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Predator cues facilitate oyster biofiltration by suppressing the density-dependent impacts of ectoparasites

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ABSTRACT: Predators commonly regulate the feeding behavior of consumers through non-consumptive effects (NCEs) generating cascading indirect effects. While parasites are ubiquitous consumers in ecosystems, it is not known whether predator NCEs can generate similar cascading impacts by regulating parasite feeding on their hosts. Ectoparasites may be particularly sensitive to predator NCEs, yet this interaction remains unexplored. We focused on a common ectoparasitic snail, *Boonea impressa*, and examined how predator-associated olfactory cues impact feeding on its host, the eastern oyster *Crassostrea virginica*. Scent-exposure assays revealed that *B. impressa* reduced feeding on its host in the presence of predator (mud crab *Panopeus herbstii*) cues. A laboratory biofiltration experiment, in which we manipulated the density of ectoparasites and the presence of predatory crab olfactory cues, showed that ectoparasites reduced oyster biofiltration rates, and these effects are mediated by both parasite density and predator cues. Mud crab NCEs switched from having negative to positive effects on oyster biofiltration as ectoparasite densities increased. While this study presents the first evidence of a predator influencing ectoparasite feeding through NCEs, this phenomenon may be common in nature.

KEY WORDS: Parasitism · Non-consumptive effects · Predator · Ectoparasite · *Crassostrea virginica* · *Boonea impressa* · Biofiltration

1. INTRODUCTION

Predators wield strong influence over the structure, functioning, and stability of ecological communities by regulating their prey (Paine 1966, Werner & Peacor 2003, Estes et al. 2011, Trussell et al. 2011). In addition to controlling prey density directly through consumption, predators indirectly regulate prey via non-consumptive effects (NCEs), trait changes that alter prey behavior, distribution, and morphology (Matassa & Trussell 2011, Weissburg et al. 2014). NCEs can generate trophic cascades of similar and greater strength to those initiated by the consumptive effects of predators alone (Schmitz et al. 2013, Belgrad & Griffen 2016, DeWitt et al. 2019). These trait-mediated trophic cascades are a key mechanism by which predators drive changes in prey activity and indirectly shape ecosystems.

Predators also shape ecosystems by mediating host–parasite dynamics (Johnson et al. 2010, Lopez & Duffy 2021). Predators regulate the spread and persistence of disease through the direct consumption of hosts, parasites, or vectors, and there is increasing evidence that predators may also alter host–parasite dynamics through NCEs, initiating trait-mediated cascades (Thieltges et al. 2024). The threat of preda-

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tion can induce changes to the distribution of hosts in space and time, altering encounter rates between hosts and disease agents or vectors (Cornelius et al. 2023). Alternatively, predators influence disease transmission by driving changes in the behavior or phenotype of the vectors themselves. For instance, exposure to predator cues affects the behavior, size, development, and survival of mosquito larvae, all traits which indirectly mediate the spread of mosquito-borne illnesses (Bond et al. 2005, Arav & Blaustein 2006, Zuharah et al. 2013, Roux et al. 2015). Predators may also facilitate hosts by driving changes in the feeding behavior (frequency, activity) of parasites, indirectly alleviating or increasing host stress. Because of their position at the interface of the host and the external environment, ectoparasites, as compared to endoparasites, may be particularly susceptible to predator NCEs and other environmental cues. However, the ability of predators to regulate feeding by ectoparasites via NCEs and, consequently, their potential to indirectly affect host performance, remains unexplored.

In eastern US oyster reef ecosystems, Atlantic mud crabs *Panopeus herbstii* (Fig. 1A) are ubiquitous mesopredators that drive cascading effects in these communities through their consumption of juvenile eastern oysters *Crassostrea virginica* (Meyer 1994, Grabowski 2004). Mud crab cues can also induce changes to oyster shell thickness and the frequency of valve closure. These changes can drive alterations in reef structure and biofiltration rate, highlighting the importance of NCEs in generating ecosystem-level cascades on oyster reefs (Scherer et al. 2017, Carroll & Clements 2019). As generalist predators, mud crabs also prey on *Boonea impressa* (hereafter '*Boonea*'), a common ectoparasitic pyramidellid snail that feeds on oysters. *Boonea* snails feed by positioning themselves along the oyster shell margin, extending their proboscis between the host's valves, and consuming hemolymph from the mantle margin (Fig. 1B,C) (Fretter & Graham 1949). *Boonea* can parasitize oysters in large numbers (>30 per oyster), reducing oyster growth by substantially increasing energetic costs, increasing mortality in post-set juvenile oysters, and inhibiting oyster filter-feeding (Robertson & Mau-Lastovicka 1979, White et al. 1984, 1988, Ward & Langdon 1986, Carroll & Finelli 2015). While parasitism by *Boonea* is well known to regulate critical aspects of their hosts' biology, no studies have examined whether mud crabs influence *Boonea* feeding behavior through NCEs and if such regulation of ectoparasite feeding may benefit oyster hosts. Here, we examined the impacts of mud crab NCEs on the feeding activity of *Boonea* to determine if, through the regulation of ectoparasite feeding activity, mud crabs can indirectly affect oyster biofiltration rate, a key functional trait (Coen et al. 1999, Vaughn & Hoellein 2018).

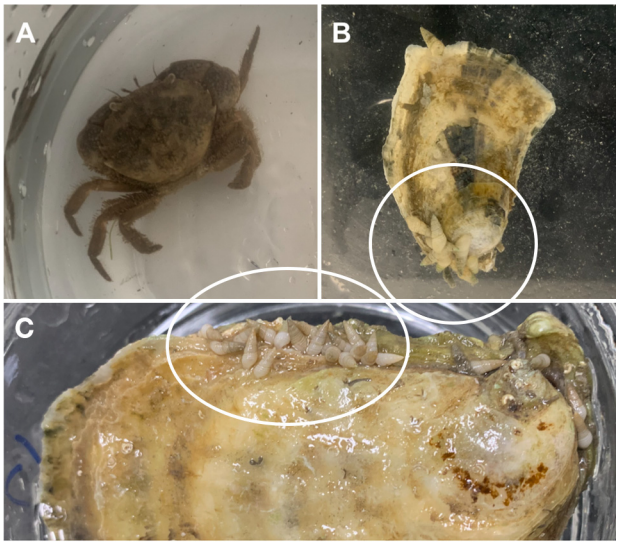

Fig. 1. Study organisms and key interactions. (A) Atlantic mud crab *Panopeus herbstii*. (B,C) *Boonea impressa* feeding (encircled) on tissue and hemolymph using a proboscis (not visible) and accessing the mantle from between the valves along the shell margins of its host *Crassostrea virginica*. Photo credits: Ryan C. Rogers

We conducted 2 laboratory experiments to analyze the interspecific interactions between mud crabs, *Boonea*, and oysters. The first was a behavioral response trial, conducted to determine if mud crab scent cues can drive changes in *Boonea* feeding activity. The second was an oyster filtration assay, where we assessed the relative effects of mud crab scent cues and ectoparasite density on oyster biofiltration rate. We predicted that (1) increasing densities of *Boonea* would reduce oyster biofiltration rates, (2) mud crab NCEs would reduce *Boonea* feeding activity, and (3) mud crab NCEs would enhance biofiltration rates of parasitized oysters by reducing the number of actively feeding *Boonea*.

2. MATERIALS AND METHODS

Mud crabs (n = 9) and *Boonea* (n = 1086) were collected by hand from an intertidal oyster reef at Pivers Island, Beaufort, NC, USA (34° 43' 05.9'' N, 76° 40' 16.5'' W). Oysters, both juvenile (n = 36, shell length 37.15 ± 5.03 mm, ±SD) and adult (n = 60, shell length 71.49 ± 8.91 mm), were collected from the

Duke Marine Lab Aquafarm in Atlantic Beach, NC (34° 42′ 01.9″ N, 76° 42′ 13.5″ W). We visually inspected all oysters for boring sponge infestation and selected only those with no or negligible infestation for use in experiments. Organisms were transported to the Duke University Marine Lab where they were maintained in individual glass dishes filled with filtered, aerated seawater prior to testing. We exposed feeding *Boonea* to predator-associated scent cues in both our laboratory feeding assay and biofiltration experiments. Mud crab scent cue concentrations were standardized using the formula: cue strength (grams per minute liter) = crab wet mass (g) / [soak time (min)/ vol (l)] (Rittschof & Hazlett 1997). To generate scent cues for NCE treatments, 3 mud crabs (combined weight ~5 g) were soaked for 5 min in 1500 ml of filtered seawater, yielding a concentration of 0.66 g (min l)$^{-1}$ crab scent across experiments. The volume of chemical cue water administered differed between our 2 experiments, where 0.5 ml (10 drops) were used in our feeding assays (see Section 2.1) and a larger volume of 13 ml was used during our biofiltration assay (see Section 2.2). This was done in part due to differences in the experimental duration (30 vs. 60 min). Likewise, cues were directly administered onto feeding snails in our cue assay with limited mixing and degradation, whereas in the biofiltration assay, cues were widely dispersed and mixed due to the presence of an aerator and adult oysters. Ultimately, the goal was to ensure the presence and persistence of cues throughout the duration of the biofiltration experiment by increasing the cue volume relative to the jars. Control treatments used the same volumes of seawater in which no crabs had been soaked.

2.1. Ectoparasite feeding assay

To assess the effect of mud crab cues on *Boonea* feeding activity, we performed group behavioral trials involving the administration of 2 randomly assigned scent cue treatments — (1) a control drop of filtered seawater with no added scent cues or (2) a drop of seawater with mud crab scent cues — to a group of *Boonea* feeding at a dosage of 1 drop per snail (therefore, for 10 snails we used 10 drops or approximately 0.5 ml), on a single juvenile oyster. Trials were conducted in arenas consisting of a cylindrical glass dish (19 cm diameter, 8 cm height) filled with 1500 ml of filtered seawater. Cleaned oyster shells were placed over the bottom of the arena to mimic the structure of a natural reef. A juvenile oyster was placed in the center of the arena and given 5 min to acclimate prior to the start of the experiment. All oysters were visually confirmed to be feeding following this period. At the beginning of each trial, 10 snails were positioned on the left valve of the oyster and allowed 5 min to acclimate before the initial number of snails feeding was recorded. Because we could not directly observe snail proboscises extending into the host, we used snails remaining stationary on the shell margin as a reliable proxy for active feeding (Robertson & Mau-Lastovicka 1979). Following the acclimation period, we administered one of 2 randomly assigned scent cue treatments: (1) a drop of filtered seawater with no added scent cues (control) or (2) a drop of seawater with mud crab scent cues. Cues were administered directly over the top of feeding snails. After 30 min, the total number of feeding snails was recorded again. We conducted a total of 24 group response trials (n = 12 trials per treatment), with cue treatments replicated evenly among the trials.

Treatment differences in the average change in the number of *Boonea* feeding at the end of the experiment were evaluated using 1-way ANOVA. All data met the normality and homogeneity of variance assumptions of ANOVA as determined by Shapiro-Wilk and Bartlett tests. All analyses were conducted in R studio (RStudio Team Version: 2024.09.1+394).

2.2. Oyster biofiltration assay

To assess how consumer NCEs and ectoparasite density may interact to influence oyster filtration rate, we conducted an oyster biofiltration assay in November 2021, selectively exposing parasitized oysters with varying *Boonea* densities to mud crab NCEs and then comparing biofiltration rates.

Adult oysters were maintained in a flow-through tank for ~24 h prior to use in our experiment. Glass jars (1300 ml) served as experimental units. Jars were assigned a *Boonea* density treatment (low: 5; medium: 10; high: 20) and a crab scent concentration (0.67 or 0 g (min l)$^{-1}$) in a 2 × 3 factorial design (n = 10 replicates per treatment combination). Jars were filled completely with filtered seawater and oxygen was delivered via a bubbler stone. Because of low winter temperatures, chlorophyll *a* (chl *a*) concentration of added seawater was low (<3 µg l^{-1}). As such, we supplemented the water in each jar with 215 ml of concentrated algal culture (*Isochrysis* sp., 15 000 cells ml^{-1}) to ensure that adequate food was available to oysters. Five min after adding algae, we collected 10 ml water samples from each jar to establish initial chl *a* concentrations, forming a baseline for oyster fil-

tration rate estimation (Δchl *a* = initial chl *a* − final chl *a*). Subsequently, a single adult oyster was placed in each jar, followed by the addition of *Boonea* density treatments directly onto each oyster. *Boonea* were given a 5 min acclimation period to attach to the oyster before administering any cue treatments. Ten jars filled with filtered seawater and algae, but no oysters, served as controls for ambient algal growth.

Unlike our feeding assay where concentrated scent cues were administered directly over the top of target organisms in shallow dishes filled with non-circulating water, bubbler stones ensured that cues were dispersed throughout the volume of each jar, potentially diluting its effects. To account for this, we used a greater volume of crab cues (13 ml) to ensure that snails and oysters were sufficiently exposed. The experiment began with the addition of crab cues (13 ml) to appropriate treatments. Control jars received 13 ml of filtered seawater. Cues were administered again after 30 min. Five min after each cue administration, the total number of *Boonea* in feeding position was observed and recorded. The total number and proportion of feeding *Boonea* recorded at these 2 timepoints were averaged to produce metrics used in analysis. A final 10 ml water sample was collected after 1 h at the conclusion of the experiment to determine final chl *a* concentrations.

Immediately following the end of the experiment, all water subsamples were vacuum filtered onto Whatman 47 mm microfiber filters, transferred to 50 ml vials of methanol, and placed in a freezer for pigment extraction. After 48 h, samples were brought to room temperature, and chl *a* content was analyzed using a calibrated Turner 10-AU fluorometer. The average change in chl *a* concentrations in algal growth controls was used as an algal growth correction factor that was added to final chl *a* values prior to analysis. The difference in initial and final chl *a* concentration served as a measurement of phytoplankton removed by oyster filtration. All oysters were dissected at the end of the experiment to determine the presence of pea crabs or other parasites.

We checked for initial treatment differences in oyster lengths and chl *a* concentration using 1-way ANOVA. Treatment differences in the average change in chl *a* concentration at the end of the experiment and the average number and proportion of *Boonea* observed feeding on oysters were evaluated using 2-way ANOVA. The average number of feeding *Boonea* was square root transformed prior to analysis to meet the assumptions of ANOVA. Additionally, we used binary logistic regression to test for treatment differences in the presence of boring sponges and pea crabs, which are potential sources of variation in oyster biofiltration.

3. RESULTS

3.1. Ectoparasite feeding assay

We found no significant differences in initial feeding between the groups ($F_{1,56}$ = 0.285, p < 0.754). The presence of mud crab scent cues reduced the number of *Boonea* actively feeding on oyster hosts (Fig. 2, p < 0.002, Tukey HSD).

3.2. Oyster biofiltration assay

The average number of *Boonea* actively feeding on oyster hosts increased with *Boonea* density (Fig. 3A, $F_{1,56}$ = 7.034, p = 0.010) and decreased in the presence of mud crab scent cues ($F_{1,56}$ = 35.022, p = 2.07 × 10^{-7}). Similarly, mud crab scent cues reduced the proportion of *Boonea* actively feeding ($F_{1,56}$ = 8.187, p = 0.005), although the proportion of *Boonea* feeding was unaffected by the density of the ectoparasites ($F_{1,56}$ = 1.246, p = 0.269). There was no significant interactive effect of mud crab scent cue addition and *Boonea* density on either the average number or proportion of *Boonea* feeding (p > 0.06, both cases).

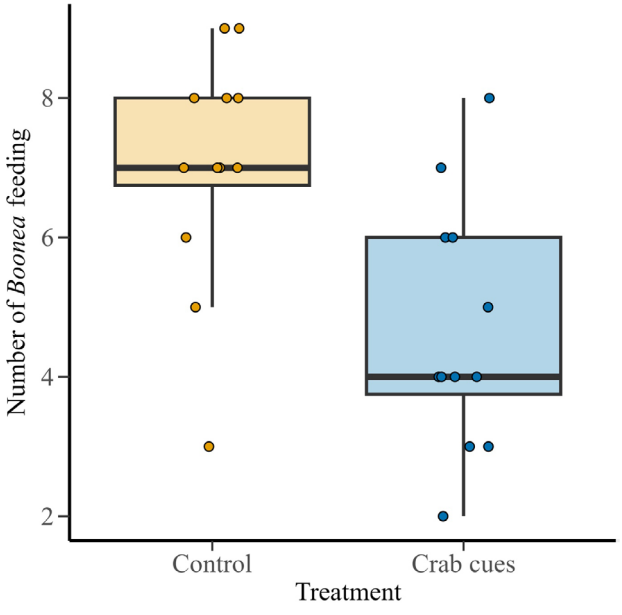

Fig. 2. Observed *Boonea* feeding activity by scent exposure treatment. Each box reports the median (thick black line), 25th and 75th percentiles (outer box edges), and ±95% confidence intervals (farthest extent of whiskers)

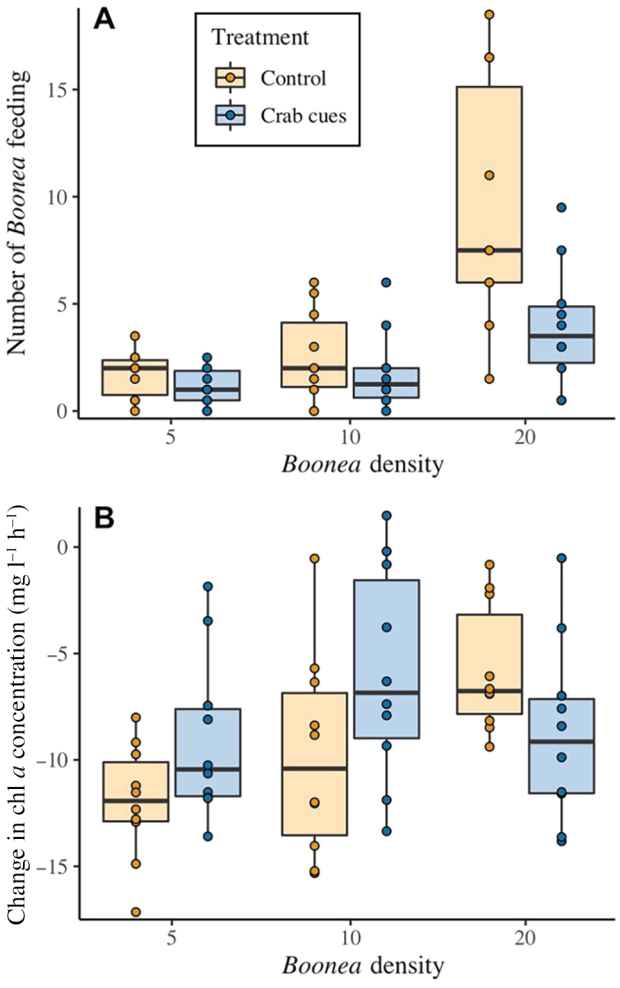

Fig. 3. Results from the oyster biofiltration assay. (A) Number of *Boonea* observed in active feeding position and (B) change in chlorophyll *a* concentration, a proxy for oyster biofiltration rate, at different levels of *Boonea* density and with or without (Control) the addition of mud crab scent cues. Note that more negative values for change in chl *a* indicate greater oyster biofiltration while less negative values indicate less biofiltration. Boxplot parameters as in Fig. 2

Increased *Boonea* density reduced oyster biofiltration rate (Fig. 3B, $F_{1,56} = 5.307$, p = 0.025). Crab scent cues alone did not influence oyster filtration ($F_{1,56} = 1.443$, p = 0.2348), but there was a significant interaction between crab scent cue addition and *Boonea* density ($F_{1,56} = 6.755$, p = 0.0119). At low and medium *Boonea* densities (5–10 snails per oyster), crab scent negatively impacted oyster filtration rate, while at high *Boonea* densities (20 snails per oyster), crab scent cues enhanced oyster filtration rate.

Initial chl *a* concentration of experimental jars did not differ by treatment ($F_{5,54} = 1.131$, p = 0.355). Initial size differences in oysters did not differ by treatment (p > 0.97). Dissection of oysters used in our biofiltration assay revealed no significant differences in pea crab infection between treatments (p > 0.18). Likewise, the frequency of boring sponge infection was similar among treatments (p > 0.53).

4. DISCUSSION

Our results suggest a pathway by which predator NCEs might generate cascading effects in ecosystems: suppressing feeding of ectoparasites. In particular, the results of our lab experiments demonstrate how NCEs of a common oyster reef predator indirectly support oyster biofiltration by regulating feeding of *Boonea impressa*. Our ectoparasite feeding assay revealed that exposure to mud crab olfactory cues strongly decreased the number of *Boonea* actively feeding on oyster hosts (Fig. 2). Our subsequent oyster biofiltration assay revealed that the effects of predator-associated olfactory cues depended on ectoparasite density: at low *Boonea* densities, the net effect of mud crab scent cues on oyster biofiltration was negative, while at high densities, crab scent cues had net positive effects on oyster biofiltration by suppressing ectoparasite feeding (Fig. 3).

Our findings also revealed that mud crab scent cues negatively impact oyster biofiltration at lower *Boonea* densities. Notably, a previous study investigating the influence of mud crab NCEs on oyster biofiltration found no discernible effects on small groups of adult and juvenile oysters within laboratory enclosures (Dodd et al. 2018). This apparent discrepancy may be because, unlike the prior study, we did not examine the effects of mud crabs on oyster feeding in the absence of *Boonea*. Mud crab cues may only decrease oyster biofiltration when other natural enemies, such as *Boonea*, are present. Additionally, the effect of crab cues on *Boonea* was relatively greater in our feeding assay compared to our biofiltration assay. This may be attributable to the use of larger adult oysters during our biofiltration assay and may indicate a role of host size/strength in affecting feeding activity; likewise, the use of an aerator and bubbler during the filtration assay likely facilitated the degradation and dissolution of scent cues. Future studies should examine the interactions between oysters, mud crabs, and *Boonea* to fully contextualize indirect consumer interactions in this system, and to understand when, and at what scales, such interactions may be occurring.

The results of our laboratory experiments support the hypothesis that perceived predation risk can contribute to the modulation of ectoparasite feeding

activity, and ultimately filter-feeding by oysters. While our study was limited to examining the relative effects of ectoparasites and mud crab scent cues on the feeding activity of individual oysters under highly controlled conditions, our results provide important insights that warrant further testing under natural conditions. If mud crabs regulate feeding by *Boonea* where they co-occur on oyster reefs from the mid-Atlantic to the Gulf of Mexico, they may influence broader patterns of ecosystem functioning. For instance, feeding *Boonea* can act as a vector for the protozoan parasite *Perkinsus marinus*, commonly associated with dermo disease (perkinsosis) in molluscan shellfish (White et al. 1989). Mud crabs may mediate the transmission of this deadly parasite through their NCEs. Additionally, considering that mud crabs readily consume *Boonea* (R. C. Rogers pers. obs.), our results may underestimate the overall positive effects of mud crabs on oysters. A more complete understanding of the extent to which consumptive and non-consumptive pressures ultimately determine the net effects of *Boonea* on oyster reef functioning will require manipulative field experiments.

While our study is, to our knowledge, the first to experimentally demonstrate that predators can influence the feeding behavior of ectoparasites on their hosts through NCEs, this type of indirect interaction might be commonplace and ecologically influential. Service–resource mutualisms where predatory cleaners remove ectoparasites from client organisms are widespread and are well known to initiate trait-mediated indirect interactions that shape the structure and functioning of entire ecosystems (Bshary 2003, Grutter et al. 2003, Bshary et al. 2007, Waldie et al. 2011). Cleaner species involved in these mutualisms may also alter the feeding behavior of ectoparasites via olfactory or visual cues, generating similar cascading effects. Predators may be more likely to influence ectoparasite feeding on hosts when ectoparasites can flee or hide on their host or within the surrounding environment. Temporary ectoparasites, such as gnathiid isopod pranzia or juvenile sea lampreys, which emerge from the benthos to parasitize marine fish, might be particularly susceptible to predator-associated cues (Nagel 2009, Artim et al. 2017). Indeed, recent studies on sea lampreys have demonstrated the effectiveness of deploying alarm cues during fish migration, guiding them into traps for population control (Bals & Wagner 2012, Buchinger et al. 2015, Mensch et al. 2022). In aquatic environments, host mobility may be a key determinant of the importance of indirect predator regulation on ectoparasite feeding. When ectoparasites target sessile benthic hosts, like those in our study, they may have more prolonged and frequent contact with scent cues of benthic predators, compared to those targeting mobile hosts like pelagic fish. Future studies examining the role of predator NCEs in modifying prey feeding may reveal when and where such interactions occur.

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