Social predation by a nudibranch mollusc

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Abstract

Social predation is a common strategy used by predators to subdue and consume prey. Animals that use this strategy have many ways of finding each other, organizing behaviors and consuming prey. There is wide variation in the extent to which these behaviors are coordinated and the stability of individual roles. This study characterizes social predation by the nudibranch mollusc, *Berghia stephanieae*, which is a specialist predator that eats only the sea anemone, *Exaiptasia diaphana*. A combination of experimental and modeling approaches established that *Berghia* preys upon *E. diaphana* in groups. The extent of this social feeding was not altered by length of food deprivation, suggesting that animals are not shifting strategies based on internal state. It was unclear what cues the individual *Berghia* used to find each other; choice assays testing whether they followed slime trails, were attracted to injured anemones, or preferred conspecifics feeding did not reveal any cues. Individuals did not exhibit stable roles, such as leader or follower, rather the population exhibited fission-fusion dynamics with temporary roles during predation. Thus, the *Berghia* provides an example of a specialist predator of dangerous prey that loosely organizes social feeding, which persists across hunger states and uses temporary individual roles; however, the cues that it uses for aggregation are unknown.

Significance Statement

Social predation is an adaptive strategy that enables predators to subdue dangerous prey while minimizing injury. Many nudibranchs specialize in predation on cnidarians, which pose unique challenges due to their potent defenses. Although nudibranchs are often characterized as solitary hunters, our study reveals that *Berghia stephanieae* exhibits social predation behaviors, forming temporary, fluid groups to feed on sea anemones. These groups lack stable social structures, with individuals adopting temporary roles such as joining or initiating feeding. Interestingly, we found no evidence that aggregation is driven by simple cues such as slime trails, conspecific activity, or prey injury, suggesting that group formation may depend on more complex or context-specific mechanisms. This work highlights the need for further research into the ecological and sensory factors underlying social predation in nudibranchs and other marine predators.

Keywords: foraging behavior, Berghia stephanieae, producing, scrounging, satiety-dependence, dangerous prey

Introduction

Social feeding behaviors has been extensively studied across taxa, from simple multicellular organisms like *Trichoplax adherans* to complex animals like cephalopods and wolves (Burford and Robison, 2020; Fortunato and Aktipis, 2019; Krause and Ruxton, 2002; MacNulty et al., 2014). Feeding in groups can be costly, leading to increased competition for food and the risk of attracting predators (Balaban-Feld et al., 2019; Sutton et al., 2015). However, hunting and feeding in groups often provides key advantages, such as increased efficiency in locating and subduing prey, improved vigilance against predators, and reduced individual handling times during dangerous interactions with prey (Barta et al., 2004; Brown and Richardson, 1988; MacNulty et al., 2014). For example, lionfish achieve higher hunting success rates in groups (Lönnstedt et al., 2014; Sarhan and Bshary, 2023) and electric eels herd prey for collective electrical strikes (Bastos et al., 2021). Social predation strategies, which range from highly choreographed attacks to loose aggregations, represent diverse adaptations to these trade-offs (Lang and Farine, 2017).

Feeding in groups covers a broad continuum, from organized hunts in which individuals have defined roles to loose aggregations attracted to the same resources. Complex social predation strategies, which include choreographed attack patterns, are used by animals that live socially (Berghänel et al., 2022) as well as by animals that are generally solitary (Lührs and Dammhahn, 2010; Twining and Mills, 2021). Thus, social living is not directly tied to social predation. In contrast, simpler strategies involve aggregation without coordinated behavior, as seen in brown bears feeding at salmon runs (Deacy et al., 2016) and predatory nematode-hunting mites that aggregate around injured prey (Aguilar-Marcelino et al., 2014). Aggregation behaviors, although independent, still confer benefits such as increased prey availability or reduced predation risk. This continuum of strategies highlights the importance of understanding the underlying mechanisms that drive group formation and predation. For the purposes of this paper, social predation is defined as encompassing behaviors where predators "find, capture and consume animals with others" (Lang and Farine, 2017).

To investigate aggregation and social predation, we studied the nudibranch sea slug *Berghia stephanieae*, a monophagous predator that feeds exclusively on the sea anemone *Exaiptasia diaphana* (Carroll and Kempf, 1990; Goodheart et al., 2022; Monteiro et al., 2020). Like other sea anemones, *E. diaphana* is dangerous due to its nematocysts and acontia, specialized structures for deterring predators. It can even kill and consume potential predators (Hayes and Schultz, 2022; Lam et al., 2017; Mehrotra et al., 2019).

Here, we addressed whether *Berghia* feeds socially, aggregating at anemones in a non-random manner and sought to determine the mechanisms underlying this aggregation behavior. In this study, we first experimentally establish that *Berghia* feeds socially even with the opportunity to feed individually. Building on this finding, we investigated potential mechanisms underlying aggregation. We also examined whether hunger state influences the likelihood of social feeding. Finally, we tested whether individual slugs consistently prefer social or solitary feeding, hypothesizing that preferences might vary among individuals, potentially reflecting personality traits or ecological strategies.

Methods

Animal Care

A colony of *Berghia stephanieae* was maintained from individuals purchased from Salty Underground (Crestwood, MO, USA) and Reeftown (Boynton Beach, FL, USA). Prior to use in this study, *Berghia* were communally housed in groups of 5-15 individuals in 1-gallon acrylic aquariums filled with artificial seawater (ASW; Instant Ocean, Blacksburg, VA, USA), made with a specific gravity of 1.020 -- 1.022 and pH of 8.0 - 8.5 with a 12:12 light dark cycle at 22-26°C. *Exaiptasia diaphana* (Carolina Biological Supply Co., Burlington, NC, USA) were housed in glass aquariums containing ASW. Unless otherwise noted, the *Berghia* were fed twice a week by placing two *E. diaphana* individuals in their home tank.

Group Feeding Assay

To test whether *Berghia stephanieae* feed on *Exaiptasia diaphana* in groups even if they have the option to feed alone, eight *E. diaphana* individuals were evenly spaced in a circle around the edge of a large clear acrylic box (25 X 25 X 25 cm). The arena was place on top of a white LED lightboard, which provided uniform illumination and facilitated visualization and analysis. Opaque black electrical tape was applied around the outside edges of the arena to block external visual stimuli. The animals were recorded from above using a Pro Stream Webcam 1080P HD at 1 FPS using Video Velocity software (Virginia City, Nevada, USA). The anemones were allowed to acclimate for 5 minutes and then eight *Berghia* were added to the center of the circle, equidistant from all anemones. After 20 minutes, the sizes of the groups and number of slugs that were not feeding were recorded and the slugs were returned to their home tanks. The slugs used in these experiments were food-deprived for either 7-days or 3-days depending on the experiment. Group sizes were counted by observers blind to the food-deprivation length.

2-Alternative Choice Assays

To identify the cues *Berghia stephanieae* might use to aggregate, we conducted a series of two-alternative choice assays. Each trial took place in a small square acrylic arena (7.62 cm x 7.62 cm x 2.54

cm) surrounded by opaque white window film to block external visual stimuli. The arena was illuminated from below by a white LED lightboard. Two anemones were placed in opposite corners of the arena and allowed to acclimate for 5 minutes before introducing a single *Berghia*. Slugs were acclimated in an identical arena using either plain artificial seawater (ASW) or anemone-treated water (ATW) depending on the experiment. ATW was prepared by incubating one anemone per 25 mL of ASW for at least 24 hours, followed by filtration through a 0.22 µm PES filter (Millipore Sigma, Burlington, MA). Acclimation in ATW for 5 minutes was used to prime the slugs and increase responsiveness to the food odor, increasing the likelihood of quickly selecting an anemone at the start of the trial.

During each trial, *Berghia* were placed equidistant from the two anemones using a placement guide to ensure consistent positioning. Trials were recorded from above, using the same equipment and frame rate as the group feeding assay. A trial ended when the slug contacted one of the anemones or after 30 minutes if no choice was made. After each trial, slugs were returned to their home tanks, and their choices were recorded. All slugs were food-deprived for 3 or 7 days, depending on the experiment.

The following experimental conditions were tested:

- Munched anemone (MA): To test attraction to an anemone injured by a conspecific, a helper slug fed on one anemone for at least 10 minutes in a separate arena before the trial. These two anemones were then placed in opposite corners of the testing arena.
- Bisected anemone (BA): To determine if slugs were attracted to injured anemones, slugs chose between an intact anemone and one bisected with a razor blade immediately before acclimation. While the injury was naturalistic, it isolated cues from an injured anemone from potential residual cues from a conspecific.
- Slime trail (ST): To test if slugs followed a slime trail, a helper slug was allowed to navigate the arena until contacting one of two intact, size-matched anemones. The helper was removed after

protruding its proboscis but before biting. Slime trail visibility was confirmed using activated charcoal in preliminary tests.

- Feeding conspecific (FC): To test if slugs were attracted to a conspecific actively feeding, a helper slug was allowed to feed on one of two anemones in a separate arena. Both anemones, along with the feeding helper, were then transferred to the testing arena. By transferring the anemones with the helper slug still attached, there was no slime trail leading to either anemone.
- Feeding conspecific + slime trail (FC + ST): To test combined cues, a helper slug navigated the arena and began feeding on one of two intact anemones. Both the feeding slug and its slime trail were present during the trial.

Helper slugs were free to choose between anemones in several trials, accounting for natural variation in anemone attractiveness across *Berghia* individuals. Trials were excluded if the focal slug failed to make a choice or, in cases involving a feeding conspecific, if the helper slug stopped feeding before the focal slug made a selection.

Consistency of Social Preferences Assay

To examine whether individual *Berghia* consistently preferred social or solitary feeding, we tested 32 slugs after 7 days of food deprivation using the group feeding assay described above. Each slug was assigned an identifier, and its feeding behavior (group vs. solitary) was recorded.

Slugs were then housed individually in clear plastic deli cups, provided with 24 hours of ad-libitum access to *Exaiptasia diaphana*, followed by 7 days of food deprivation. Each slug was subsequently tested in the FC + ST two-alternative choice assay and its anemone choice was recorded. This cycle of feeding and deprivation was repeated until each slug completed four tests (see Fig. 4a).

The total number of times each slug chose the social option (anemone with a feeding conspecific and slime trail) was used to calculate a social preference score. Slugs unable to complete all four tests were excluded from analysis.

Statistical Analysis

To statistically compare the group sizes observed with the null hypothesis that each slug chose independently of each other, we constructed a model with *m* slugs each selecting one of *n* anemones with equal probability (Eq. 1). Using this model, we simulated a trial and calculated the mean and maximum group sizes. This was repeated for the same number of trials in each dataset and then the mean of the mean and maximum group sizes were calculated for each simulated dataset to create the null distribution. The experimental means of the mean and maximum group sizes were then compared to the null distribution and the probability of the null model producing the same result or larger than the experimental data for a *p* value was calculated. 100,000 datasets were simulated for each statistical test.

$$(eq. 1)\ P(slug\ selects\ anemone\ i)\ = \frac{1}{n}$$

Additionally, we used the social dining model (SDM; often referred to as the “Chinese Restaurant Process”; (Antoniak, 1974; Pitman, 2002)) to estimate a concentration parameter representing the propensity of individuals to select an anemone with feeding conspecifics. The social dining model is a discrete process that simulates a set of individuals, *m*, each sequentially selecting a dining location, *i* (Eq. 2). A concentration parameter, α, dictates how likely individuals are to select a dining location that is already occupied (Eq. 2). This model assumes that the number of anemones, *n*, is greater or equal to the number of slugs, *m*. The model also assumes that the order in which the slugs choose does not affect the final probability distribution. We estimated the concentration parameter using a bisection method to iteratively determine the parameter that fits the experimental data. We used this parameterized model to calculate a p-value similarly to above.

$$(eq. 2)\ P(slug\ selects\ anemone\ i) = \frac{m_i}{m + \alpha}$$

In addition to the models described above, the group feeding assay for 3- and 7-day food-deprived animals were compared using a t-test. For the 2-alternative choice assays, the proportion of individuals that selected the manipulated anemone was compared to random chance (50%) using a binomial proportion test.

The consistency of social preferences assay was analyzed using a Fisher's Exact Test. We also tested if the distribution of social feeding scores (number of trials social option was selected) was bimodal using the Silverman (1981) critical bandwidth test as implemented by the *multimode* package (v1.5; Ameijeiras-Alonso et. al., 2021). To assess the individual repeatability of 2-alternative choice test outcomes, we estimated individual repeatability using the *rptR* package (v0.9.22; Stoffel et. al., 2017) with their choice in the predator-prey ratio assay as a predictor and individual identity as a random intercept.

All modeling, visualization and statistical analysis was performed in R version 4.2.3 (R Core Team 2023). Data manipulation used the *dplyr* (v1.1.4; Wickham et. al., 2023a) and *tidyr* (v1.3.0; Wickham et. al., 2023b) packages. For visualization, we used the following packages: *ggplot2* (v3.4.4; Wickham, 2016), *ggpubr* (v0.6.0; Kassambara, 2023a), *rstatix* (v0.7.2; Kassambara, 2023b) and *cowplot* (v1.1.1; Wilke, 2020). All code to reproduce this analysis and the figures in this paper is available on Github.

Results

Berghia fed in groups more than expected by random chance

This study was inspired by observations of large groups of slugs forming during feeding in the laboratory (Fig. 1A). We quantified the distribution of slugs 20 minutes following a routine feeding and found that when fed with two anemones per tank, the slugs did not evenly distribute between the two anemones (Fig. 1B,C). A one-sample Wilcoxon signed-rank test indicated that the mean proportion of slugs feeding on one of the anemones, 0.85, was significantly different from 0.5 ($Z = 231$, $p = 0.000052$, effect size= 0.887).

To test whether *Berghia* feed on *E. diaphana* in groups even if they have the option to feed alone, we performed a group feeding assay. When given the opportunity to feed individually with a 1:1 ratio of *Berghia* to *E. diaphana* (Fig. 1D), *Berghia* fed in groups larger than expected if each individual *Berghia* was selecting an anemone independently of one another. Across 28 trials, the mean of the average group sizes observed in each trial was 1.82 (Fig. 1E*i*; median = 1.75, SD = ± 0.62) and the mean of the maximum group sizes observed in each trial was 3 (Fig. 1E*iii*; median = 3, SD = ± 1.25).

To distinguish an active choice to aggregate around prey from random grouping, we simulated a scenario where each slug selected an anemone with equal probability (eq. 1), which is representative of conditions wherein each individual slug was selecting prey independently of one another. 100,000 datasets with 28 trials each were simulated. There was no overlap between the experimental dataset mean and the simulation distribution; the experimental mean average group size was significantly more than expected by the simulated data ($p = 0.00002$; Fig. 1E*ii*) and the mean max group size of the experimental data was similarly larger than the simulated data (Fig. 1E*iv*; p = 0). Thus, the slugs are not choosing the anemones independently of each other.

Fig. 1

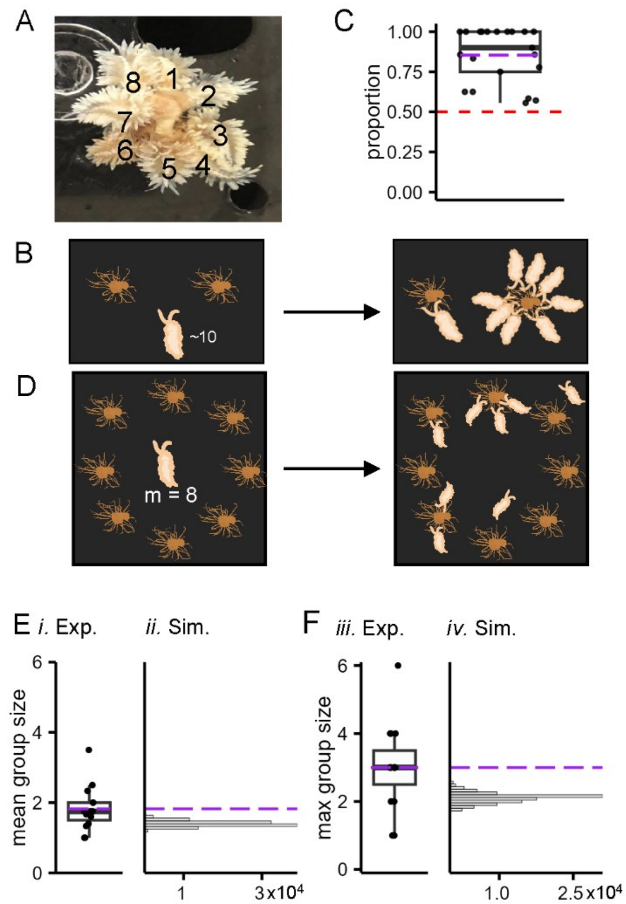

Fig. 1 *Berghia stephanieae* form groups larger than if they each selected an anemone independently of each other. **A** Eight *Berghia* feeding on a single *E. diaphana* anemone in an aquarium. The slugs are numbered for clarity. **B** A schematic showing the experiment used to quantify the grouping during routine feeding in their home tanks. Two anemones were placed into each home tank, which contained about ten slugs. After 20 minutes, the proportion of slugs feeding in the larger group was counted. **C** A boxplot of the proportion of slugs feeding on one of the two provided anemones. The slugs did not distribute evenly between the two anemones and tended to form large groups around one of them (Z =

231, p = 0.0000258). Purple line represents the mean. Red dashed line represents even distribution between the anemones. **D** A schematic of the group feeding assay (GF). **E** A boxplot representing the mean group sizes observed in each trial (left) and a histogram of the mean group sizes for each simulated dataset with the same number of trials as the experimental data of the null hypothesis where each slug selects an anemone independently of each other (right). The purple dashed line represents the mean group size of the experimental dataset. The observed mean does not occur within the distribution of the simulated data. **F** The same plots as **E**, using the maximum group size observed. Similarly, the observed mean of the max group sizes in the dataset does not occur in the simulated data. The simulated data sets have units of 10,000 datasets.

Berghia did not use the presence of feeding conspecifics or slime trails to select anemones to feed on

A series of 2-alternative choice assays were performed to examine potential cues that *Berghia* could be using to aggregate (Table 1). One such cue is that the animals could be following the slime trail (ST) left by a conspecific animal. In the testing arena, a helper slug was placed in the middle of the arena and allowed to navigate the arena until it contacted one of two intact, size-matched anemones. Once the helper slug protruded its proboscis, it was removed from the arena before it could bite the anemone (Fig. 2A*i*). The target slug was then placed in the arena to determine which anemone it would choose, the one with the slime trail leading to it or the other. The slugs did not choose to feed on an anemone with a slime trail laid by a conspecific leading to it more than chance (p = 0.43, 23 out of 40). The slugs were also tested following an acclimation in ATW, to test whether prey scent would cause them to feed in groups due to heightened arousal. The target slug did not choose to feed on anemone with the slime trail leading it regardless of whether it was acclimated in ASW or in anemone-treated water (ATW) (Fig 2B; $p = 0.61$, 6 out of 15).

To test whether slugs were simply attracted to a feeding conspecific (FC), a two choice test was constructed; a helper slug was placed in the center of a separate arena and allowed to begin feeding on one of two intact, size-matched anemones. Once the helper slug had chosen, both anemones were transferred to the testing arena with the helper slug still feeding on the anemone it had chosen. Thus, no slime trail led to the anemone. When given the choice to feed on an anemone with a feeding conspecific, the focal slug preferred the intact anemone (Fig. 2B; $p = 0.023$, 6 out of 24). However, this preference went away when the target slug was acclimated in ATW (Fig. 2B; $p = 0.85$, 13 out of 28).

To determine whether the slugs needed the combination of a slime trail plus a feeding conspecific (ST+FC), a helper slug was placed in the middle of the testing arena and allowed to navigate the arena until it began feeding on one of two intact, size-matched anemones. The target slug was then placed in the arena. There was no preference shown for either anemone despite the presence of both a slime trail and feeding conspecific (Fig 2B; $p = 0.52$, 9 out of 22).

Fig. 2

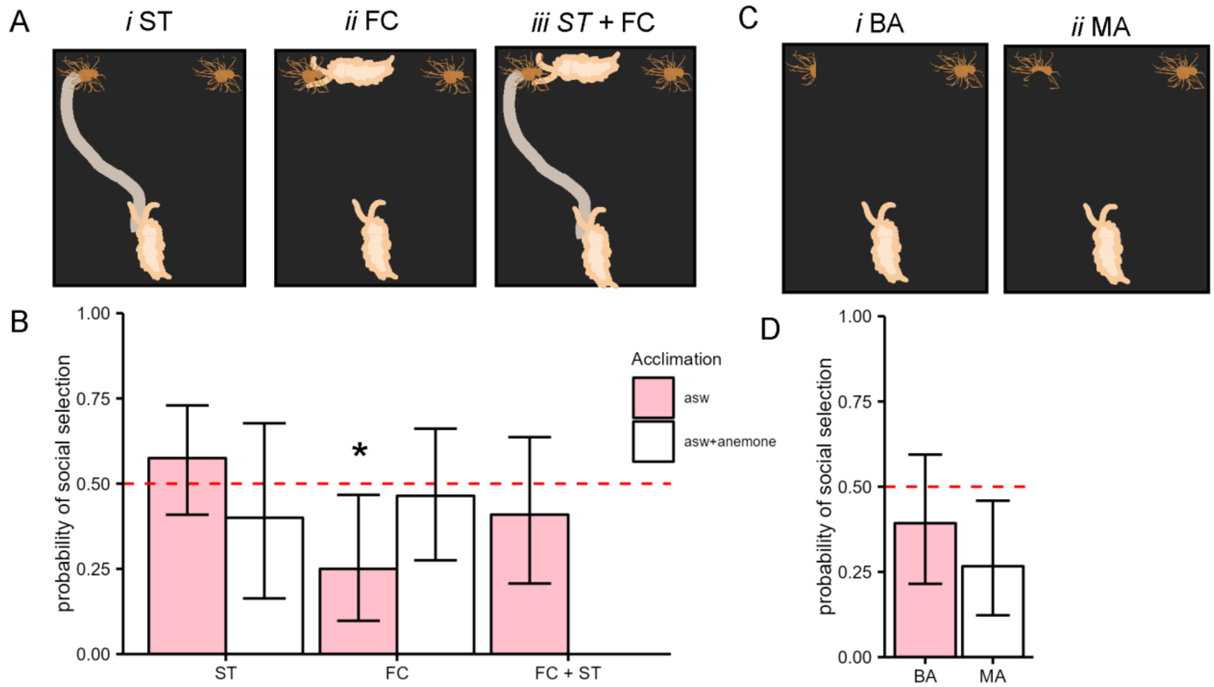

Fig. 2 Behavior in 2-alternative choice tasks. **A** Schematics of the choice between an intact anemone and an anemone with a slime trail (ST), a feeding-conspecific (FC) or both (FC + ST). **B** Bar plots showing the proportion of animals that selected the manipulated anemone for each of the choices depicted in A. The red dashed line indicates random choice. Error bars represent 95% credible intervals of the binomial test. Pink bars represent slugs that were acclimated in filtered ASW and white bars represent slugs acclimated in anemone-treated water (ATW). All choices were not significantly different from random chance, except FC when acclimated in ASW which was selected lower than chance, meaning the slugs preferred an anemone without a feeding conspecific (8/30, p = 0.016). **C** A schematic of the choice between an intact anemone and an anemone that had been cut in half (BA) and an anemone that had been previously fed on by a conspecific (MA). **D** Bar plots showing the same as in **B**. None was significantly different from random chance.

Berghia did not prefer anemones that have been injured

The potential influence of kairomones from injured *E. diaphana* was tested with a 2-alternative choice assay. Two size-matched anemones were selected and one was cut in half with a razor blade (bisected anemone, BA). After 5 minutes, a target slug was added to the arena. *Berghia* showed no preference when given a choice between a bisected anemone and an intact anemone, (Fig 2D; $p = 0.35$, 11 out of 28).

To test whether slugs preferred an anemone that had been injured by a conspecific (munched anemone, MA), a helper slug was placed in the center of an arena and allowed to begin feeding on one of two intact, size-matched anemones. After 5 minutes of feeding, the anemones were removed and placed in the testing arena. The target slug was then placed in the test arena. Contrary to our prediction, slugs showed a preference for intact anemones over anemones that had been previously fed on by a conspecific (8/30, $p = 0.016$; Fig. 2D).

Although the slugs did not show a preference to various social cues, they might have contacted the manipulated anemone more quickly, which could lead to aggregation. A three-way ANOVA was used to compare the effect of the slugs' choices, the acclimation method, and the anemone manipulation on the time it took them to make a choice. The latency to choose was log-transformed to normalize. Slugs that selected the social option did not do in less time than animals that selected the control anemones for any of the treatments (Supplementary Figure S1, Supplementary Table S1). There was no effect of choice ($F(1) = 1.113$, $p = 0.293$), nor a statistically significant interaction effect ($F(3,3) = 0.617$, $p = 0.605$). Although was an effect of the assay type on the latency to select an anemone ($F(3) = 8.851$, $p = 1.89e-05$), this was not a main effect of interest (Supplementary Table S2). Slugs that were acclimated in ATW were faster to choose an anemone ($F(1) = 18.578$, $p = 2.88e-05$), likely due to heightened arousal from the scent of their prey prior to entering the arena, which differs from previous findings that food-deprived slugs in an empty arena move slower when presented with a food odor (Quinlan and Katz, 2023). This effect interacted significantly with their choice ($F(1,1) = 5.864$, $p = 0.0166$), such that their latency was impacted the most when the slugs selected control anemone and ATW acclimation caused them to choose faster. There was no interaction effect between acclimation and manipulation ($F(1,3) = 0.734$, $p = 0.3931$), nor was there a three-way interaction between the terms ($F(1,1,3) = 1.658$, $p = 0.1998$).

To test whether slugs preferentially selected the larger anemones, a nested ANOVA was used to compare the mean difference in the chosen anemone diameter from the anemone that was not chosen to 0 and test for an effect of anemone manipulation. The mean difference in anemone diameter between the anemone choices was not significantly different from 0 for any of the manipulations (Supplementary Figure S2; $F(6) = 0.594$, $p = 0.735$).

Social predation was not facilitated by intermediate levels of food-deprivation

Animals might be changing their social feeding strategies because of a trade-off between food-acquisition and injury. To test the prediction that social predation is more prevalent in animals that are intermediately hungry, we compared 3-day and 7-day food-deprived animals in a group-feeding assay. Across 13 trials, the mean of the average group sizes observed per trial was 1.85 for the 3-day group and 1.82 for the 7-day food deprived group (Fig. 3A*i*; 3-day median = 1.67, SD = 0.75, 7-day median = 1.75, SD = 0.62). The mean maximum group size was 3.00 for both groups (Fig. 3B*i*; 3-day median = 3.00, SD = 1.25; 7-day median = 3.00, SD = 1.29). The mean group sizes for the 3-days food deprived animals were not significantly different from those of the 7-days food deprived animals (Fig. 3A; $t = 0.11074$, df =

23.553, p = 0.9128). The maximum group sizes were also not significantly different (Fig. 3B; t = 0, df = 25.201, p = 1).

Similarly to the 7-day food deprived data, we compared the 3-day food deprived experimental data to the distribution of simulated dataset means of the mean and max group size when each slug chose an anemone independently of one another with equal probability (eq. 1). These simulated datasets had 13 trials each, like the experimental dataset (Fig. 3A*ii*,B*ii*). The observed mean average group size and the mean maximum group size were significantly larger than the simulations (mean p = 0.00037, max p = 0.00084). Thus, 3-day food-deprived animals are also not choosing anemones independently of each other.

We also parameterized the social dining model (SDM) using the 3-days food-deprived dataset. The concentration parameter, α, was estimated to be 4.063. The distributions of the simulated dataset means for the mean and maximum group sizes included the experimental mean average group size (Fig. 3A*ii*; p = 1) and mean maximum group size (Fig. 3B*ii*; p = 1). Additionally, the 7-day food-deprived experimental mean of the mean and maximum group size was also within the simulated distribution parameterized with the 3-days food deprived dataset. This indicates that the grouping as indicated by the α parameter is similar for both levels of food-deprivation.

We also tested 3-days food-deprived animals in some of the 2-alternative choice assays. Like the 7-day food-deprived animals, 3-day food-deprived slugs showed no preference for any of the cues (Fig 3C). There were no differences between anemones with a slime trail (p = 1.00, 9 out of 18), anemones that were previously fed on by a conspecific (p = 0.63, 7 out of 17); or anemones with a feeding conspecific and a slime trail (p = 0.45, 10 out of 16).

Fig. 3

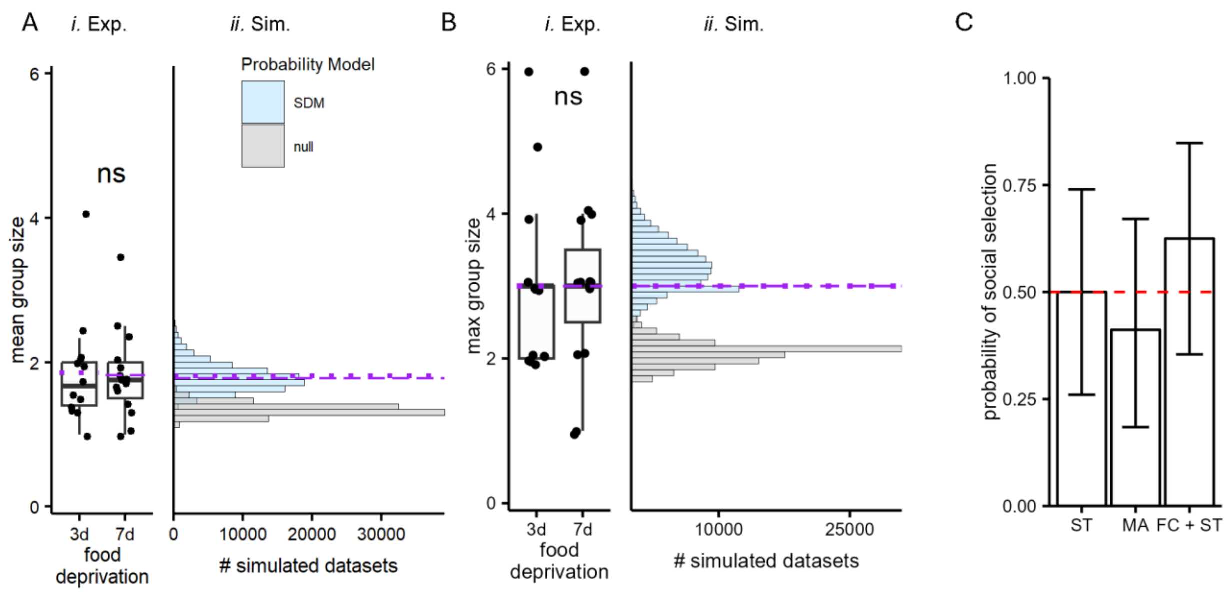

Fig. 3 There is no difference in group size between intermediately food-deprived animals and 7-day food-deprived animals. **A** Boxplot of the mean group size for trials that were 3-days food-deprived and 7-days food-deprived (left). Histogram of the dataset mean of the mean group sizes observed in 10,000 simulated datasets (right). The light blue bars represent the parameterized social dining model (SDM), and the grey bars represent the null model. The dotted purple line is the experimental dataset mean for the 3-day food-deprived animals and the dashed purple line is the experimental mean for the 7-days food-deprived animals. There is no difference between the experimental means and they fall within the SDM simulated dataset means and do not overlap with the null simulated dataset means. **B** Similar plots as A for the dataset mean of the maximum group sizes. **C** The probability of selecting the manipulated anemone in 2-alternative choice assays comparing feeding conspecifics and slime trails (FC + ST), anemones previously fed on by a conspecific (MA) and anemones with slime trails (ST). None was significantly different from random chance (0.5).

Berghia did not show consistent individual preferences to feed in groups

It is possible that the reason that no cue or hunger state was found to account for aggregation in social feeding could be that individual slugs have consistent preferences to feed socially or not. This individual preference might have been lost in the group data. Therefore, we gave individual identifiers to 32 slugs that were 7-days food-deprived and run in a group-feeding assay, recording whether each slug fed in a group or alone (GF, Fig 4A). In this first test, 13 of 24 animals fed socially. Six animals were removed from the analysis because they did not complete four of the subsequent tests.

After testing in the GF assay, the slugs were housed individually in clear plastic deli cups and underwent a 24-hour period of ad-libitum access to *E. diaphana* followed by 7-days of food-deprivation. They were then tested in the FC+ST 2-alternative choice assay and their choice was recorded (T1). Then, they were allowed to eat for 24-hours and then were food-deprived for another 7 days. This process was repeated such that each animal was tested four times (Fig. 4A). Their choices in the subsequent assays were used to create a score for each animal that represented the total number of times each individual chose the social option (anemone with a feeding conspecific and a slime trail).

Their first choice was compared to subsequent choices. In the first 2-alternative choice trial (T1) 10/24 of animals selected the social option and 8/13 of them had fed socially in the GF assay and 7/13 of them fed socially in the second 2-alternative choice trial (T2; Fig. 4B). The choice to feed socially in the GF assay was not predictive of how many times an animal would select the social option in the 2-alternative choice assays (Fisher's Exact Test, $p = 0.1548$). If individual animals had consistent preferences to feed in groups, we would also expect a bimodal distribution in the number of trials they selected the social option, but the distribution was unimodal (Silverman (1981) critical bandwidth test, Critical bandwidth = 0.3612, p = 0.738; Fig. 4C). Their choices were not repeatable (R = 0, 95% confidence interval (CI) = 0., 0.136, p = 0.5).

Fig. 4

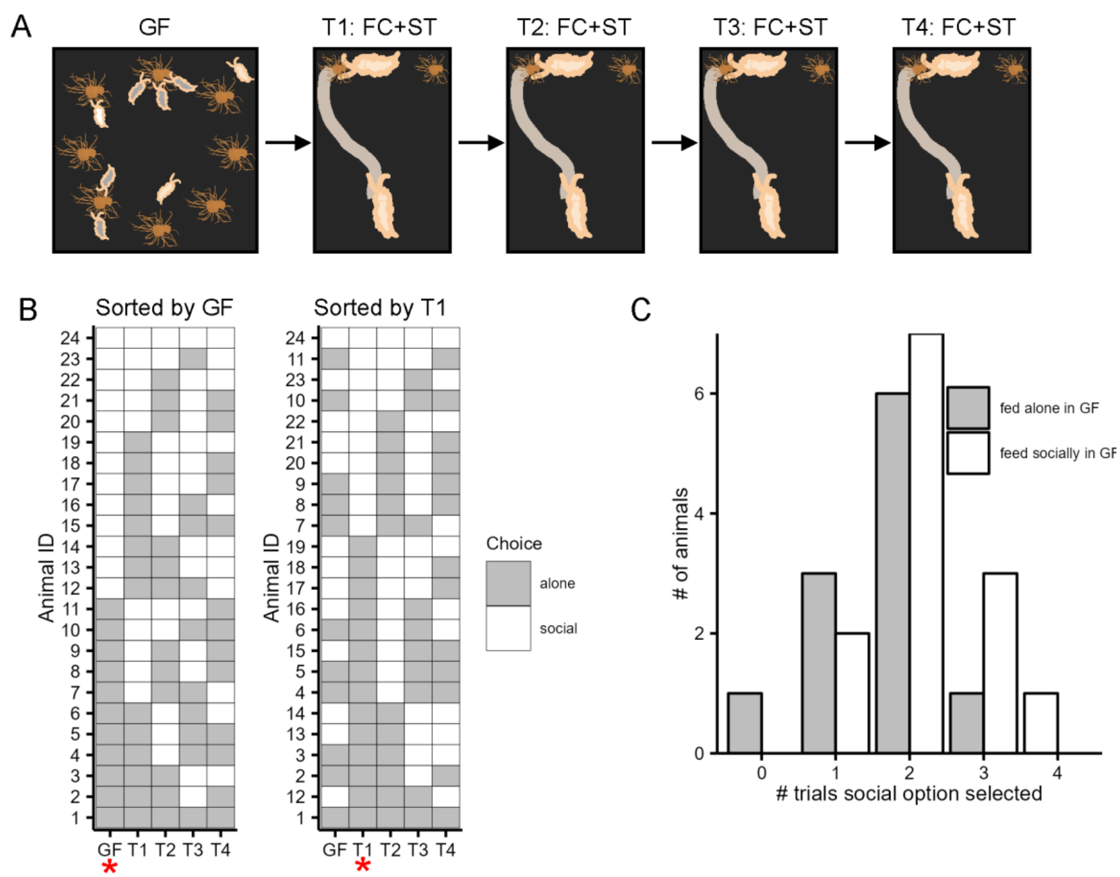

Fig. 4 The choice to feed socially is not consistent within individuals. **A** Schematic showing the experimental design for this dataset. Animals were first tested in the group feeding assay (GF and then individually labeled and housed. Then they were tested 4 times (T1-T4) in a 2-alternative choice assay with a feeding conspecific and slime trail (FC+ST). **B** A plot showing the choices of each individual animal in the 5 different assays organized by their choice in the GF assay (left) and their choice in the T1 assay (right). **C** A histogram showing the number of animals that fed socially in the 2-alternative assays (T1-T4) 0 – 4 times. White represents animals that fed alone in the GF assay and grey represents animals that

fed socially in the GF assay. The distribution is not bimodal and animals seem to randomly switch between feeding socially and alone.

Discussion

Our study revealed that *Berghia stephanieae* feed on their prey socially, forming groups to feed on prey more often than would be expected if each individual chose anemones independently. An alternative explanation is that the grouping behavior observed in these assays is not driven by social attraction but rather by differences in the attractiveness of the prey. For example, in mosquitos some individual humans are more attractive to mosquitoes due to their specific combinations of kairomones (Ellwanger et al., 2021; Giraldo et al., 2023). However, we can discount this hypothesis because if analogous mechanisms exist in *E. diaphana*, some individual anemones may emit cues that universally increase their attractiveness to *Berghia*. If these combinations of cues reliably increased attraction across the species, the 2-alternative choice assays that use helper slugs would likely have captured this effect, leading to a selection rate for the manipulated anemone higher than random chance. Thus, differential prey attractiveness alone does not explain social feeding in *Berghia*.

We hypothesize that social feeding minimizes the risk of injury posed by the radially symmetric defensive structures of the anemone prey by allowing multiple slugs to attack simultaneously from different sides. This aligns with broader patterns in social predators, where cooperation enables individuals to subdue larger or more dangerous prey (MacNulty et al., 2014; Mukherjee and Heithaus, 2013). Our findings suggest that group feeding in *Berghia* is likely an evolved strategy to mitigate these risks.

Contrary to our expectations, *Berghia* showed no preference for anemones associated with conspecific slime trails or active feeding by conspecifics in two-alternative choice assays. This result challenges the assumption that conspecific cues, such as mucus trails, drive aggregation at prey sites. Nudibranchs, like other gastropods, rely on deposition of mucus that they glide on using cilia on their muscular foot. In terrestrial and aquatic gastropods, trail following is a mechanism that many species use to find mates (Ng et al., 2013), hunt other gastropods (Leonard and Lukowiak, 1984; Patel et al., 2014) and otherwise aggregate (Bretz and Dimock, 1983; Davies and Beckwith, 1999). However, this was not a cue that mediated aggregation at anemones in 2-alternative tests.

Conspecific cues are often key drivers of social behavior in other species, and may include the role of social influence, where the actions of conspecifics drive behavioral changes and/or shifts in motivational states of an individual (Webster and Fiorito, 2001; Whiten and Ham, 1992). For example, some crabs locate food by observing other crabs eating; the presence of crabs eating acts to stimulate eating (Kurta, 1982). Similarly, meat traps for *Vespula germanica* wasps are facilitated by the presence of conspecifics at the trap (D'adamo et al., 2003). That said, the presence of a feeding conspecific also was not sufficient to cause slugs to aggregate in this study.

The absence of attraction to these cues in *Berghia* could indicate that more complex or context-dependent signals facilitate group formation, such as a critical density of individuals or a threshold of sensory input not captured in our assays. The group-feeding assay demonstrated that slugs often feed in pairs, and in cases where they feed in larger groups, the first slug to join a group must have responded to cues from a single conspecific. This highlights the need for further exploration of alternative mechanisms, such as chemical signaling or tactile interactions, which may occur under natural conditions or at higher population densities.

We found no evidence that *Berghia* were attracted to injured anemones, which contrasts with findings in other predator-prey systems where kairomones or alarm cues attract predators (Aguilar-Marcelino et al., 2014; Schoeppner and Relyea, 2005). For example, kairomones released by injured prey have been shown to stimulate aggregation in nematode-hunting mites and frogs (Bilgrami, 1994; South et al., 2020). It is possible that injury-related chemical cues from anemones are less relevant to predation strategies in *Berghia* or that such cues are masked or altered in the controlled laboratory setting. However, the 2-alternative choice assay may not be sufficient for identifying cues in social feeding because it captures only the initial attraction and choice. In the nematode *Caenorhabditis elegans*, injury induces social feeding through activation of nociceptive neurons (de Bono et al., 2002). Since the 2-alternative choice assays were stopped at first contact between the slugs and their prey, it may not have allowed them to experience injury and then re-evaluate their decision to ultimately select the other anemone. Individual *Berghia* may need to interact with their prey for a longer time period and then be allowed to make a selection. These results suggest that further experiments incorporating prolonged interactions and dynamic decision-making contexts could clarify whether injury or other post-contact cues play a role in the feeding behavior of *Berghia*.

Food deprivation did not influence the propensity of *Berghia* to feed in groups, as slugs deprived for three or seven days showed similar levels of social feeding. We hypothesized that comparing seven- and three-day food-deprived animals would reveal a trade-off where hungrier animals were more likely to feed alone to maximize food intake at the risk of injury while intermediately hungry animals would feed in groups. In *Berghia*, the lack of a satiety effect suggests that social feeding is not primarily motivated by hunger but may instead serve other purposes, such as reducing predation risk or overcoming prey defenses. For instance, in freshwater amphipods, aggregation behavior increases in response to perceived predation risk (Kullmann et al., 2008). Similarly, social feeding in *Berghia* may be an evolved strategy to mitigate risks associated with their prey, independent of individual energy needs. In this species, social feeding behaviors appear to be a strategy used by most individuals regardless of satiety.

These conflicting results led to the hypothesis that individual slugs have different likelihoods of using social predation as a strategy. If the animals preferring social predation and animals that prefer to feed alone are random in the overall population of *B. stephaneiae*, then randomly sampling from the animals for the 2-alternative choice assay would show a null result. However, we found no evidence of stable individual preferences for group feeding.

Many social predators have stable individual roles across hunting bouts such as the social spider *Australomisidia ergandros*; individuals specialize in a feeding tactic as a producer or a scrounger (Dumke et al., 2016). Similarly, individual dolphin specialize as divers and blockers when herding prey for capture (Gazda et al., 2005). This hypothesis also was not supported, indicating that individuals take on temporary roles as leaders and followers that drive fission-fusion social dynamics in the presence of prey. Each individual is not foraging randomly, however their roles seem to differ depending on context and specific foraging bout. This is similar to false cleaner fish, which have temporary roles when predating upon fish eggs (Sato et al., 2024) and the yellow saddle goat fish whose role is determined by spatial position in relation to the prey (Steinegger et al., 2018). The absence of such specialization in *Berghia* suggests that individuals may adopt temporary roles, such as scrounging or producing where individuals either use the strategy of joining groups feeding at specific food sources or locate their own sources, respectively (Vickery, 2020).

In other species, the choice of tactics is influenced by an individual's early life experience (Katsnelson et al., 2008), perceived predation risk (Barta et al., 2004), hunger (Lendvai et al., 2004), and the availability and quality of food sources (Kurvers et al., 2012). Modeling studies support the idea that social predation can be maintained in populations where individuals may inhabit temporary roles such as scrounging or producing where individuals either use the strategy of joining groups feeding at specific food sources or locate their own sources, respectively (Vickery, 2020). Group formation in *Berghia* is likely context-dependent and flexible, with individuals participating opportunistically rather than adhering to fixed roles. By exploring individual variation in social behavior, our study aimed to understand the mechanisms driving group feeding, and these findings suggest that group dynamics in *Berghia* are fluid and influenced by yet unknown external factors.

This study focused on the feeding behavior of adult *Berghia* under controlled laboratory conditions, providing insights into their social feeding tendencies and the potential mechanisms driving these behaviors. However, several important avenues remain unexplored. For instance, unpublished observations of juvenile post-metamorphosis *Berghia* indicate social feeding behavior similar to that of adults (KO). Juvenile social interactions may carry unique costs and benefits compared to adults, given that mixed-size groupings can hinder growth and survival. Juvenile *Berghia* experience higher mortality and reduced growth rates when housed with adults (Monteiro et al., 2020), highlighting potential trade-offs between the benefits of social foraging and the pressures of competition or predation risk. These dynamics are not unique to *Berghia*; for example, juvenile ground squirrels forage in groups more frequently than adults but maintain higher vigilance levels, even when group foraging reduces vigilance in adults (Ortiz et al., 2019). Similarly, in the algae-eating saccoglossan sea slug *Placida dendritica*, feeding conspecifics stimulate others to feed, and smaller individuals benefit from group foraging more consistently than larger individuals, except when grouped with conspecifics of similar size (Trowbridge, 1991). These examples highlight the importance of developmental stage in shaping social foraging behavior.

The developmental stage of *Berghia* is likely to play a complex role in their social foraging behavior, shaping trade-offs in ways that remain to be fully understood. Additionally, the laboratory setting of this study may not fully capture the natural ecology of *Berghia*. Social predation and grouping behaviors are likely influenced by population density and environmental conditions in the wild, neither of which has been extensively studied for this species. Future research should investigate these dynamics across developmental stages and natural populations to better understand the ecological and evolutionary pressures shaping social foraging in *Berghia*.

Data Availability

The datasets generated and analyzed in the current study are available on Github (https://github.com/OtterLabGroup/nudibranch_social_predation_2024). Behavioral videos are available upon request.

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Author Contributions

All authors contributed to the study conception and design. Data collection and analysis were performed by Kate Otter and Saida Gamidova. The first draft of the manuscript was written by Kate Otter and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Conflict of interest

The authors declare that they have no conflicts of interest.

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