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SYMPOSIUM

Den-Associated Behavior of *Octopus rubescens* Revealed by a Motion-Activated Camera Trap System

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Synopsis Dens are a crucial component of the life history of most shallow water octopuses. However, den usage dynamics have only been explored in a few species over relatively short durations, and *Octopus rubescens* denning behavior has never been explored *in situ*. We built four underwater camera traps to observe the behavior of *O. rubescens* in and around their dens. To distinguish individuals, octopuses were captured and given a unique identifiable visible implant elastomer tag on the dorsal side of their mantle. After being tagged and photographed, each octopus was released back to its original capture site within its original den bottle. The site is unique in that octopuses reside almost exclusively in discarded bottles, therefore aiding in locating and monitoring dens. Motion-activated cameras were suspended in a metal field-of-view above bottle dens of released octopuses to observe den-associated behaviors. Cameras were regularly retrieved and replaced to allow continuous monitoring of den locations in 71 h intervals for over a month. We found that *O. rubescens* was primarily active during the day and had frequent interactions with conspecifics (other members within the species). We also found that rockfish and red rock crabs tended to frequent den locations more often when octopuses were not present, while kelp greenling both visited dens more frequently and stayed longer when octopuses were present. Our results, demonstrate the utility of motion-activated camera traps for behavioral and ecological studies of nearshore mobile organisms.

Introduction

Octopuses’ soft, unarmored bodies and limited swimming ability means that small octopuses must rely upon crypsis and dens for protection from predators, such as large fish, sharks, pinnipeds, and cetaceans (Dorsey 1976; Oxman 1995; Clarke 1996). Due to the security provided by a denning site, many octopuses spend the majority of their time within their dens, revealing the importance of shelter in their ecology and life history (Kayes 1973; Mather 1988). *Octopus vulgaris* has been shown to spend up to 88% of daylight hours in a den (Mather and O’Dor 1991), with only 7.3% of *O. vulgaris* encountered outside dens (Katsanevakis and Verriopoulos 2004). This necessity for a den often leads to octopuses occupying any available den types, such as discarded shells (Mather 1982), rocky dens/outcroppings (Anderson 1997), and human refuse, for example, discarded bottles (Anderson et al. 1999; Katsanevakis and Verriopoulos 2004; Freitas et al. 2022). Den availability has been found to constrain population sizes in *O. briareus* and *O. Joubini* (Mather 1982; Aronson 1986; Katsanevakis and Verriopoulos 2004). Since refuge from predation is so important for survival, it is no surprise that octopuses compete for dens (Dorsey 1976; Cigliano 1993; Edsinger et al. 2020). Limited denning sites also cause lower localized population densities, to minimize competition and reduce interactions (Kayes 1973; Aronson 1986; Scheel et al. 2016; O’Brien et al. 2021). These observations of reduced population densities helped form the long-held concept of the “asocial octopus,” as suggested by Mather (1982) when describing the absence of territorial ranges and the rarity of conspecific interactions in *O. joubini*, limiting interactions to those necessary for procreation

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(Huffard et al. 2008, 2010). In recent years, the concept that octopuses are asocial has been contradicted by the discovery of social aggregations and non-aggressive interactions in several species, although many of these aggregations could be influenced by population density, feeding success, protection from predators, mate accessibility, or localized resources (Hunt 1996; Huffard 2007; Godfrey-Smith and Lawrence 2012; Caldwell et al. 2015; Scheel et al. 2016; Scheel et al. 2018; O'Brien et al. 2021). While these types of social behaviors are not widespread among octopuses, they indicate species-specific behavioral plasticity, which would be expected from such an intelligent animal (Mather and Dickel 2017).

Due to the difficulty of observing wild octopus behavior the majority of social behavior in cephalopods has been observed *ex situ*, with very few studies examining *in situ* denning behavior or ecology in octopuses (Aronson 1986; Voight 1992; Katsanevakis and Verriopoulos 2004; Mereu et al. 2018), leading to biased data on cephalopod social behavior due to laboratory confinement (Dorsey 1976; Tricarico et al. 2011). Confinement in an aquarium has been found to cause profound changes in social behavior. Aggression level has been related to aquarium size in cichlid fish (Oldfield 2011), zebrafish (Granquist and Berges 2013), and common cuttlefish (Geary 1999). In Atlantic salmon (*Salmo salar*), social behavior is significantly different between fish that have been raised in the wild and those raised in hatcheries (Fenderson and Carpenter 1971).

When space is limited, such as in an aquarium, interactions with other inhabitants of that space become more common and dominance hierarchies or territories may be formed, even within species otherwise considered solitary or asocial (Yarnall 1969; Van Heukelem 1977; Boyle 1980; Mather 1980). These types of social interactions can be a strategy to reduce aggression between conspecifics, such as through the "dear enemy effect" (Fisher 1954), which posits that neighboring animals will become less aggressive towards each other when territorial borders have become established. In a previous study with laboratory-confined *O. rubescens*, 47% of octopus interactions were found to result in den evictions, possibly due to territorial constraints (Dorsey 1976).

Due to the impacts of aquarium confinement on the behavior of aquarium animals, observing the den usage and behavior of wild animals is preferred. Much of the previous work on octopus den-associated behavior has relied on direct observation (Ambrose 1982; Forsythe and Hanlon 1997; Huffard 2007) or tagging studies (Hartwick et al 1984; Hofmeister and Voss 2017). Direct observation suffers from the limited time a human diver or snorkeler can continuously remain with the den and the disturbance caused by the observer. Tagging studies in octopuses have been impeded by poor tag retention and health impacts to the octopuses (Barry et al 2011). More recently, use of visible implant elastomer (VIE) tags have shown promise in octopus studies, with long retention times and minimal injury to the animal (Barry et al 2011; Brewer and Norcross 2012). To date, VIE tagging has only been employed in physical recapture studies in octopuses, and not used to study den-associated behavior. The ruby octopus (*Octopus rubescens* Berry 1953) occurs from Southeastern Alaska to Northern Mexico from intertidal regions to 200 m subtidally in kelp beds, sandy mud buttons, and rocky areas (Hochberg 1998). Ruby octopuses in the study region do not appear to have a distinct breeding season, as egg clutches can be found throughout the year (pers obs). Within its range *O. rubescens* is one of the smaller octopus species, growing to an adult mass of up to 500 g (Hochberg 1997). *Octopus rubescens* is thought to forage at night, feeding on a variety of gastropods, crustaceans, euphausiids, bivalves, and even fish, although they prefer small crabs and hermit crabs (Dorsey 1976; Hochberg and Fields 1980; Laidig et al. 1995; Onthank and Cowles 2011). *Octopus rubescens* has been observed living in clumped dens (∼1 m apart) in California (Hanlon and Messenger 1996), while the occurrence of glass bottles in Puget Sound have allowed *O. rubescens* to utilize habitat where naturally occurring dens are rare (Anderson et al. 1999). Additionally, juvenile *O. rubescens* have been found exhibiting schooling behavior as they move through the water column (Hunt 1996). In addition to observations of wild conspecific interactions, several examples of interspecific associations have also been found. Octopuses have been found engaging in cooperative interactions with non-octopus species, such as hunting with fish (Kayes 1973; Bayley and Rose 2020; Sampaio et al. 2021), utilization of cleaning stations (Johnson and Chase 1982; Sazima et al. 2004), and attraction of scavengers to midden piles (Hartwick and Thorarinsson 1978). Our research investigates the individual, interspecific, and conspecific social behaviors of *O. rubescens*.

To understand the wild denning behavior of *O. rubescens,* this study attempts to answer the following questions: (1) What is the general diel activity pattern of *O. rubescens*? (2) What interspecific interactions can be observed surrounding *O. rubescens* den locations? (3) What trends of conspecific social interactions can be observed among *O. rubescens* at denning locations?

Methods

Octopus capture and transport

Twenty-seven octopuses over 15 g (140 ± 101.5 g, mean ± SD) (52% female: 48% male) were collected from a depth of 15–18 m using SCUBA from Driftwood Park, in Island County, Washington state (48.16397, -122.63746). All octopuses were gathered opportunistically from June to August and housed for the shortest duration possible before release (typically 3–5 days). The majority of octopuses collected were found inhabiting discarded glass bottles. Our study location represents a unique opportunity for the observation of conspecific and interspecific interactions among octopuses due to the substantial number of discarded glass bottles at the site, lack of alternative denning locations on the shell-hash/sediment bottom, and high octopus density of at least one octopus per 26.3 m^2 (about the size of a parking space), (Chase and Verde 2011). On shore, openings of collected bottles containing an octopus were covered with flexible nylon mesh and secured with rubber bands to allow water flow while preventing octopus escape. Bottles containing octopuses were transported to Rosario Beach Marine Laboratory (RBML) inside a ∼130 L (about 34 gal) cooler filled with fresh seawater and aerated with a battery-powered aquarium air pump. At RBML, octopuses were housed in individual 11 L flow-through aquaria with their original bottle dens. Octopuses were fed a diet of purple shore crab (*Hemigrapsus nudus*) and a variety of small commercially available clams *ad libitum*.

Octopus tagging

Weight, sex, health, and identifying characteristics (missing arms, etc.) were recorded for each octopus, before assigning each octopus a unique color pattern (green, yellow, orange, blue, and/or red) that would be injected into the dorsal side of the mantle using VIE tags produced by Northwest Marine Technology, Inc. (NMT), Anacortes, Washington. To apply the VIE tags, octopuses were anesthetized by submersion in an aerated 2.5% ethanol seawater mixture (Estefanell et al. 2011). Once an octopus was sedated, VIE was injected below the chromatophore layer using a 1 mL syringe and 27-gauge needle. After tagging, octopuses were returned to their individual saltwater tanks to recover. Tagging had a negligible impact on octopus health, no necrosis or mortalities were observed throughout the experiment and tags were still unchanged at the termination of the study (∼3 months later).

Open-source motion-activated camera system

Camera trap systems were designed using a Raspberry Pi 3B+, The Raspberry Pi Foundation, Cambridge, United Kingdom, and a Raspberry Pi HQ camera, The Raspberry Pi Foundation, Cambridge, United Kingdom (Fig. 1B and C) outfitted with a 6 mm lens. A custom hat-type PCB (an expansion board that connects to the Raspberry Pi GPIO pins) was used to additionally connect the Raspberry Pi to far-red (FR) and ultra-violet (UV) LED strobes (Fig. 1B and C), a microcontroller board to trigger the LED strobes, a real-time clock, batteries and associated power management systems, and a small LED screen to monitor the system. The camera system is powered by six 12 V 4500 mAh Ni-Mh batteries wired in parallel to produce a total charge of ∼27 Ah, yielding an ∼71 h camera runtime (Fig. 1B). Cameras were housed in a 1 m section of schedule 80, 3-inch (7.62 cm) PVC pipe with three clear ports, two covered by 1.27-cm-thick acrylic for the camera and loading port and one covered by 0.635-cm glass for the strobes (to allow UV transmittance) (Fig. 1B). The camera trap system detects motion by capturing low-resolution (320 × 240) monochrome evaluation images at 1 s intervals while illuminating with the FR strobe. These evaluation images are saved and analyzed using a Mixture-of-Gaussian foreground detection algorithm (Aslam and Sharma 2017) from the python version of the OpenCV library version 3.4.1. (Bradski 2000). If a test image shows sufficient change in foreground pixels, indicating motion in the image, a 2040 × 1520 pixel color image is taken using combined illumination of FR and UV lights to illuminate the subject and any VIE fluorescent tags present. Once a full resolution image was triggered, the system would wait 5 s before restarting motion detection. To optimize camera motion detection settings for field deployments in both daytime and nighttime, variable underwater current strengths, and expected animal motion characteristics, cameras were tested over several weeks on captive, tagged *O. rubescens* in a large outdoor 700-gallon (about 2650 L) flow-through aquarium in addition to several short field deployments at RBML. During these evaluations, we were able to determine that we could successfully read VIE octopus tags in 87% of photos with visible octopus present. System construction files and software have been banked at the Zenodo repository (DOI: 10.5281/zenodo.6543944).

Camera deployment and octopus release

Cameras were mounted in deployment frames 61 cm above the sea floor, facing down upon bottle entrances (Fig. 1D and E). This setup resulted in a field-of-view of ∼ 0.5 × 0.35 m. Deployments varied from 10.5 to 70.7 h durations (49 h ± 20.0, mean ± SD), some running short of the maximum ∼71 h due to battery difficulties. After at least 71 h of deployment, cameras were collected and immediately replaced with a fully charged camera system.

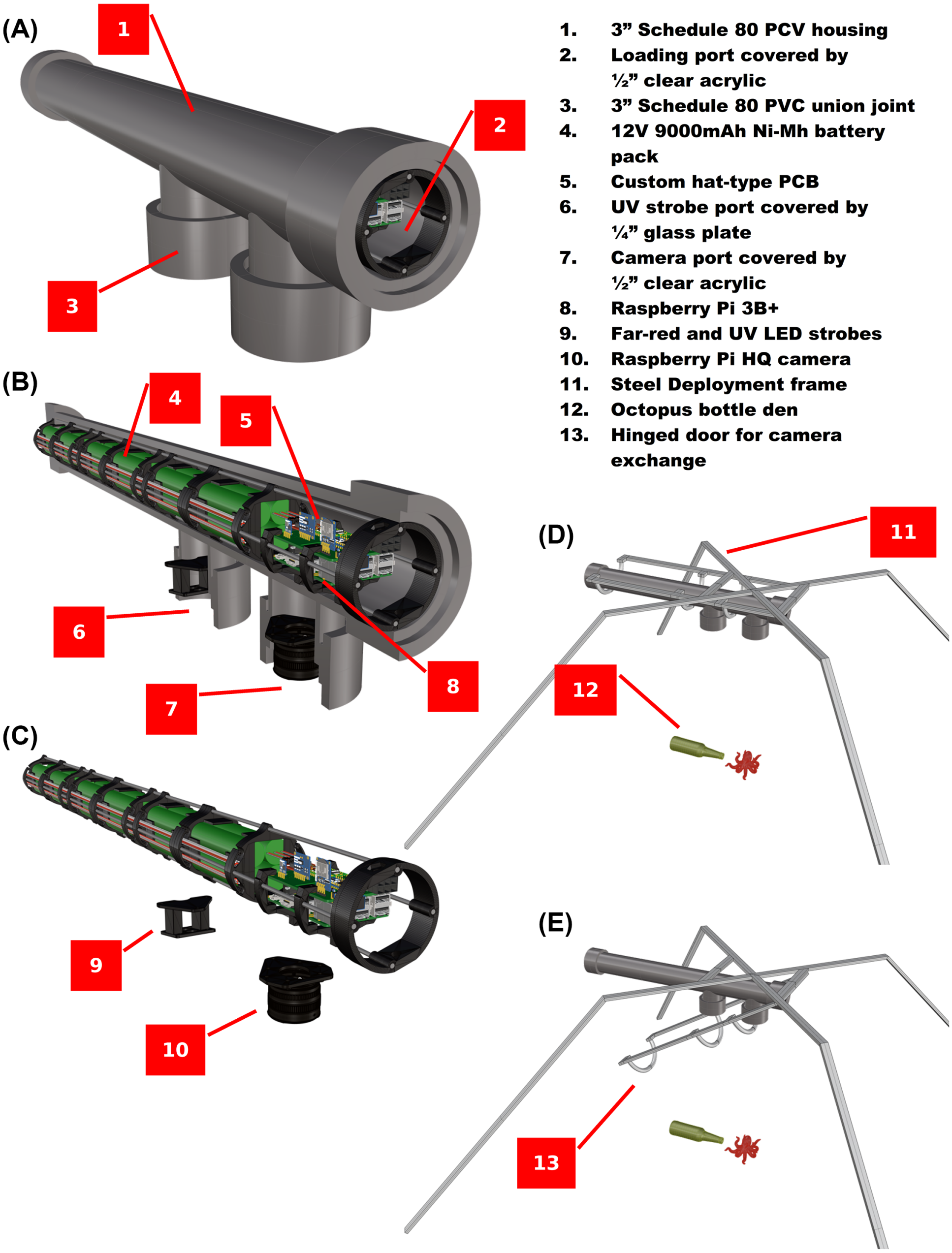

Fig. 1 Camera trap assembly and field deployment system. (**A**) Camera PVC housing with installed system and union joints demonstrating port locations. (**B**) Camera schematics showing port cover locations, battery packs, and attached components. (**C**) Lighting array and camera placement. (**D**) Deployment frame with installed camera, ready for deployment over den site. (**E**) Deployment frame open and ready for camera exchange.

Two cameras with frames were deployed at depths between 15 and 18 m and octopuses released on the same dives at the Driftwood Park site. Octopuses were released in their original collected denning bottle. One octopus, chosen at random, was placed beneath each deployment frame and camera. On occasion one to four additional octopuses would be released haphazardly over 8 m away from the deployment frames, to minimize captivity durations. To maintain octopus densities similar to those encountered at the start of the study, octopuses were only collected and released within the study area. During subsequent deployments, the camera systems were swapped with another system with charged batteries, but deployment frames were not relocated. Deployment frames were built to include a hinged door, allowing cameras to be exchanged quickly. After exchanging the camera, divers would evaluate the bottles within the camera's field-of-view to determine if an octopus was present. If no octopuses were found within these bottles, a newly tagged octopus within its original denning bottle would be placed beneath the camera and an unoccupied bottle removed. If non-tagged octopuses were encountered, they were collected for VIE tagging and identification.

Data analysis

All triggered photos were examined, and when any animal (except shrimp and small crabs, which were exceptionally abundant) was captured in the photos, the event was recorded into a spreadsheet (hereafter referred to as the "event log"). For each event date and time, the deployment number, animal species observed, octopus ID for tagged octopuses, behavior observed, and event type were recorded into the event log. Because of the high rate at which we could read tags during early tests (∼87% of tagged octopus photos), coupled with the slow approach of octopuses to bottles ensuring that >10 photos were taken of each octopus, we have high confidence that we did not miss any tags on octopuses. In addition, in any case in which a tag is visible on an octopus, there was always at least one image in which the tag was readable. Behaviors were assigned for each photo based on a set of pre-defined behaviors that could be readily discerned from still photos (Supplementary Table S1). Event types were categorized into those involving a resident octopus, defined as an octopus that entered a bottle in the camera field-of-view during the deployment, a non-resident octopus, or a combination thereof., We also noted events involving an interaction between octopuses or between an octopus and interspecific animal. Over 4200 events were extracted from the triggered photos and this event log was used for all further statistical analyses. All analyses were performed using R (R Development Core Team 2021). Frequencies of common octopus behaviors during day and night were compared using chi-squared tests. Day was defined as the period between sunrise and sunset, while night was defined as the period between sunset and sunrise. Changing sunset and sunrise times were determined for the specific location of the Driftwood Park site on the date the behavior occurred using the sunriset() function in the maptools package in R (Bivand et al. 2022). Expected probabilities for the chi-squared analysis were generated by calculating the proportion of day and night for each 24 h period when the behavior in question occurred.

Frequencies of observation for the four most observed species were compared by chi-squared between periods when an octopus was present versus when no octopus was present. Octopuses were judged to be "present" from the time the octopus entered the camera field-of-view until it left the field-of-view, even if it was inside a bottle or obscured by algae and not directly visible. To generate expected probabilities for used in the chi-squared analysis, for each interspecific animal observation, the probability of the observation occurring when an octopus was present was calculated based on the proportion of time when octopuses were present versus absent in the day or night, depending on if the observation was during the day or night. For example, for an observation of a kelp greenling at night the probability of that event occurring when an octopus was present was calculated by dividing the total amount of time cameras were deployed at night when octopuses were present by the total amount of time that cameras were deployed at night. The mean of the probabilities for each individual observation of a species to occur when an octopus was present was used as the probability for the whole analysis for that species. The probability of that event occurring when an octopus was not present was calculated by subtracting the probability of it occurring when octopuses were present from 1. The distinction between day and night observations was made to avoid biases that could be introduced by diurnal or nocturnal animals. The visitation duration, defined as the time difference between the first and final photos in a continuous set of photos containing an individual animal, of the four most observed species, was also compared between periods when an octopus was present versus when no octopus was present using a two-sample permutation test. Similarly, the frequency of observations and visitation duration were compared for non-resident octopuses when resident octopuses were present or were not present by chi-square and two-sample permutation tests, respectively. The frequency of non-resident octopuses reaching into bottles versus not reaching into bottles when a resident octopus was present were compared by chi-squared with expected values set by the relative proportion of those behaviors performed by non-resident octopuses when resident octopuses were absent.

The frequencies of occurrence for two common octopus behaviors, fortify (pulling material over the bottle entrance) and periscope (placing eyes out of the bottle entrance while leaving arms and mantle inside the bottle), were compared when octopuses were alone (no other octopuses) in the field-of-view to frequency of occurrence when multiple octopuses were in the field-of-view by chi-squared. The expected probabilities for these chi-squared tests were generated using the proportion of time when one octopus versus multiple octopuses were present in the camera field-of-view, weighted by the number of octopuses present (for instance, a particular behavior is twice as likely to be observed when two octopuses are present versus one octopus).

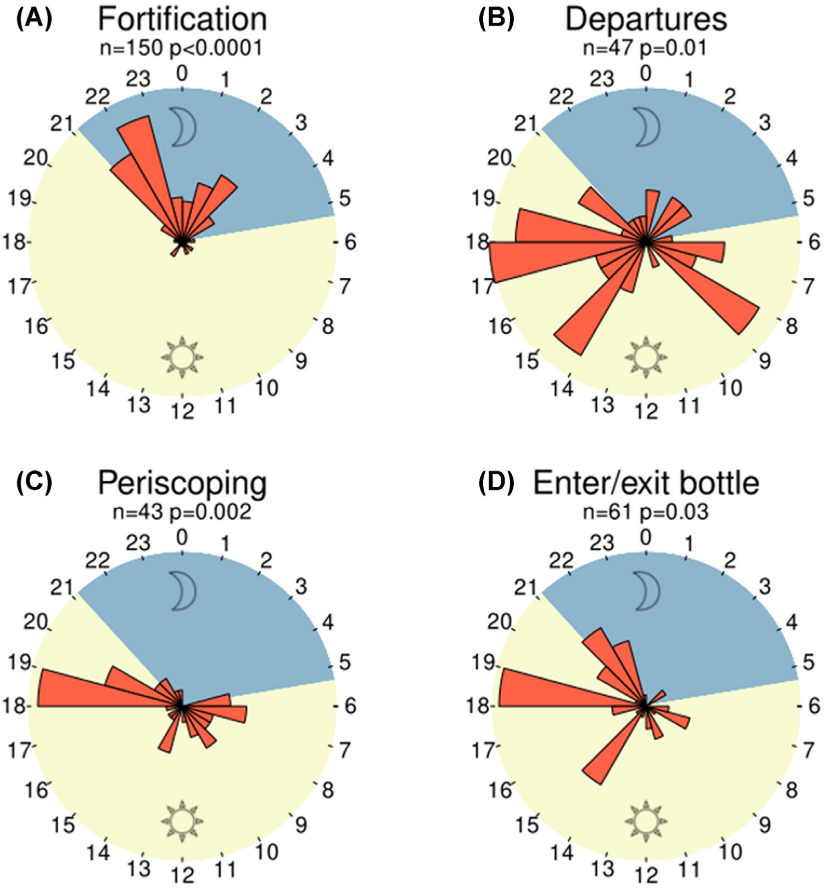

Fig. 2 Radial histograms representing the absolute frequencies of hourly daily activities for *O. rubescens* recorded by marine camera traps throughout the day. Categorical behaviors were graphed individually, (**A**) represents observed fortification events, $n = 150$, chi-squared test; $X^2 = 148$, df = 1, *P*-value <0.0001, (**B**) all observed field-of-view departures, $n = 47$, chi-squared test; $X^2 = 6.04$, df = 1, *P*-value = 0.014, (**C**) periscoping behaviors observed, $n = 43$, chi-squared test; $X^2 = 9.24$, df = 1, *P*-value = 0.002, and (**D**) entering and exiting of bottles, $n = 61$, chi-squared test; $X^2 = 4.61$, df = 1, *P*-value = 0.032

Results

Collected data

Cameras produced a total of 249,163 motion-activated photos with ∼2.8 million additional low-resolution evaluation photos. Motion-activated cameras recorded the activity of octopuses and other common animals near octopus bottle dens for over 785 total hours (33 days). Individual octopuses were never observed leaving or arriving twice in succession, which demonstrates the cameras were not missing arrivals or departures of octopuses. Thus, we conclude the system is effective at capturing octopus arrivals and departures without missing important data. In total, 31 non-resident octopuses and 14 resident octopuses were observed. Non-resident octopuses were observed for a mean of 2.9 ± 3.5 min (mean ± SD) per octopus, while resident octopuses were observed for a mean of 1309 ± 1384 min (mean ± SD) per octopus.

Daily activity patterns

Octopus activity was higher during daylight hours than at night. Departures, the behavior defined as an octopus leaving the camera field-of-view, were significantly greater during the day (Fig. 2B, chi-squared, $\chi^2 = 6.04$, df = 1, $P = 0.014$). The frequency of octopuses entering and exiting bottles was also significantly higher during the day (Fig. 2D, chi-squared, $\chi^2 = 4.61$, df = 1, $P = 0.032$). A high rate of fortification, the behavior defined as an octopus pulling in material to cover the den entrance, was observed within the first two hours post-sunset, followed by reduced fortification events throughout the remainder of the night. While fortification was one of the most frequently observed octopus behaviors, it was almost never observed during daylight hours, occurring significantly more often at night (Fig. 2A, chi-squared, $\chi^2 = 148$, df = 1, $P < 0.0001$).

Interspecific interactions

Direct interactions between octopuses and other animals were rarely observed; however, the behavior of some animals appeared to change when octopuses were present or absent at the den (Fig. 3). When an octopus was present in the camera field-of-view kelp greenling (*Hexagrammos decagrammus)* spent significantly more time per visit ($n = 291$, permutation two-sample t-test, P-value $= 0.0002$), and also visited at a higher frequency (although not significant) when octopuses were present ($n = 291$, $\chi^2 = 3.2$, df $= 1$, $P = 0.072$). In addition to increased visitation frequency and duration when octopuses are present, *H. decagrammus* were regularly observed in close proximity with *O. rubescens* (Fig. 4). Octopuses were repeatedly observed entering and exiting the camera field-of-view while closely accompanied by *H. decagrammus* (Supplementary Figs. S1 and S2). *Sebastes sp.* rockfish and *Cancer productus* crabs were observed significantly less frequently when octopuses were present (*Sebastes* sp.: $n = 612$, $\chi^2 = 43.21$, df $= 1$, $P = <0.001$, *C. productus*: $n = 368$, $\chi^2 = 13.56$, df $= 1$, $P < 0.001$).

Conspecific social interactions and spacing

Conspecific interactions were frequently observed, with multiple octopuses present >40% of the time that octopus were present within the camera field-of-view (6,535 min with multiple octopuses out of 15,972 total minutes of octopuses within the camera field-of-view). Despite the substantial amount of time with octopuses near each other, these interactions never resulted in den evictions or any apparent aggressive behaviors. Non-resident octopus visitation duration and frequency were compared when a resident octopus was present versus absent to understand social tolerance. Among the 42 visitations by non-resident octopus, 28 occurred while no resident octopuses were denning within the camera field-of-view, a non-significant difference (Fig. 3, chi-squared, $\chi^2 = 1.72$, $P = 0.189$, df $= 1$), but non-resident octopus visitation durations were significantly longer when a resident octopus was present (138 s ± 121, mean ± SD), more than double the average when a resident octopus was not present (64 s ± 48, mean ± SD) (Fig. 3, two-sample permutation test, $P = 0.012$). Octopuses also alter their behavior when in close proximity to other octopuses, with periscoping behavior (an octopus placing its eyes outside the den, while its arms and mantle remain inside) occurring at a higher frequency when octopuses were alone than when multiple octopuses were present (Table 1, chi-squared, $\chi^2 = 16.2$, df $= 1$, $P < 0.0001$) although fortification behavior (an octopus pulling in material to cover the den entrance) appears to favor periods when only one octopus is in the field-of-view (Table 1, chi-squared, $\chi^2 = 0.754$, df $= 1$, $P = 0.39$*)*. To determine if visiting non-resident octopuses were interacting with resident octopuses, the number of times each visiting octopus reached inside a bottle was recorded, in addition to the bottle's occupancy (with or without a resident octopus). When passing through the camera field-of-view, non-resident octopuses were found to reach inside bottles significantly more frequently (68% of visits) if a resident octopus was present; however, if no resident octopus was present, visiting octopuses would reach inside bottles less frequently (32%) (Table 1, chi-square, $\chi^2 = 2.58$, df $= 1$, $P = 0.024$).

Table 1 The influence of conspecific presence on octopus behaviors.

	Bottle interaction by non-resident octopuses when a resident octopus is present	
	Do not reach	**Reach into bottle**
Observed	6	13
Expected	10.9	8.1
Pearson's residuals	−1.47	1.70
χ^2	5.07	
P-value	**0.024***	
	Fortification behavior	
	Octopus alone	**Octopus not alone**
Observed	68	82
Expected	62.8	87.2
Pearson's residuals	0.66	−0.56
χ^2	0.75	
P-value	0.39	
	Periscoping behavior	
	Octopus alone	**Octopus not alone**
Observed	31	12
Expected	18.0	25.0
Pearson's residuals	3.07	−2.60
χ^2	16.17	
P-value	**<0.001***	

* is used to indicate statistical significance.

Discussion

This study represents the first examination of wild *O. rubescens in situ* denning behavior, with observations of conspecific and interspecific interactions occurring at den locations. This study observed octopus dens for 33 days over a 44-day period. Any organisms and behaviors encountered within the camera field-of-view were recorded for analysis. *Octopus rubescens* is believed to be nocturnal (Hochberg and Fields 1980). We found that *O. rubescens* departs from the camera field-of-view andenters and exits their bottle den significantly more

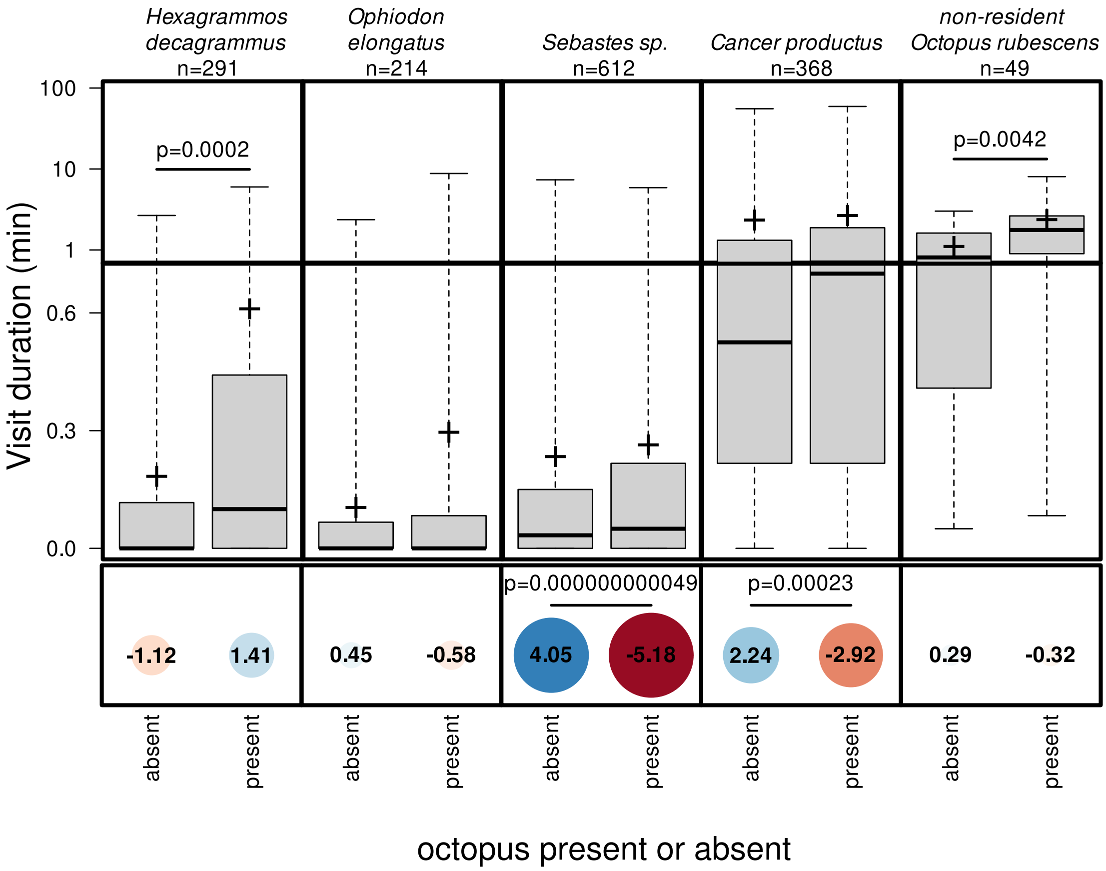

Fig. 3 Commonly encountered species were evaluated for visitation duration and frequency, with and without a resident octopus present. Four non-octopus species were examined with a fifth comparison of non-resident octopus visitations. The top panel displays a boxplot of visitation durations for each species when an octopus was not present or present in the camera field-of-view. Plusses (+) indicate average visitation durations. Y-axis is broken at 0.7 min, above which is logarithmic to display long tails. The bottom panel displays Pearson's residuals of chi-squared analysis of visitation frequency when octopuses were not present or present in the camera field-of-view.

frequently during the day. In contrast, *O. rubescens* engaged in closing their den entrances with material (fortifying behavior), the most common octopus behavior observed, occurred virtually exclusively at night. These findings indicate that *O. rubescens* at the Driftwood Park site are diurnal. This is surprising as this species has been exclusively reported as being active primarily at night (Dorsey 1976; Anderson 1987; Hochberg 1997, 1998). However, these have relied on data from the behavior of *O. rubescens* in captivity or anecdotal encounter rates by SCUBA divers. The larger, sympatric giant Pacific octopus (*Enteroctopus dofleini)* is considered nocturnal, through the use of sonic tagging telemetry in multiple studies (Mather et al. 1985; Scheel and Bisson 2012). Diurnal activity in *O. rubescens* could lessen competition between this species and similar sized *E. dofleini,* which have remarkably similar diets (Anderson et al. 1999; Onthank 2008; Scheel and Anderson 2012).

Throughout the study, *O. rubescens* regularly interacted with conspecifics with virtually no antagonistic behavior observed. In a previous study of captive *O. rubescens*, 47.8% of 69 conspecific interactions resulted in den evictions, in which one octopus successfully removed another octopus from a bottle den (Dorsey 1976). However, among the 43 wild conspecific interactions observed throughout this study lasting a total of 6,535 min, no evictions were observed. Octopus interactions are not rare in this population, and there is not a strong avoidance of conspecifics. Nearly half (40.9%) of the time at least one octopus was within the camera's field-of-view (a total of 15,972 min, about one and a half week), it would be accompanied by at least one more octopus. Further, during periods when a resident octopus is present, a significant increase in non-resident octopus visitation duration was seen, although no significant difference in visitation frequency was observed. This seems to indicate a preference for interaction over avoidance of conspecifics. This conflicts with the long-held belief that octopuses avoid interacting with conspecifics (Mather 1982). These results could indicate a level of social tolerance and behavioral plasticity previ-

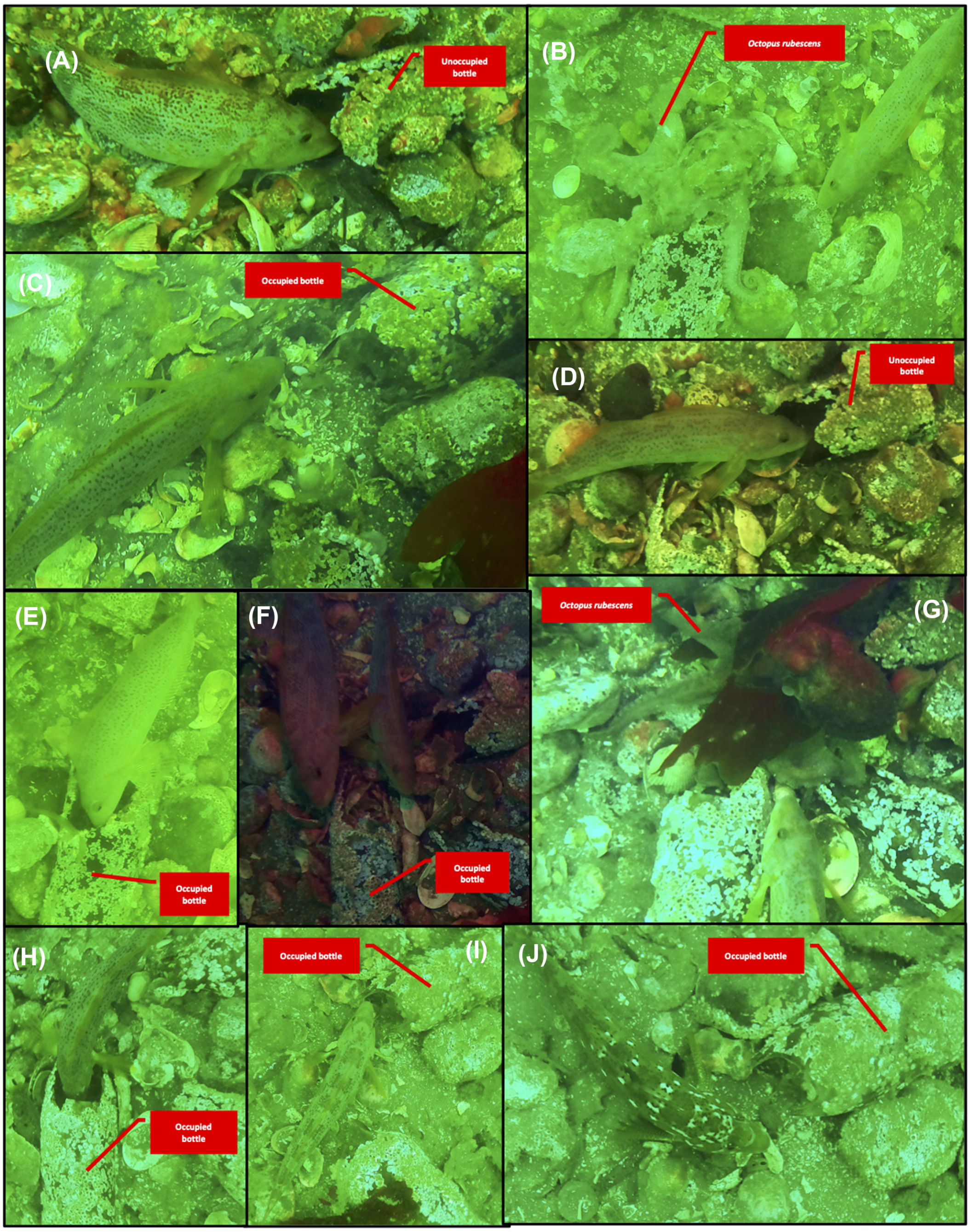

Fig. 4 Photo data demonstrating interspecific interactions between *H. decagrammus* and *O. rubescens*.

ously unobserved within this species. This behavioral change may also be influenced by an abundance of denning locations, which could reduce aggressive behaviors by removing the need to compete for a key resource.

During conspecific interactions, non-resident octopuses were found to reach inside the bottle den significantly more when octopuses were inhabiting the bottle, despite rarely seeing the bottle interior successfully prior to an interaction. Although octopuses are highly visual, they may struggle to see within the bottle interior (due to biofouling of the bottle's surfaces, fortification material blocking the bottle entrance, or approaching the bottle from the rear). The use of sucker-to-sucker contact as an effective means of interaction may indicate the importance of chemotactile reception within octopus social behavior, or simply an alternative when visual recognition fails (Polese et al. 2016).

In some instances, the behavior of fish and crabs was influenced by octopus presence. At times when octopuses were present, both *Sebastes* sp. and *C. produc-*

tus visited significantly less frequently, indicating active avoidance of areas where octopuses occur. Repantian crustaceans, such as crabs and lobsters, are common prey items of virtually all shallow water octopuses, including *O. rubescens* (Anderson et al. 1999; Onthank 2008) and the other common octopus species occurring in the area, *E.dofleini* (Vincent et al. 1998; Scheel and Anderson 2012). Crabs are in fact preferred by *O. rubescens* over other prey taxa (Onthank and Cowles 2011). It is unsurprising, therefore, that several species of crustaceans have been shown to avoid octopus chemical cues (Brooks 1991; Berger and Butler IV 2001). Juvenile *C. productus* specifically have been found to be consumed by *O. rubescens* (Onthank 2008), and *C. productus* of all sizes are consumed by *E. dofleini* and are likely the most common prey item of this octopus species in the Puget Sound area (Scheel and Anderson 2012). The avoidance of octopus chemical cues would, therefore, be quite adaptive in this species and consistent with our data.

It is less easy to explain why rockfish (*Sebates* sp.) avoid octopus dens when an octopus is present. Rockfish are not major predators of octopuses, nor are octopuses predators of rockfish. Despite an intensive investigation of rockfish diet in this area, only *S. caurinus* has been found to rarely prey on *O. rubescens* (Dorsey 1976; Palsson et al. 2009). Rockfish are not eaten by the larger sympatric octopus *E. dofleini* (Cosgrove 2002), and in contrast *S. caurinus* and *S. nebulosus* have both been observed sharing dens with *E. dofleini* (Love 1996; NOAA 2004). Competition may be a more likely explanation for this interesting interaction between *O. rubescens* and *Sebates* sp. fish. Crustaceans make a substantial component of the diet of many species of rockfish found in the Puget Sound area (Palsson et al. 2009). If crustaceans avoid the areas near bottle dens when octopuses are present, as we found with *C. productus*, it is understandable that rockfish seeking out those crustaceans would also be less likely to visit the area.

Instead of avoidance, kelp greenling (*H. decagrammus)*, appeared to be attracted to *O. rubescens*. Kelp greenlings were observed significantly more frequently when octopuses were present (11.4 observations per 24 h) than when octopuses were absent (8.7 observations per 24 h), and the mean visit duration more than tripled when octopuses were present (mean visit duration of 36.4 ± 70.0 s) than when octopuses were absent (mean visit duration of 10.9 s ± 25.6 s). During these visits when octopuses were present, *H. decagrammus* was regularly observed in close proximity (within 10 cm) of *O. rubescens* without noticeable indications of aggression or predatory behavior from either species (Fig. 4). On several occasions, *H. decagrammus* was observed closely following an octopus. In each instance, as the octopus entered the camera field-of-view, it was closely followed by an individual *H. decagrammus,* which remained within arm's reach of the octopus throughout the entire observation, before leaving the camera field-of-view still accompanying the visiting octopus (Supplementary Figs. S1 and S2). This data suggest some form of non-aggressive interspecific relationship between *H. decagrammus* and *O. rubescens*. Examples of cooperative hunting between octopus and fish have been documented (Kayes 1973; Bayley and Rose 2020; Sampaio et al. 2021); this relationship may be a similar example of such behavior. Our data, however, are not able to shed further light on this interaction, and future studies should explore the relationship between *H. decagrammus* and *O. rubescens.*

The use of motion-detecting camera systems for this study proved essential to its success, providing a comprehensive look at octopus conspecific and interspecific social interactions while allowing daily behavioral trends to be quantified. The use of motion activation over a time lapse system reduced the number of images to be reviewed by ∼10×, in addition to reducing storage space and download times. By combining the camera's UV lighting and VIE tagging, subjects too small for other forms of tracking could be identified, allowing the examination of organisms whose biology is otherwise only known from captivity or brief encounters in the wild.

The behavior and daily den use of *O. rubescens* show a significant preference for out-of-den activity during daylight. This is the first evidence contradicting the long-standing belief based on SCUBA and captive observations that *O. rubescens* is primarily nocturnal. Additionally, *O. rubescens* were found to interact with *H. decagrammus* in a way perhaps similar to previously reported fish-octopus interactions. Finally, we show that conspecific interactions between individual *O. rubescens* are common *in-situ*, adding further evidence that octopuses are not as asocial as once believed. Among all the direct conspecific interactions found throughout this study, no behaviors were observed that could be categorized as aggressive.

Informed consent

No human subjects were used in this study and informed consent was therefore not applicable.

Ethical Approval

All octopuses collected for this project were permitted under a Washington Department of Fish & Wildlife collection permit (ONTHANK 21–153). All applicable laws concerning the ethical use of animals for scientific research were followed during the course of this study.

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Supplementary Data

Supplementary Data available at *ICB* online.

Conflict of Interest

The authors declare no conflict of interest.

Data Availability

All datasets and code used for this study are available on Zenodo
Photos DOI: 10.5281/zenodo.6403880
Statistical analysis code DOI: 10.5281/zenodo.6407342
Camera construction and system files DOI: 10.5281/zenodo.6543944

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