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Wave of mutilation: Scavenging hermit crabs use social information to locate carcasses

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Abstract

Carcasses are patchily distributed and often short-lived resources, placing scavenging animals under pressure to locate them before they rot or are depleted by competitors. Scavengers may search for carcasses directly, or indirectly, using social information. Aggregations of feeding animals and their conspicuous competitive behaviour may be more readily detectable to searching scavengers than the carcass itself. Moreover, the actions of attendant scavengers upon the carcass, breaking it apart and releasing odour or chemical cues, may further enhance its detectability to others foraging nearby. Here we test this idea. In the first of two experiments performed in the field, we found that hermit crabs (*Pagurus bernhardus*) were attracted to shelled mussels (*Mytilus edulis*) that other hermit crabs were already feeding on. They showed no strong tendency to approach aggregations of conspecifics in the absence of food, nor conspecifics that were confined close to mussels but prevented from feeding on them. We speculated that through breaking up the carcass, the feeding hermit crabs released chemical cues and drifting particles of mussel tissue that further attracted other hermit crabs. We tested this in a second experiment, finding that finely chopped mussels attracted significantly more hermit crabs than did intact mussels. We suggest that scavenger feeding action upon carcasses makes these more detectable to others by releasing odour and particle plumes, a form of inadvertently produced social information.

KEYWORDS
competition, foraging, grouping, public information, scrounging, social foraging

1 | INTRODUCTION

For scavenging animals carcasses can be patchy and unpredictable resources. Because carcasses can rot, or be consumed by competitors, or may be moved by currents, they might only be exploitable for a limited period of time. Effective scavenging therefore depends upon being able to locate and reach carcasses quickly (Kane et al., 2017). Scavengers might achieve this by using visual or chemical cues emanating from the carcass itself. They may also use social information produced by others that have already found the

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resource. An aggregation of other scavengers, along with conspicuous, noisy competition that occurs between them, might be a particularly salient cue that a carcass is present (Danchin et al., 2004; Krause & Ruxton, 2002; Ward & Webster, 2016).

In terrestrial environments, the scavenging behaviour of vultures, obligate carrion-specialising birds that typically feed on the carcasses of large mammals, has been studied extensively. Vultures can locate carcasses independently, using visual cues (Mundy et al., 1992), however they also make extensive use of social information from con- and heterospecifics. Griffon Vultures (*Gyps fulvus*) use social cues to locate carcasses, with locations where amassed conspecifics can be seen sinking to the ground attracting others (Cortés-Avizanda et al., 2014). Wheeling aggregations are likely visible over many kilometres and are more conspicuous a cue than the carcass itself, while sinking, as birds alight around the carcass provides finer-scale information on its location. In East Africa, vultures (*Gyps* sp.) exploit carcasses alongside several species of eagles (*Aquila* sp.). Arrival times suggested that vultures use social cues provided by the eagles to locate carcasses (Kane et al., 2014). Five species of vultures were also attracted to playbacks of aggressive competitive calls from mammalian carnivores, supporting the idea that eavesdropping on heterospecific social information in the form of auditory cues is another means by which carcasses can be located (Jackson et al., 2020).

In the marine environment, whale falls represent sources of nutrients that can persist for decades. These occur when whale carcasses sink into deeper waters, where the low temperature and high pressures prevent rapid decomposition, allowing communities of specialised scavengers to develop and persist (Smith et al., 1989; Smith & Baco, 2003). Four stages of succession are recognised in the development of a whale fall ecosystem, the first of which is dominated by the consumption of soft tissues by mobile scavengers (Aguzzi et al., 2018; Smith & Baco, 2003). A diverse range of species feed on whale carcasses during the mobile scavenger succession phase. Aguzzi et al. (2018) observed species of molluscs, arthropod, echinoderm and fishes among the first visitors to a tethered and intensively monitored whale carcass. Laboratory experiments revealed that hagfish (*Eptatretus stouti*) and amphipods (*Orchomene obtusus*), common scavengers of marine carcasses, could survive without feeding for extended periods, but quickly commenced active searching for food after being exposed to carcass odour cues (Tamburri & Barry, 1999). Smith et al. (2014) observed large numbers of fish, amphipod and decapod scavengers feeding on a recent whale fall in Antarctica, inferring that they were attracted by the odour plume emanating from the carcass. Auster et al. (2020) suggest that while odour plumes from dead marine megafauna might be the means by which many scavengers locate them, acoustic cues produced by sharks and large fishes as they use their teeth and rapid tail movements to tear and twist tissue away from carcasses might also provide socially transmitted cues that attract other scavengers.

In shallow coastal waters, sunken carcasses also provide rich resources for diverse ranges of scavenging animals, though they usually persist for much shorter periods compared to whale falls before being depleted. Davenport et al. (2016) placed cameras baited with dead fish (mackerel, *Scomber scomber*) at depths of 1–2 and 16–18 m at a site on the south coast of Ireland and noted a variety of scavengers in attendance at the deeper locations. Highly mobile fishes and swimming crabs arrived soonest, followed by crawling crabs and molluscs, with large starfish, spider crabs and small sharks arriving later. They also noted that feeding by crab species detached particles of tissue that drifted away from the carcass. These supported indirect scavengers, species that consumed material detached by other species, but which tended not to feed from the carcass itself. The authors also noted that the detached material also likely contributed to the odour plume associated with the carcass, which may have enhanced its detectability to other scavengers.

The terrestrial and marine examples discussed here highlight the sources of information that scavengers might use to locate carcasses. They might use cues coming from the carcass itself, likely visual and chemical. They can also use social information. This may be provided by the presence of other scavengers in or around the resource, or indirectly, via the actions of other scavengers upon the carcass (Danchin et al., 2004). As they feed, they break the carcass up, increasing the surface area from which chemical cues can be released, exposing new tissues and any associated volatile compounds and detaching small pieces of tissue that can be entrained and dispersed by local currents. This action has the potential to disperse carcass cues and enhance carcass detectability over a wider area (Kamio & Derby, 2017).

In this field-based experiment, performed in rockpools on the rocky shore, we investigated how the hermit crab *Pagurus bernhardus* uses direct, social and socially derived feeding cues to locate carcass resources. This species of hermit crab is a generalist forager that sifts sand for detritus (Thorson, 1966), consumes invertebrates found on and amongst the substrate (Ramsay et al., 1996) and filters suspended zooplankton and algae from the water column (Gerlach et al., 1976). They also readily consume carrion, including dead fish and molluscs, often gathering in aggregations to exploit these (Ramsay et al., 1997).

In a first experiment, we compared five treatments, presented in stimulus chambers placed on the bed of the rockpool. These consisted of either a group of hermit crabs, a dead mussel, a group of hermit crabs that were feeding on a dead mussel, or a group of hermit crabs and an inaccessible mussel (so that they could not feed) and a no-stimulus control. We predicted that hermit crabs would amass in front of the stimulus boxes in the greatest numbers when feeding conspecifics were present, using direct, social and socially produced food cues to locate the mussel. In a second experiment, we presented an empty stimulus box as a control, an intact dead mussel as before, and a dead mussel that had been chopped into fine particles. This simulated a mussel that had been broken up by foragers but controlled for any direct social stimulus. We predicted that the greatest numbers of hermit crabs would be seen in front of the stimulus boxes in the chopped mussel treatment, reasoning that the greater surface area of the mussel in this treatment would lead to a greater concentration of chemical cues escaping the stimulus box and drawing in the hermit crabs.

2 | METHODS

2.1 | Study site

Experiments were conducted at low tide in rockpools on the lower shore of East Sands, St Andrews on the east coast of Scotland between 23rd November 2021 and 19th August 2022 (experiment 1) and 6th June and 27th July 2023 (experiment 2). The study site consisted of a stretch of rocky shore with rockpools that were connected by the rising tide and inundated completely twice daily. The study site was typically covered by the sea for 9 h of each tidal cycle, during which time we could not access it to perform experiments. No experiments were performed as the tide was flowing into the pool as the water was usually too turbid for use to see the apparatus or animals. The beds of the rockpools consisted of sandstone bedrock with loose pebbles and coarse sand, large boulders and patches of macroalgae. The typical depth of the rockpools was 5–60 cm and we focussed on areas of 30–60 cm depth. Hermit crabs were abundant at the study site (estimated at $>20/\text{m}^2$). A variety of other crustaceans and fish were also present, with green shore crabs (*Carcinus maenas*), common prawns (*Palaemon serratus*), sculpin (*Myoxocephalus scorpius*), two spotted goby (*Gobiusculus flavescens*), juvenile whiting (*Merlangius merlangus*), shannies (*Lipophrys pholis*) and corkwing wrasse (*Symphodus melops*) commonly seen close to the experimental apparatus.

2.2 | Ethics approval

Decapod crustaceans are not currently included under UK animal welfare legislation. The Animal Welfare and Ethics Committee of the University of St Andrews has confirmed that no ethical approval was required for this work.

2.3 | Experiment 1: Hermit crab recruitment via social and resource cues

2.3.1 | Overview

In this experiment, we sought to determine the importance of social cues (the presence of aggregations), resource cues (the presence of a food resource) and combinations of these in attracting hermit crabs to carcasses. We used a stimulus chamber (Figure 1), a small Perspex tank, placed on the bed of the rockpool to present five different stimuli treatments. These were as follows:

(i) *Feeding conspecifics*, in which a group of five hermit crabs were allowed to feed on a thawed frozen mussel.

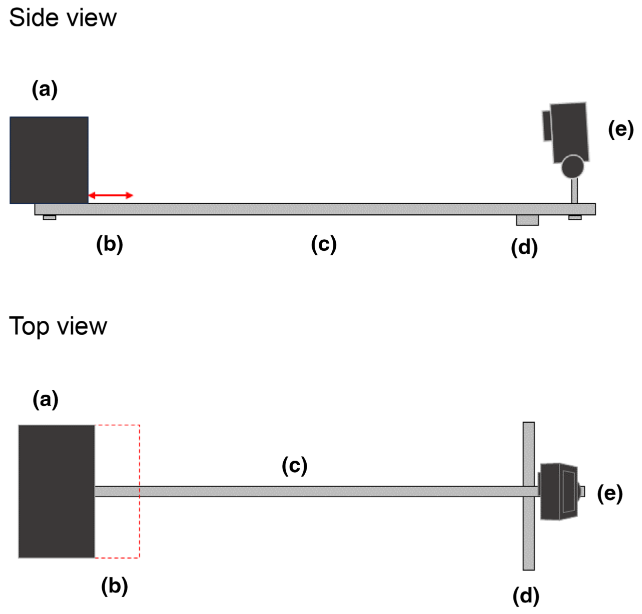

FIGURE 1 Side and top-down view diagrams of the apparatus used in experiments 1 and 2. (a) the stimulus chamber (15 × 6.2 × 7.6 cm) used to hold the treatment stimuli, (b), the stimulus goal zone within which recruited hermit crabs were counted (note that this was not physically marked but was delineated using a drill hole in the fixing plate), (c) stainless steel fixing plate (length: 47 cm), (d) 20 cm fixing plate for stability, (e) GoPro Hero 5 camera with screw-on mount. Diagrams not to scale.

(ii) *Conspecifics and food present but no feeding*, in which the five hermit crabs were presented alongside, but were unable to access a frozen mussel.

(iii) *Conspecifics only*, a group of five hermit crabs presented without any food.

(iv) *Food only*, a thawed frozen mussel was present in the stimulus chamber.

(v) *Control*, an empty stimulus chamber containing no hermit crabs or food.

We performed 15 replicates (hereafter: trials) of each treatment, for 75 trials in total. The testing schedule was randomly pre-determined. Note that a number of trials were abandoned or discarded (described below). These trials were re-run in order to achieve 15 per treatment.

2.3.2 | Apparatus

The stimulus chamber consisted of a Perspex box measuring 15 × 6.2 × 7.6 cm (length × width × height). The side and rear walls and base were painted black using matte acrylic paint. The front and lid were left colourless transparent. We drilled three 10 mm holes in the front of the chamber, 20 mm apart. We also drilled five 10 mm holes in the base. Four of these were 20 mm in from each corner. The fifth was in the centre and was used to bolt the chamber to a fixing plate, described below. The lid had two 10 mm holes, 30 mm apart from each other in the centre. A plastic cable tie was looped through this, but they were otherwise left open (this was used to secure a mussel in place in the second treatment condition, described below). The holes facilitated water flow between the chamber and surrounding water, allowing food and conspecific chemical cues to leave the chamber.

The chamber was attached to a stainless-steel fixing plate measuring 47 cm long and 2.5 cm wide using stainless-steel wingnuts and bolts. A second T-shaped fixing plate measuring 20 cm wide by 10 cm long was bolted to the first to provide stability. At the opposite end of the apparatus to the stimulus chamber was a 50 mm bolt, placed thread-end up. We used this to screw on a camera (GoPro Hero 5 with screw-on housing mount). This was positioned towards the clear, unpainted side of the stimulus chamber. We constructed three of these devices and used either two or three simultaneously when performing trials. We attached a balloon as a buoy to each apparatus using a 1.5 m nylon rope attached to the end of the rig where the camera was located. This was extended away from the rig in a downwind direction to prevent it from drifting over the apparatus. This allowed us to quickly locate and retrieve rigs at the end of the trials. When placing the apparatus, we avoided areas with larger boulders and patches of macroalgae as these prevented us from placing the apparatus flat on the bed and obscured the camera view of the study area.

The hermit crabs placed in the stimulus chambers were collected from the margins of the rockpools, held in a bucket of seawater for no more than 10 min and five individuals were then added to the stimulus chambers immediately before they were deployed. We only used hermit crabs occupying common periwinkle (*Littorina littorea*) shells measuring 15–20 mm tall. Hermit crabs within this shell-size range were haphazardly added to the stimulus chambers. Periwinkle shells are the most commonly occupied at this location (we conservatively estimate >90% of hermit crabs use these shells) and this size range is typical. Mussels (*Mytilus edulis*) were purchased from Tesco supermarket. These were supplied shelled and chilled. They were frozen until required for use and thawed in seawater immediately prior to use. All mussels were 15 mm in length. Pilot observations confirmed that these were readily consumed by hermit crabs at the study location.

2.3.3 | Experimental procedure

We performed a set of two to three trials simultaneously. Typically, on any given day, we only performed one set of trials before the tide began to inundate the study area but on some days we were able to perform two sets of trials. We randomly pre-determined the order of the treatments at the start of the experiment. When we placed the three pieces of apparatus we systematically allocated to open areas free from boulders or macroalgae within the rockpools.

Hermit crabs were collected and added to the stimulus chambers for the *Feeding conspecifics*, *Conspecifics and food present but no feeding* and *Conspecifics only* treatments. A single mussel was added to the floor of the chamber for the *Feeding conspecifics* and *Food only* treatment. In the *Conspecifics and food present* treatment, in which the hermit crabs were prevented from feeding on the food, the mussel was secured to inside of the chamber lid using a cable tie, where the stimulus hermit crabs could not reach it.

The apparatus was immediately deployed, and the camera was switched on (1920 × 1080 resolution, 30 frames per second). They were deployed by hand; researchers walked to the location, placed the apparatus and then immediately exited the water. The apparatuses were left in place for 20 min before being retrieved. The videos were downloaded and used for data analysis. We discarded the first 10 min of each video, reasoning that the manual deployment likely disturbed the hermit crabs in the area. The second 10 min was used for analysis. Using a drilled hole in the fixing plate as a marker we designated an area 5 cm in front of the stimulus chamber as a goal zone and we counted the number of hermit crabs that were attracted to this area (Figure 1). To do this, we scan samples for 20 s every minute, counting the number of hermit crabs in the stimulus goal zone. This yielded 10 counts per trial.

2.4 | Experiment 2: Hermit crab recruitment to broken-up mussels

In this experiment, we tested the idea that by breaking up mussels as they fed, hermit crabs might attract further conspecifics. To achieve this we used chopped mussels, comparing recruitment to apparatus containing these, intact mussels or empty control. In each case, the chopped and intact mussels were placed within black nylon gauze bags within the stimulus chamber, this was necessary to prevent the chopped mussel pieces from washing out through the holes in the chamber as the apparatus was deployed. The empty control conditioned used an empty gauze bag only. The intact mussels were purchased from Tesco supermarket, as in experiment 1. The chopped mussels were produced by Gamma Foods (Tropical Marine Centre.com) in the form of blisters of pre-chopped (.5–1 mm piece size) mussels sold as aquarium fish food. Though produced by different manufacturers, the mussels were the same species (*Mytilus edulis*). We used equal masses of chopped and intact mussel (mean mass ± standard error, intact 2.79 ± .04 g, chopped 2.72 ± .01 g, *T*-test: $n = 20, 20$, $T = 1.89$, $p = .08$). Both intact and chopped mussels were thawed in seawater at the moment of use, as in experiment 1. The experiments proceeded as described for experiment 1. Fifteen replicates were completed in each of three conditions, in a randomised order, using either two or three simultaneously deployed camera rigs. An alternative version of experiment 2 was also conducted. We decided to redesign it, replacing it with the version presented here, which we consider an improved design. For transparency, however, we describe the design and findings of the alternative version of the experiment in Data S1.

2.4.1 | Excluded trials

A total of 14 trials were discarded in Experiment 1 and 12 trials in Experiment 2 due to predator presence or equipment failure. Predatory green shore crabs, wrasse or shannies sometimes approached the apparatus and attempted to access the stimulus chamber to reach the mussel. When they were present hermit crabs tended to avoid the area. Equipment failures usually consisted of videos failing to record or save, batteries failing, loose macroalgae snagging on the camera and covering the lens or the camera rotating on its mount and facing away from the stimulus chamber. Some trials were abandoned due to poor visibility arising from suspended sediment entering the sea from a nearby stream following floods. Finally, a set of trials was discarded after it became clear that strong winds were agitating the water surface sufficiently to move the apparatus and disturbing the hermit crabs in the vicinity. All discarded trials were rerun to ensure that each treatment had 15 trails. A full list of abandoned trials is presented in Table S1.

2.4.2 | STRANGE statement

The STRANGE framework encourages researchers to declare and discuss potential sources of bias that might limit the representativeness of their test subject pool relative to the wider population of animals that they seek to understand (Rutz & Webster, 2021; Webster & Rutz, 2020).

In this study, hermit crabs self-selected in so far as they were free to interact, or not, with the experimental apparatus. In a laboratory study that tested hermit crabs from this population, we found that hermit crabs collected from open areas behaved different than those collected from beneath cover, emerging from their shells sooner following disturbance (Hills & Webster, 2022). By placing our apparatus in open areas within the rockpool we may have included more of these bolder individuals in our sample. We also note that we used a short acclimation period and short observation period of 10 min each, which may have excluded visits by neophobic individuals. We have no cause to believe that this may have affected the differences in recruitment that we saw between treatments.

While hermit crabs were highly abundant at the study site (estimated at >20/m^2), we cannot exclude the possibility the same crabs were recorded more than once in different trials. Similarly, because stimulus hermit crabs were released after being used we cannot rule out that they were recaptured and reused later or that they were recorded visiting stimulus goal zones in later trials. Hermit crabs could not be marked because they were too numerous and because they regularly exchange shells, and had no obvious features that could be used for individual recognition. We have no data on either site fidelity or dispersal in this species that might provide information on potential for repeated sightings. Our experimental design, which spread each experiment over several weeks or months and used rigs placed in different areas of the rockpools should have reduced the potential for pseudoreplication but cannot exclude it completely.

Finally, we saw no effects of time of year (days since start of study) upon hermit crab recruitment numbers. While this suggests no evidence of a seasonal effect we highlight that we do not have data spanning multiple years and that we only focused on a single population, so this should be interpreted with caution.

2.5 | Statistical analyses

For both experiments, we used a general linear model with Poisson distributed errors to compare the recruitment of hermit crabs to the stimulus goal zone between treatments. For each treatment in each experiment, we first plotted the average number of hermit crabs seen per minute (see Figures S1 and S2). We saw no trend for changes in hermit crab numbers over the observation period in any condition. For this reason, we used a mean average of these visit scores for each trial as the dependent variable in the models. Averaging point counts within trials are also guarded against repeated visits by the same hermit crabs within trials. We included treatment as a categorical factor and day of testing since the start of the experiment as a continuous covariate. This allowed us to test for changes in hermit crab numbers of the duration of the experimental period. To calculate this, we designated the first day of testing as day 1 and counted whole days from that point for subsequent trials. By this approach, Experiment 1 began in November 2021 and ran for 239 days until August 2022, encompassing winter to summer seasons. Experiment 2 ran for a shorter period during the summer only, from early June 2023 to late July 2023. In each model, we used simple contrasts to compare recruitment to the stimulus goal zone against the treatment where stimulus hermit crabs were present and feeding (experiment 1) and the treatment where an intact mussel was present (experiment 2). Analyses were performed in R version 4.0.2 (R Core Team, 2023), using the lme4 package (Bates et al., 2015). Box plots were produced using (Postma & Goedhart, 2019).

3 | RESULTS

3.1 | Experiment 1

A general linear model revealed an effect of treatment upon hermit crab recruitment to the stimulus zone, but no effect of day of testing nor any interaction between these [Intercept: $F_{(1,74)} = 20.70$, $\eta p^2 = .24$, $p < .001$; Treatment: $F_{(4,74)} = 4.65$, $\eta p^2 = .22$, $p = .002$; Day: $F_{(1,74)} = 1.03$, $\eta p^2 = .01$, $p = .31$, Treatment × Day: $F_{(4,74)} = .96$, $\eta p^2 = .05$, $p = .43$, Figure 2]. Contrasts revealed that more hermit crabs were attracted to the stimulus zone in the treatment where hermit crabs were present and feeding within the apparatus compared to the empty condition ($p < .001$), when the stimulus chamber contained hermit crabs

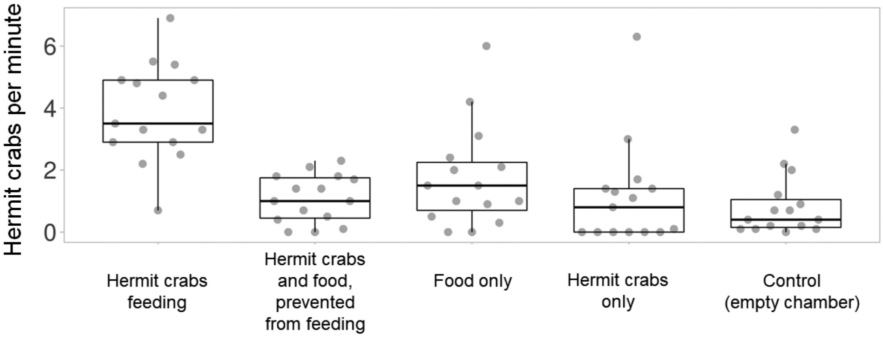

FIGURE 2 The number of hermit crabs per trial recorded in the stimulus goal zone. Bold black lines, boxes and whiskers depict median, interquartile range and 95% confidence intervals respectively. Grey points indicate the mean number of crabs per trial. Significantly more hermit crabs visited the stimulus goal zones in the treatment where stimulus hermit crabs were feeding than they did in any of the other treatments.

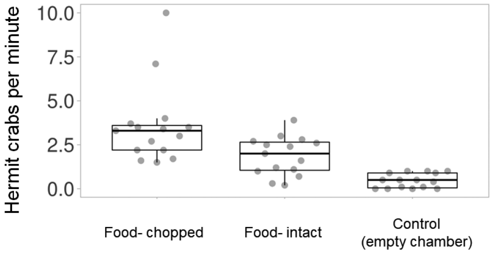

FIGURE 3 The number of hermit crabs per trial recorded in the stimulus goal zone. Bold black lines, boxes and whiskers depict median, interquartile range and 95% confidence intervals respectively. Grey points indicate the mean number of crabs per trial. Significantly more hermit crabs visited the stimulus goal zones in the treatment where the food was chopped than they did in either of the other treatments and significantly more visited in the intact food treatment than in the control treatment.

only ($p=.003$), food only ($p=.006$) or when it contained food and hermit crabs that were unable to access the food ($p=.023$).

3.2 | Experiment 2

As in the first experiment, a general linear model revealed an effect of treatment upon hermit crab recruitment to the stimulus zone, but no effect of day of testing nor any interaction between these [Intercept: $F_{(1,44)}=43.01$, $\eta p^2=.52$, $p<.001$; Treatment: $F_{(4,44)}=9.12$, $\eta p^2=.32$, $p<.001$; Day: $F_{(1,44)}=1.66$, $\eta p^2=.04$, $p=.21$, Treatment × Day: $F_{(4,44)}=.17$, $\eta p^2=.01$, $p=.84$, Figure 3]. For this model, we specified the intact mussel treatment as the comparator category when performing contrasts, since we wanted to test the prediction that more hermit crabs would be attracted when we used a chopped mussel than an intact one, and also that fewer hermit crabs would recruit when the chamber was empty. Contrasts confirmed that significantly more hermit crabs were attracted in the chopped than intact mussel treatment ($p<.001$) and significantly fewer to the empty treatment than the intact mussel treatment ($p<.001$).

4 | DISCUSSION

We performed two experiments to investigate the role of social and food-derived cues in attracting scavenging hermit crabs. In the first experiment, we saw that significantly more hermit crabs approached the apparatus when it contained conspecifics that were actively feeding, compared to other conditions. The presence of conspecifics alone, food alone or conspecifics and inaccessible food did not result in more hermit crabs approaching the apparatus compared to when the apparatus contained no food or social stimulus at all. As stimulus hermit crabs fed, they broke the mussel into fine pieces, many of which drifted away into the water beyond the apparatus. This feeding action also increased the surface area of the mussel, allowing for a greater exchange of chemical cues into the surrounding water. We suggest that the action of the feeding stimulus hermit crabs upon the mussel created a stronger odour cue and / or particle cloud compared to an intact mussel that attracted further hermit crabs to the area (Kamio & Derby, 2017). While further hermit crabs were attracted to cues from the mussel, these were socially facilitated through the actions of the stimulus hermit crabs as they fed.

Our second experiment supports this interpretation. Here we saw that more hermit crabs were attracted to the apparatus when it contained a finely chopped mussel, compared to an intact mussel. Davenport et al. (2016) also observed scavenging crabs producing clouds of particles as they fed on fish carcasses. These drifted away from the carcass and may have attracted further scavengers. The feeding hermit crabs in our study were constrained in a stimulus chamber in our first experiment and absent in the second one. We speculate that under natural conditions the feeding and movements of the crabs might serve to displace and disperse the food particles further, potentially attracting even more scavengers to the area. It is however, important to note that in an alternative version of our second experiment, we saw that hermit crabs were attracted to apparatus containing intact or chopped mussels at similar rates (described in Data S1). This observation is likely due to the preparation of the mussels in the alternative experiment 2. For the chopped mussel treatment in the alternative experiment, we had cut the mussels into fewer larger pieces. This resulted in a lower surface area and thus limited opportunity for release of chemical cues. The larger size also prevented pieces from drifting away. This preparation of the mussels did not replicate the chemical and particle plume produced by the feeding hermit crabs and this may explain the discrepancy in the findings between experiment 2 and the alternative experiment 2.

The particles and odour plumes provided by the feeding hermit crabs constitute a form of inadvertent social information. Social information is defined as information produced by another animal or its products (Hoppitt & Laland, 2008). Here, products include the actions of the scavengers upon the carcass and the released material, which provides a cue to others as to the presence and location of a food resource. Inadvertent social information differs from signals, which are defined as cues that have evolved to alter a receiver's behaviour that evolved which is effective because the receiver's response has also evolved (Smith & Harper, 2003). Instead, inadvertent social information arises passively as a by-product of a 'demonstrator' interacting with the environment, in this case, a scavenger consuming a resource (Danchin et al., 2004). Other examples of inadvertently produced social information in a feeding context come from foraging finches and fishes. Within flocks of foraging spice finches (*Lonchura punctulate*), greater rates of movement of the head as the birds stooped to pick up seeds from the ground were associated with a greater likelihood of other birds joining the feeding individuals (Coolen et al., 2001). Foraging ninespine sticklebacks (*Pungitius pungitius*) became more active in the presence of food and performed more 'feeding strikes', bursts of acceleration as they lunged at food to capture it. Other sticklebacks were more strongly attracted to more active fish and to groups that were performing more feeding strikes (Webster et al., 2019). In both cases, the feeding birds and fish inadvertently produced social cues as they fed, as a by-product of postures and movements involved in food capture, and other foragers were able to use these socially transmitted cues to locate food patches. We suggest that the detached food particles produced by feeding hermit crabs are also an inadvertently produced social cue, a byproduct of feeding behaviour that others can use to locate resources.

As scavengers break apart carcasses they likely produce a variety of cues to others. Odour and chemical cues are one source of information, and depending upon the size of the carcass and the strength of local wind or water currents these cues may be dispersed over long distances (Kamio & Derby, 2017). Scavenger action on carcasses may also produce visual cues. Though the integuments of intact animals may be drab or cryptically coloured, to provide camouflage, the exposed tissues or internal organs of scavenged carcasses may be more conspicuous, often being pale in colour, and may be detected by other scavengers passing by. In addition, those scavengers already present may produce acoustic cues as they feed or contest the resource (Auster et al., 2020; Laidre, 2013), while aggregations of animals around resources, although not found to be a strong attractant in the present study, can also attract others in other species (e.g. Riddell & Webster, 2017; Webster & Laland, 2013).

Being joined by others might be costly to the first scavengers to locate and begin to feed on a carcass. Further arrivals at the resource inevitably lead to competition, including scramble competition, where more individuals mean that the resource is depleted sooner, contest competition, where scavengers actively compete to monopolise the whole carcass or pieces of it and kleptoparasitism, where they attempt to steal pieces from each other (Ward & Webster, 2016). There may be a finder's benefit, in which the first to arrive enjoy a period of relatively uninterrupted feeding before competitors join them (Ranta et al., 1996). On the other hand, if the carcass requires some processing before it can be exploited, for example, a thick hide that needs to be opened, then it might be beneficial to arrive later, allowing others to pay the energetic and time costs of making the edible parts available (Broom & Ruxton, 2003). The costs and benefits of scavenging on a given resource are likely to be affected by the size of the carcass, the net energy gains associated with processing it before feeding on it, the changing intensity of competition, opportunities to kleptoparasitise others and the expected likelihood of detecting further carcasses in the future.

In summary, in this study, we have shown that hermit crabs are attracted to cues from mollusc carcasses that are being fed upon by other hermit crabs. They were not strongly attracted to intact mussels or aggregations of conspecifics alone. We suggest that the action of feeding hermit crabs upon a carcass, breaking them up and releasing chemical cues and tissue particles, inadvertently provides social cues that other hermit crabs can use to recruit to the carcass. Hermit crabs are a useful model system for further work exploring the economics of scavenging behaviour, being readily amenable to study in the laboratory and field, for example by manipulating resource size, competitor density and frequency and predictability of carcass provision and relating these to joining decisions and time spent at the carcass. Our study only focussed on the behaviour of the hermit crabs themselves. Predation of scavengers by predators has been documented at carcasses however (Auster et al., 2020) and exploitation of material detached by primary scavengers, by smaller or specialised secondary scavengers is also reported (Davenport et al., 2016). The hermit crab-scavenger system has potential as a useful system for exploring the community ecology of carcass scavenging.

AUTHOR CONTRIBUTIONS

Annie Rowe: Conceptualization; investigation; writing – review and editing. **Arantzazu Pagonabarraga Altisen:** Conceptualization; investigation; writing – review and editing. **Adèle Dubosque:** Conceptualization; investigation; writing – review and editing; formal analysis. **Anna Hills:** Conceptualization; validation; writing – review and editing. **Akanksha Shah:** Investigation; writing – original draft. **Anna Vegh:** Investigation; writing – review and editing. **A. Li Veiros:** Investigation; supervision; writing – original draft. **Mike M. Webster:** Conceptualization; investigation; funding acquisition; writing – original draft; writing – review and editing; formal analysis; project administration; data curation; supervision; resources; methodology; validation; visualization.

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CONFLICT OF INTEREST STATEMENT

The authors have no relevant financial or non-financial interests to disclose.

DATA AVAILABILITY STATEMENT

The datasets generated during the current study will be made available in the FigShare repository after the paper has been accepted.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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