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DIFFERENCES IN THE DIURNAL AND NOCTURNAL DEFENSE MECHANISMS OF *OCTOPUS BOCKI* (ADAMS, 1941)

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Abstract. Octopuses are known for the advanced behaviors and elaborate displays used in predator avoidance. Although studies have provided anecdotal evidence on the defense mechanisms of these animals, whether these behaviors vary under light and dark conditions is unknown. This study investigated the diurnal and nocturnal predator defense mechanisms of *Octopus bocki* (Adams, 1941) in Moorea, French Polynesia. Seven behaviors were identified as primary defense mechanisms for protection from fish predators during daylight and nighttime hours. Rates of occurrence and durations for defense behaviors significantly differed between diurnal and nocturnal conditions, as *O. bocki* frequently Crawled during the daylight hours, but sat still and Curled during the nighttime hours. Results indicate that *O. bocki* modifies predator defense behaviors for survival under light and dark conditions.

Key words: octopus signal transmission, antipredator defense mechanisms, diurnal and nocturnal behaviors, predation

INTRODUCTION

Animals evolve antipredator defenses that account for biotic and abiotic factors that may inhibit successful signal transmission to the predator (Bradbury and Vehrencamp, 1998). Biotic factors include the predator's sensory system, while abiotic factors can include phenomena such as ambient lighting. (Bradbury and Vehrencamp, 1998)

Octopuses are known for their elaborate visual displays used to deter predators. Some of the best-studied antipredator displays include crypsis, aposematic coloration, mimicry, and polyphenism (Hanlon and Messenger, 1996, Hanlon, et al., 1999). Although these defenses are well known, it is not known whether they are used during both daylight and nighttime hours.

Octopus bocki is a pygmy octopus found on Moorea, French Polynesia. Individuals are nocturnal and inhabit dens in dead coral rubble along coral reef crests. Past studies on the species have looked at their learning abilities (Lebensohn, 1999) sensory cues (Johnson, 1995), as well as intraspecific den defense (Logan, 2001). Although some of their defenses have been studied, the identification and usage of their

antipredator defenses remains to be investigated.

This study investigated the antipredator defense mechanisms of *Octopus bocki* under diurnal and nocturnal conditions. I tested three hypotheses: 1) octopuses would adjust their defense mechanisms for daylight and nighttime hours; 2) octopuses would ink and jet away more frequently during the daylight hours, as ambient lighting would increase the predators' detection

MATERIALS AND METHODS

Biology of Octopus bocki

Octopus bocki is a nocturnal species of pygmy octopus found in Moorea, French Polynesia (Cheng, 1996, Caldwell, 2005). It inhabits cavities in coral rubble distributed along coral ridge crests throughout the island (Cheng, 1996). Juveniles are transparent to light brown in coloration and flash red chromatophores, while adults are a solid dark brown but turn transparent or speckled when disturbed (Valencia, pers. obs.). Males with 5mm mantle length (ML) or greater can be distinguished from females by the presence of a hectocotylus, a modified third right arm used in the transfer of spermatophores (Cheng, 1996).

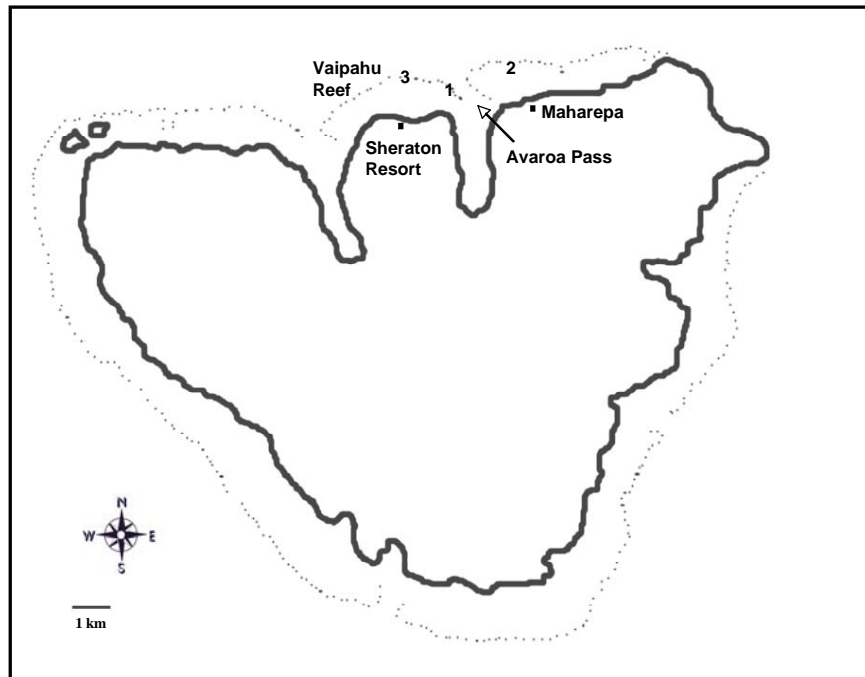


Figure 1. Map of Moorea showing sites from which octopuses were collected. Animals were collected from three sites: 1) Vaipahu Reef near Cook's Bay; 2) a reef located 1 km east of Avaroa Pass; 3) Vaipahu Reef across from the Sheraton Resort. (Adapted from Cheng, 1996.)

Collection and Maintenance Individuals were collected from three sites around Moorea: (1) northwest of Cook's Vaipahu Reef (Fig. 1; Table 1). A boat was necessary to reach sites 2 and 3 however, a kayak was sufficient to reach site. 1. Large bins containing one brick each were taken out to the crests where they were filled with porous coral rubble collected from areas with strong wave action (Fig. 2). The bins were left undisturbed for at least 30 min, allowing water to drain from the rocks. After sitting for at least 30 min, the bottoms of the bins were searched for octopuses (Lebensohn, 1999). Twenty-one octopuses were collected and placed in plastic cups with lids and were transported to the University of California, Berkeley, Richard B. Gump Research Station. Each animal was kept in individual plastic containers at the wet lab, which provided running seawater

for daily water changes. In keeping with the octopuses' nocturnal habits, feedings took place every night after testing was completed. A red light was used to feed the animals in the dark to

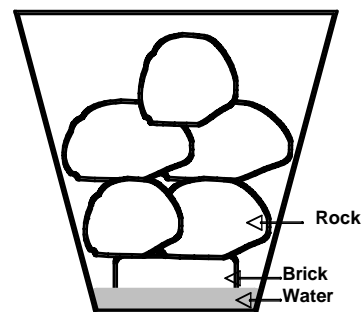


Figure 2. Sample bin used for collecting octopuses. Bins were taken out to reef crests, where they were filled with porous rocks. They were then left undisturbed for 30 min, emptied and searched for octopuses.

prevent disturbance of their circadian rhythms. Juveniles were provided with freshly- collected marine zooplankton.

Table 1. GPS coordinates, water depth, and description of habitat for sites from which octopuses were collected. GPS coordinates are given in UTM. Coordinates for location 2 were not taken.

Site	Location	GPS Coordinates (utm)	Water Depth (m)	Habitat Description
1	Vaipahu Reef, northwest of Cook's Bay	WGS 1984 Datum 01999806South8064842	0-1	Barrier reef crest; frequent wave action; sparse dead rubble
2	1 km east of Avaroa Pass, across from Maharepa		0-4	Reef flat; strong wave action; large coral heads; dense patches of dead coral rubble
3	Vaipahu Reef across from Sheraton Resort	WGS 1984 Datum 01975956South8065043	0-4	Reef flat; strong wave action; large coral heads; dense patches of dead coral rubble

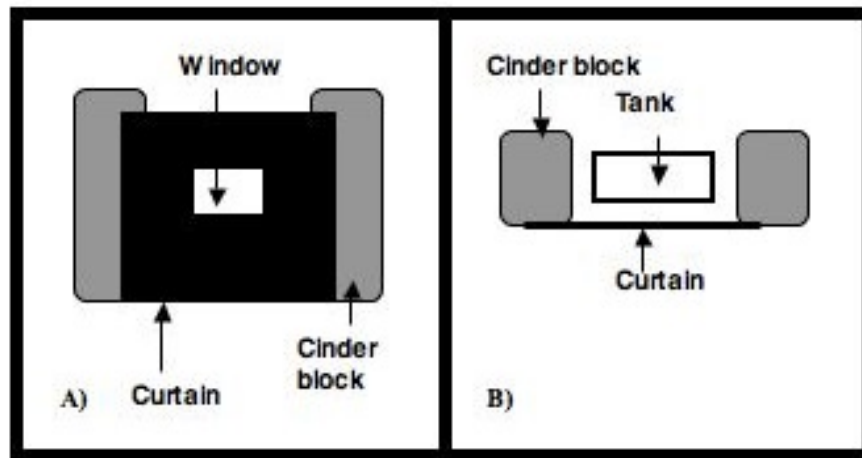


Figure 3. Experimental design. A) Front view; B) Top view. A tank (arena) was placed between two cinder blocks. The front wall of the tank was covered by a curtain attached to both blocks. A small window on the curtain allowed the researcher to observe interactions between fish and octopus.

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plastic containers at the wet lab, which provided running seawater for daily water changes. In keeping with the octopuses' nocturnal habits, feedings took place every night after testing was completed. A red light was used to feed the

animals in the dark to prevent disturbance of their circadian rhythms. Juveniles were provided with marine zooplankton collected fresh every night, while adults were fed live crustaceans collected throughout the day.

Testing for Differences Between Diurnal and Nocturnal Predator Defense

Fish were collected off the station dock to serve as predators during testing. A baited fish line with a small hook and sinker was used to catch the fish with little injury to the animals. After collection, the fish were identified to species before being placed in a tank with flowing seawater. Each fish was immediately returned to its collection site after testing, and no fish was kept for more than 4 day

Testing was done twice a day during daylight and nighttime hours. One *O. bocki* and one fish were randomly chosen for each test using an EXCEL random number generator. An arena was set up outside for natural lighting. The arena consisted of a tank sitting between two cinder blocks. The front wall of the tank was covered by a curtain on one side to minimize the effects of the behavior (Fig 3). Tests conducted at night were visualized under red lighting, and all tests lasted for 5 min. This same procedure was done using an empty arena to control researcher's presence on the animals' for the effects of human handling on the animals' behavior. Twenty tests were run for both diurnal and nocturnal conditions; ten controls were run for both treatments.

Preliminary Tests

Preliminary tests were done using the experimental design described above. Tests were used to identify *O. bocki* defensive postures and body movements relevant to the study (see Results). As it was difficult to assess body coloration and texture at night under red lighting, these behavioral parameters were excluded from the study.

Statistical Analysis

Rate data for defense mechanisms were not normally distributed and were, therefore, square root transformed prior to statistical testing. Similarly, duration data for all mechanisms were log transformed prior to analysis. T-tests were done using JMP statistical software to test for differences between the mean rates and durations of diurnal and nocturnal defense mechanisms. As treatments consisted of 20 replicates and controls consisted of 10 replicated, these data could not be compared for differences between means.

RESULTS

Octopus bocki Predator Defense

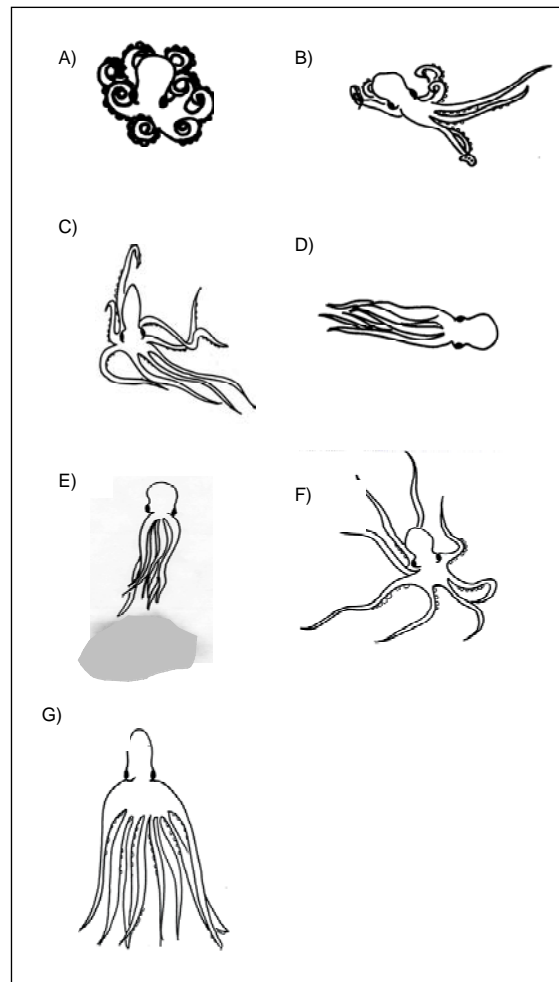


Figure 4. Line drawings of *Octopus bocki* defense mechanisms used for diurnal and nocturnal treatments. See text next page.

Seven defense strategies were identified for both diurnal and nocturnal tests (See Fig 4A-G):

- A. Curl:** Sitting still with arms held (tightly or slightly extended) against the body and curled around the mantle.
- B. Crawl:** Walking with arms extended.
- C. Mantle Erect:** Mantle is stretched and narrow while crawling or sitting still.
- D. Jet Propulsion:** Expulsion of water via the funnel, resulting in rapid swimming (Hanlon and Messenger, 1996).
- E. Spread:** Sitting still with the body flat against the substrate and all arms extended.
- F. Ink:** Release of black ink.
- G. Ballooning:** The web, head, and mantle are lifted with arms held against the substrate.

Assessing Differences Between Diurnal and Nocturnal Predator Defense

Octopuses were mobile in the presence of a predator during the daylight hours, but were less mobile at night. Crawling had the highest rate of occurrence (18.98 ± 7.36 defense/sec) followed by Spread (10.91 ± 5.07 defense/sec) and Curl (9.15 ± 4.54 defense/sec) (Fig. 5A, Table 2). There were significant differences in the mean rates of Crawl (t -test, $P < 0.0001$) and Curl (t -test, $P < 0.0001$) between diurnal and nocturnal treatments (Table 2). All other defenses were rarely observed during the day (Fig. 5A, Table 2). Inking, in particular,

was very rare, occurring in only 3 out of 40 tests, when the fish was 0 to 1 cm away from the octopus (Table 3) The most frequent antipredator defense used at night was Spread (8.87 ± 3.71 defense/sec). There were no significant differences in the mean rates of Spread between treatments (t -test, $P = 0.1477$).

Mean durations for defenses differed between diurnal and nocturnal conditions. Curls were held the longest during both daylight (1.23 ± 0.54 sec) and nighttime (1.47 ± 0.94 sec) (Fig. 5B, Table 2). Spread had the second longest durations during the day (0.90 ± 0.50 sec) and night (1.41 ± 0.62 sec) (Fig. 5B, Table 2). Mean durations for Spread significantly differed between daylight and nighttime hours (t -test, $P < 0.0001$) (Table 2).

DISCUSSION

Octopus bocki Predator Defense

Data suggest that the type of defense mechanism does not depend on time of day. *Octopus bocki* used the same seven antipredator defense mechanisms for diurnal and nocturnal treatments. The horned lizard, *Phrynosoma cornutum*, elicits blood-squirting in the presence of a predator (Middendorf and Sherbrooke, 1992). Frequencies of blood-squirting did not significantly differ between diurnal and nocturnal hours, but were affected by predator type (Middendorf and Sherbrooke, 1992). Similarly, *O. bocki* did not change the type of antipredator mechanisms to account for the time of day, but mechanisms varied in rates of occurrence and durations.

Assessing Differences Between Diurnal and Nocturnal Predator Defense

Crawling appears to be a primary antipredator behavior during light hours.

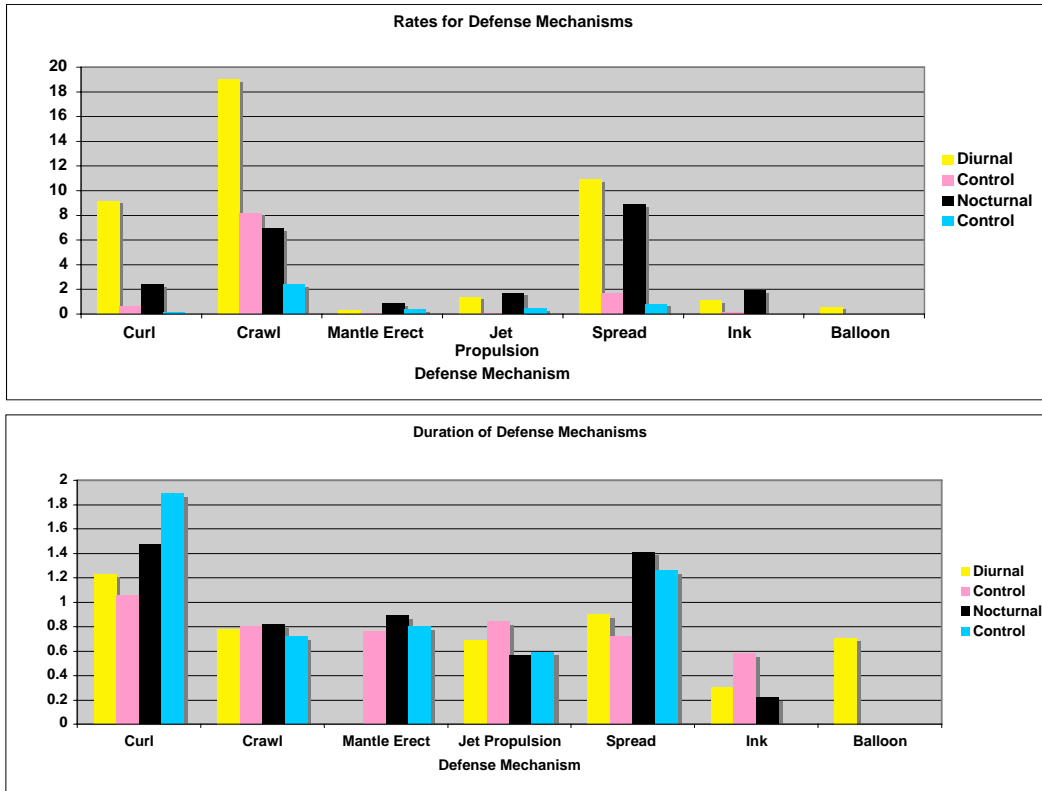


Figure 5. A) Mean rates of defense behaviors for diurnal (N=20) and nocturnal treatments (N=20), and controls (N=20). Crawl had the highest rate of occurrence under diurnal conditions (18.98 ± 7.36 defense/sec), while Spread was the most common behavior under nocturnal conditions (8.87 ± 3.71 defense/sec). Crawl was the most common defense behavior for both diurnal (8.18 ± 4.61 defense/sec) and nocturnal (2.87 defense/sec ± 2.38) controls; B) Mean durations of defense behaviors for diurnal and nocturnal treatments, and controls. Curls were held the longest during diurnal (1.23 ± 0.55 sec) and nocturnal (1.47 ± 0.94 sec) treatments, as well as for diurnal (1.06 ± 0.5 sec) and nocturnal (1.89 ± 0.74 sec) controls. Blue bars indicate results for diurnal treatments; red bars indicate results for diurnal controls; yellow bars indicate results for nocturnal treatments; green bars indicate results for nocturnal controls.

Results revealed that Crawling was used more than any other behavior during diurnal treatments. Daylight hours provide more sunlight and increase a predator's ability to detect prey. Easy detection by the fish may have induced a flee response in the octopuses, resulting in frequent crawling to escape the predator. This hypothesis, however, does not explain the infrequent occurrence of jet propulsion. If the octopuses had indeed attempted to rapidly escape the predator, jet propulsion would have occurred frequently, as it is a rapid escape response in cephalopods (Anderson, 2001, Hanlon and Messenger, 1996). Alternatively, *O. bocki* may actively seek for dens for protection during the day.

Nocturnal octopuses are known to spend the day in their dens, leaving them only at night to forage (Hanlon and Messenger, 1996). It is likely that *O. bocki*, a nocturnal pygmy octopus, spends most of the day hidden from predators in its den, and, therefore, searches for cavities in response to predation during the daylight hours.

Immobility may be an effective antipredator defense at night, increasing crypticity when visibility is difficult for the predator. Curling and Spreading, both resting states, had the highest rate of occurrences at night. Cryptic animals resemble their surroundings so that predators cannot distinguish them from their background environment (Bradbury and Vehrencamp, 1998).

Table 2. Mean rates and durations of defense mechanisms for diurnal and nocturnal treatment. Results for t-test testing for significant differences between diurnal and nocturnal means are also given. Crawl had the highest rate of any other behavior (18.98±7.36 defense/sec, Mean±S.D.) under diurnal conditions. Spread occurred at a higher rate (8.87±3.71 defense/sec, Mean± S.D.) under nocturnal conditions. There were significant differences between the diurnal and nocturnal rates of Curl and Crawl (p<0.0001). The duration of Curl was highest under diurnal (1.23±0.54 sec, Mean±S.D.) and nocturnal (1.47±0.94 sec, Mean±S.D.) conditions. Mean durations of Spreads significantly differed between treatments (p<0.0001).

Defense	Mean Rate±S.D. (defense/sec)		P-value*	Mean Duration±S.D. (sec)		P-value*
	Diurnal (N=20)	Nocturnal (N=20)		Diurnal (N=20)	Nocturnal (N=20)	
Curl	9.15±4.54	2.42±3.10	<0.0001	1.23±0.54	1.47±0.94	0.4478
Crawl	18.98±7.36	6.92±5.81	<0.0001	0.78±0.31	0.82±0.50	0.6098
Mantle						
Erect	0.29±1.23	0.87±2.12	0.4252678	0	0.89±0.27	n/a
Jet						
Propulsion	1.37±2.92	1.68±3.05	0.7552266	0.69±0.46	0.56±0.66	0.64
Ink	1.08±2.75	1.91±3.93	0.3863901	0.30±0.55	0.22±0.94	0.83
Ballooning	0.57±1.78	0	0.1624	0.71±0.67	0	n/a
Spread	10.91±5.07	8.87±3.71	0.1477078	0.90±0.50	1.41±0.62	<0.0001

* Significant values (p<0.05) are highlighted in bold.

As crypticity involves a match to the surroundings, immobility is crucial to its effectiveness (Hanlon, and Messenger, 1996, Bradbury and Vehrencamp, 1998) Shallow-water cephalopods are known to exploit this phenomenon; *Octopus cyanea*, a common nocturnal species in Tahiti, spends most of it's life hidden in it's den and lies in a vigilant position at the entrance of its home, cryptically mimicking its surroundings and remaining still as it monitors its surroundings (Hanlon and Messenger, 1996). In addition, ambient lighting influences the effectiveness of camouflage; lower light levels increase survival via camouflage, as the predator's vision is restricted (Hanlon and Messenger, 1996, Bradbury and Vehrencamp, 1998). It has been suggested that one function of the vertical migration in cephalopods is to keep the animal in water with low-light levels to protect it from predators (Hanlon and Messenger, 1996). As cryptic behavior is a common primary defense in cephalopods, it is not surprising that it was used frequently by *O. bocki* during test trials (Hanlon and

Messenger, 1996). The combination of *O. bocki*'s dark brown coloration along with immobility, may make it difficult for a fish to detect the animals at night.

Inking was surprisingly rare in *O. bocki*, refuting the hypothesis that inking would occur at high frequencies during daylight hours. Inking behavior in *O. bocki* was observed in only 3 out of a total of 40 tests. Energy costs associated with inking may limit the frequency of inking in cephalopods. Nolen and Johnson (2001) showed that that seahare, *Aplysia* spp., required at least three days between ink extractions to replenish ink supplies. Individuals in this study were given at least 5 days to rest between tests, however, data showed that no octopus inked in more than one test. Thus, inking may have been rare in *O. bocki* because individuals require several days to replenish their ink sacs. Moreover, inking was elicited when the fish was at close distances for ingestion of the octopus (between 0 and 1 cm), suggesting that the octopuses conserve ink for extreme situations.

Table 3. Raw data showing occurrences of inking. Inking occurred in 3 out of 40 tests, when the fish was between 0 and 1 cm away from the octopus.

Octopus ID	Diurnal		Nocturnal	
	# Ink Puffs Released	Distance from Predator (cm)	# Ink Puffs Released	Distance from Predator (cm)
O.24	3	0	0	n/a
O.30	0	n/a	3	1
O.19	0	n/a	2	0
Total	3		5	

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