attention may be focused on the group, moving away from the group may therefore be the best defense for the individual crab.

It could be possible that the crabs confuse the predator by scattering. However, the crabs moved away from the group at different times, not in a confusing simultaneous scatter.

Our third hypothesis was that individuals in larger feeding groups would emerge and scatter faster than individuals in smaller groups when under continuous threat of predation. With a large number of crabs in a group, an individual crab has a lower risk of being singled out when the crabs scattered, and so would be faster to leave the high risk group. We found no significant correlation between size of feeding group in 60 seconds, we conclude that time of emergence and movement depends on the individual crab and not on the size of the group.

In conclusion, we found larger (and presumably older) hermit crabs to be more cautious than smaller crabs. Most organisms would show increasing caution towards predation with increasing age due to learning and experience. Natural selection may also favor a trend to greater caution as crabs grow if predation risk increases with size. We found the groups of crabs to behave unlike many other known groups of animals (including many fish and birds) that aggregate to reduce predation risk. For the crabs, the group may actually attract predators without benefits to offset this increased risk. Thus, leaving the group under threat of predation is the best defense. For other organisms that group together only to feed, and are solitary of other times, a similar response may exist.

Table 1 Response to disturbance of Paguridea paguridae in feeding groups and in solitary individuals at Corcovado, Costa Rica.

Trail No.	Group Size	Ratio Leaving by 60 sec. of constant disturbance
1	16	0.50
2	20	0.70
3	12	0.83
4	5	0.6
5	8	0.75
6	16	0.56
7	9	0.88
8	4	1.0
9	10	0.60
10	6	0.17
11	7	0.71
12	2	0.50
13	4	0.25
14	4	0.75
15	7	0.57
16	26	0.77
		x=0.63

n=18 Individual crabs; ratio leaving by 60 seconds of constant disturbance = .166

Figure 1 Time of emergence as a function of shell size of Paguridae at Corcovado, Costa Rica.