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Ecology and Evolution of Social Information Use

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Ecology and Evolution of Social Information Use

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in

Ecology, Evolution, Environment, and Society

by Clare Doherty

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Abstract

Sociality is a strategy many animals employ to cope with their environments, enabling them to survive and reproduce more successfully than would otherwise be possible. When navigating their environments and making decisions, social individuals often use information provided by conspecifics (in the form of social cues and signals), thereby increasing the scope and reliability of the information they can gather. However, social information use may be influenced by many factors, including key differences in context across the physical and social environment. My thesis asks and answers a series of questions regarding the trade-offs in social information use across different contexts, with particular focus on signals (chapters 1 and 2) and movement (chapters 3 and 4). Using experimental manipulations of the highly social terrestrial hermit crab (*Coenobita compressus*) and the less social marine hermit crab (*Pagurus bernhardus*) I explored social information use across four key areas of behaviour critical to the success of most social organisms: (1) communication, (2) signal evolution, (3) movement, and (4) information transmission. For (1) communication, I tested the production of and response to threat displays across species, examining the evolutionary loss of these displays in species from dramatically different physical and social environments. For (2) signal evolution, I tested the correlation between red colouration and resource holding potential (RHP) across body parts with different signalling potential, based on whether they are exposed or covered by surrounding shell architecture. For (3) movement, I tested whether individuals were biased in their movement by their social group, and whether the level of movement bias changed in different contexts, with individuals having their own private source of protection—a shell—that supersedes the group. Finally, for (4) information transmission, I tested the capacity for information gathering via antennal contact, experimentally seeding social information in the wild to examine whether social information is beneficial to receive and costly to bear. Ultimately, by synthesizing social information use across these four important contexts, I have addressed key questions about how and why social context modifies behaviour, and the ways in which a highly valuable and limiting resource—architecturally remodelled shells—shape social behaviours.

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Introduction

Sociality is one method animals use to make the most of their environments, and access to social information is arguably one of the key benefits of sociality (Sumpter, 2010; Ward and Webster, 2016). Social individuals often use information provided by conspecifics—in the form of social cues and signals—when navigating their environments and making decisions. The use of social information can, theoretically, greatly increase the span and reliability of information that an individual can gather, well beyond what an individual can achieve alone. However, many factors may affect whether individuals use social information, including features of both the physical and social environment. While there has been much research on social information use (Ward and Webster, 2016), the majority of findings are still based on experiments in the lab or on observational studies in the wild. Each of these approaches offers insight, but they are limited. I have built on this work by undertaking novel experimental manipulations in wild populations, altering aspects of both the physical and social environment to test impacts on social information use and decisions. My studies span four key areas of behaviour, critical to the success of most social organisms: (1) communication, (2) signal evolution, (3) movement, and (4) information transmission.

To conduct these experiments, I used the highly social terrestrial hermit crab (*Coenobita compressus*) and the less social marine hermit crab (*Pagurus bernhardus*). Hermit crabs are a powerful system for addressing questions about sociality as they have a rich repertoire of behaviours that have that been studied for over half a century (Hazlett and Bossert, 1965), they span environments from sea to land, and they have a well-established molecular phylogeny (Bracken-Grissom et al., 2013). The highly social terrestrial hermit crabs also form fission-fusion groups (Couzin and Laidre, 2009), with a tension between behaving competitively (Laidre, 2010a) and cooperatively (Laidre, 2021a). Furthermore, hermit crabs are highly experimentally manipulatable, including in the wild, which allows us to ask questions that are often more challenging with organisms that do not lend themselves to experiments. Highly social terrestrial hermit crabs (*C. compressus*), in particular, due to their extreme dependence on socially-derived, architecturally remodelled shells, offer a powerful system for understanding the adaptive functions of architecture and its ecological and evolutionary impacts on sociality (Laidre, 2018), including social information use.

One important aspect of sociality, with clear fitness consequences, is effective communication. Communication is key to most successful interactions between organisms (Searcy and Nowicki, 2005; Laidre, 2010b; Bradbury and Vehrencamp, 2011; Laidre and Johnstone, 2013), including during contests, mate finding, and territory defence (Bradbury and Vehrencamp, 2011; Rubenstein, 2022). If the evolution of communication is shaped by different social pressures, then the same signal in different social environments will have a different meaning or efficacy. In **Chapter 1** of my thesis, ‘Evolutionary loss of threat display in more social species’ I addressed the question: Have production and response to threat displays been completely lost in more social species of hermit crabs? And why, given the benefits of such communication, would this ever happen? First, we synthesised literature and observations on the presence versus absence of threat display across hermit crab species, mapping this information onto a phylogenetic tree. We found that all ‘less social’ species, regardless of whether they are marine or terrestrial, produce threat displays, whereas ‘more social’ terrestrial species, which are highly derived, do not. This suggests that threat display is likely the ancestral state and that there has been an evolutionary loss in those that do not produce it. We then observed natural interactions in the wild within a less social species (*Pagurus bernhardus*), and within a more social species (*Coenobita compressus*) and found a stark contrast. Less social species, despite a lower rate of social encounter, had a higher rate of display per encounter (24%) whereas, the more social species' rate of display per encounter was negligible (<1%), effectively indicating a loss in production. To then test whether receivers in the wild retained any responsiveness to threat displays, we used postured models to experimentally reanimate threat display in the more social species. Receivers did not differentiate between models in threat and non-threat postures, regardless of whether the models were stationary or dynamically moving, and notably were always quick to contact models. Our results suggest that there has been a complete collapse of communication involving threat display in more social species, for which we implicate the social environment. In more social species, an extreme dependence on conspecific-derived shells likely drove a 'desperado effect', which led to the loss of threat displays, as they were no longer effective at deterring others from pursuing these valuable resources.

Despite instances of evolutionary loss, signals are still vital to successful communication between conspecifics (Searcy and Nowicki, 2005), particularly signals of resource holding potential (Pryke and Andersson, 2003), as these can often be used for assessment (Green and Patek, 2018), both by competitors and potential mates. Where on the body such signals are presented may greatly impact their effectiveness, a fact that may be of particular importance for species that inhabit architectural structures (e.g., burrows, nests, shells; Laidre, 2021b) and therefore only have certain areas of their body that are visible. In **Chapter 2** of my thesis, 'Doors to the homes', I addressed the following questions: Is red colouration an intraspecific signal of resource holding potential? And are exposed areas of the body, relative to their surrounding architecture, likely to function as signalling platforms (via colouration)? We systematically quantified red coloration in social hermit crabs (*Coenobita compressus*), which inhabit architecturally remodelled shells. We contrasted red colouration within individuals between an area of the body that is always covered by their shell (the carapace) and an area of the body that is always exposed (the claw, which is positioned at the shell entrance and acts as a door). We hypothesised that red colouration of claws may be a signal of RHP. Consistent with this RHP signalling hypothesis, we found that exposed claws showed significantly greater red colouration than unexposed carapaces within the same individuals' bodies. Furthermore, body size and red colouration were positively correlated, specifically in males. These results were unlikely to be explained by competing hypotheses (e.g., interspecific signalling, camouflage, or UV protection). Red claw coloration may therefore function as an intraspecific signal, and we outline future experiments that can examine recipient responses and further test this hypothesis. Ultimately, for many taxa, exposed body surfaces, relative to surrounding architecture, offer rich potential as signalling platforms for colouration, and merit further investigation, especially in other architecture-dwelling species.

Cues and signals from conspecifics can improve an individual's probability of successfully finding and exploiting essential resources such as food and shelter (Pitcher et al., 1982), a ubiquitous challenge for all animals. Social foraging theory (Giraldeau and

Caraco, 2000) has shown that individuals in groups can gather more information about the environment than when foraging alone. On top of this, selfish herding (Hamilton, 1971), wherein an animal tries to reduce its own predation risk by putting a conspecific between itself and a predator, has been proposed as the origin of social grouping in the animal kingdom. Being in a group can effectively reduce predation costs by diluting the chance of any individual being predated (Williams, 1966; Hamilton, 1971), and by increasing vigilance (Lima, 1995; Roberts, 1996). Therefore, the most fundamental measurements of social influence on individuals are attraction to others and movement in relation to others (Couzin et al., 2002). Collective movement may emerge if coordinating one's movement with others produces a greater benefit to oneself than can be achieved alone. In **Chapter 3** of my thesis, 'Individual versus collective movement during travel', I addressed the questions: Are individuals biased in their movement by the collective? Using large architectural arrays of shells, we experimentally simulated the movement of collectives of social hermit crabs (*Coenobita compressus*) in the wild, and then measured the direction travelled by live individuals to test for a social bias in movement. We systematically varied the simulated collective's travel direction as well as the context (i.e., danger level). Although there was considerable engagement with the collective, individuals' directions were not significantly biased by the collective. Individuals consistently expressed substantial variability, regardless of stimulus direction or context. We did, however, find a potential impact of traffic, as individuals typically achieved shorter displacements in the presence of the collective compared with the control stimulus. The lack of a directional bias in individuals in response to the collective suggests a high level of independence, with each crab, in effect, being a 'rugged individualist'. This autonomy of movement is likely due to the considerable personal protection offered by the portable shell individuals inhabit. Importantly, manoeuvring whole collectives in the wild and measuring individual responses is a novel technique and provides a powerful means of answering further questions at the intersection of individual and collective movement.

Even in systems where individual autonomy of movement supersedes collective movement, the adaptive advantages of attending to social information (Danchin et al., 2004) could be vast. Conspecifics can provide social information about the presence or absence of features such as predators or food resources. Such information about food is particularly useful where resources are patchily distributed (Torney et al., 2009) and unpredictable over space and time. Social information may therefore serve as a heuristic to help navigate one's environment. Of course, different types of information are likely to evoke different behavioural responses. While social information use may benefit receivers, costs associated with bearing social information are less often considered. Many passive cues, such as chemically-based social information borne on the breath or body (Galef and Stein, 1985; Galef, 1993) must be obtained via close-range encounters with non-kin, which inherently comes with increased risk. In **Chapter 4** of my thesis, 'Experimentally-seeded social information in the wild' I addressed the questions: Does social information benefit receivers? And is social information costly to bear? We experimentally seeded three types of chemicals onto conspecifics in the wild: (1) a chemical indicative of the presence of a positive feature (a food source), (2) a chemical indicative of a neutral feature (water), and (3) a chemical indicative of the presence of an ambivalent feature (a predator, which is simultaneously a danger and an opportunity, since if the predator kills a fellow conspecific, then its left behind shell can be moved into). The 'benefits to receivers' hypothesis predicts that receivers will use social information to orient towards valuable resources; and the 'costs to bearers' hypothesis predicts that bearers of social information will experience direct or indirect costs due to interaction with receivers. Our results support both hypotheses. Naïve individuals followed focal individuals bearing social information about a food resource more often than other types of social information. Furthermore, bearers of social information about a food resource incurred direct costs (i.e., were flipped more) and indirect costs, (i.e., achieved shorter displacements) than bearers of other types of social information. We conclude that experimentally-seeded social information in the wild conferred both benefits to receivers and costs to bearers. The direct and indirect costs of bearing social information, revealed here, highlight the importance of considering costs to bearers more generally in studies of social information use.

My thesis thus synthesizes multiple elements of social behaviour across a series of important contexts. I have answered key questions about when and why animals use social information, based on the underlying costs and benefits of social life. I have also revealed how and why an animal's architecture—in the form of a shell—impacts many elements of its social life. My thesis highlights that the extreme value of a limited, conspecific-derived architectural resource can impose an obligate sociality among non-kin, impacting which forms of communication and signalling are viable. I found that living within the confines of an architecturally remodelled structure has favoured the loss of threat displays, and also appears to have favoured the use of exposed body areas as platforms for colour signals, relative to the underlying architecture. In addition, carrying one’s own personal architecture and armour can alleviate some pressures from the surrounding physical and social environment, effectively granting individuals freedom of movement. Finally, I have shown that social information use entails both benefits to receivers and costs to bearers. In summary, social life and animal architecture are deeply intertwined ecologically and evolutionary, with experimental manipulations in the wild revealing the resulting impacts on social information use.

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CHAPTER 1

Evolutionary loss of threat display in more social species: phylogenetic comparisons, natural interactions in the wild, and experiments with models

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Abstract

Fitness can be increased dramatically by communication. So why, given the benefits of communication, would displays ever be completely lost evolutionarily? Threat displays, in particular, are relatively cheap to produce and are precursors of attack, so should be especially hard for both senders and receivers to lose completely. Here we explore an evolutionary transition in sociality, testing whether complete evolutionary loss of threat display has occurred in 'more social' hermit crab species, which interact more frequently with conspecifics. First, we synthesised literature and observations on the presence versus absence of threat display across hermit crab species, mapping this information onto a phylogenetic tree. We found that all 'less social' species—marine and terrestrial—produce threat displays, consistent with threat display being the ancestral state. But 'more social' terrestrial species, which are highly derived, do not produce a threat display, suggesting an evolutionary loss. Next, we contrasted natural interactions in the wild within a less social species (*Pagurus bernhardus*) versus within a more social species (*Coenobita compressus*), finding that the less social species, despite a lower rate of social encounter, had a higher rate of display per encounter (24%). In contrast, the more social species' rate of display per encounter was negligible (<1%), effectively indicating a loss in production. Finally, we experimentally reanimated threat display in the more social species, using postured models to test whether receivers retained any responsiveness to threat display. Starkly, receivers were not deterred by threat display, showing equal responsiveness across both threat and non-threat models, regardless of whether the models were stationary or dynamically moving. Our results thus reveal a case of complete collapse of communication involving threat display, implicating the social environment in this loss. In more social species, an extreme dependence on conspecific-derived shells likely drove a "desperado effect", with threat displays being lost because they could not stop others from pursuing these valuable resources.

Keywords: communication; desperado effect; displays; evolutionary loss; shells; signals; sociality; threats

“The most dangerous creation of any society is the man who has nothing to lose.”

—James Baldwin

Introduction

Communication evolved to increase fitness (Bradbury and Vehrencamp 2011). Across a variety of contexts, signallers produce acts or structures, which convey information, and this information is then responded to by receivers, with these responses ultimately impacting both parties’ fitness (Laidre and Johnstone 2013). As a consequence of communication, mutual benefits can be gained by signallers and receivers. For example, in the context of mating displays between males and females, displays can enable signallers to attract mates (e.g., Murai and Backwell 2006) and receivers to differentiate high vs. low quality mates (e.g., Holzer et al. 2003). Likewise, in the context of threat displays between rivals, displays can enable signallers and receivers to assess one another, driving off opponents (Maynard Smith and Harper 2003) and avoiding escalated conflicts (Searcy and Nowicki 2005). Given the benefits communication offers, why would displays ever be lost evolutionarily?

Theoretically, the starting point for evolutionary loss of a display can be from either the signalling party (i.e., a loss of the production component) or from the recipient party (i.e. a loss of the response component). In both cases, the loss is based on one party (signaller or recipient) no longer benefiting from the communicative arrangement (Searcy and Nowicki 2005). In one scenario for display loss, it is the production component that is lost initially due to the display becoming too costly to produce. This could either be costly physiologically (e.g., based on changes in the environmental matrix, such as if signalling in air versus water involves an increased physiological cost), or costly due to the types of responses it elicits (e.g., from conspecifics or from heterospecific eavesdroppers; Gray et al. 2014). In an alternative scenario, it is the response component that is lost initially, due to the display being replaced by another source of information, the display becoming unreliable, or the display remaining reliable but ceasing to convey information that is useful to the receiver (Andersson 1980). All these alternatives ultimately favour receivers that cease responding to the display. Regardless of which component (production or response) is lost first, the loss of one may lead secondarily to the loss of the other. Ultimately, a complete evolutionary loss of a display entails not only the display ceasing to be produced, but also receivers ceasing to respond to the display were it ever produced again.

Empirical examples of the complete evolutionary loss of displays are well established in mating and sexual selection contexts. In such contexts, displays are frequently costly (which can cause signallers to cease producing them; e.g., Zuk et al. 2006) and receiver responses are often based on arbitrary preferences (which are evolutionarily fickle and thus subject to change; Ryan 2004; Pilakouta and Alonzo 2013). In contrast to such sexual selection contexts, few empirical cases exist of the complete evolutionary loss of threat display (Maynard Smith and Harper 2003; Bradbury and Vehrencamp 2011). Threat displays are ritualised visual displays that can convey information to conspecific opponents about potential aggression or fighting ability (Számadó 2003, 2008). Theoretically, the rarity of threat display loss makes sense, given that threat displays should be among the hardest of displays to lose, both on the production and response sides (Andersson 1980). Indeed, most threat displays involve minor postural alterations (Számadó 2003, 2008), which would be unlikely to ever become prohibitively costly for signallers to physically produce (Laidre 2005). Also, unlike conciliatory displays (Laidre and Yorzinski 2005), which occur in non-aggressive contexts, threat displays occur in aggressive contexts and often represent incipient fighting movements, which predict attack (Laidre 2009) and hence should never completely cease to be responded to.

Hermit crabs (Crustacea, Decapoda, Anomura) have been a model system for the study of threat display for over half a century (e.g., Hazlett and Bossert 1965; Hazlett 1966a, b, 1968; 1981; Elwood et al. 2006; Laidre 2007; Arnott and Elwood 2007; Laidre and Elwood 2008; Laidre 2009; Arnott and Elwood 2010), with these displays being found broadly in many hermit crabs, especially marine species. Indeed, ritualised visual threat displays involving the claw are ubiquitous across marine crustaceans broadly (Hazlett 1972), often being used in contests (Számadó 2003, 2008; Briffa 2013; Hardy and Briffa 2013). Yet despite detailed studies of the behaviour of terrestrial hermit crabs, such threat displays have rarely been mentioned within species of terrestrial hermit crab (Burggren and McMahon 1988; Greenaway 2003). While the difference in physical environment—sea versus land—could seemingly account for a partial loss of threat displays in terrestrial hermit crabs (e.g., signallers stop displaying because displays are too costly to perform on land), performance costs can in some cases actually be lower on land, which is a key explanation for greater evolutionary innovation on land versus in the sea (Vermeij 2017). A more fundamental basis, therefore, for testing for a potential loss of threat displays in terrestrial hermit crab species may relate to their change in sociality, which is linked to the differential resource value of conspecific-derived shells.

Unlike all other species of hermit crab, only terrestrial hermit crab species in the genus *Coenobita* use architecturally remodelled shells (Vermeij 1993), which has made them highly socially dependent on conspecifics (Laidre 2012a) and ultimately ‘more social’ (Laidre 2014; Bates and Laidre 2018; reviewed in Laidre 2018a, b). Within the clade of hermit crabs, these ‘more social’ terrestrial hermit crab species are highly derived evolutionarily (Bracken-Grissom et al. 2013). Their greater sociality, in comparison to their marine ancestors, is ultimately due to an extreme dependence on conspecifics for architecturally remodelled shells, without which individuals cannot survive (Laidre 2012a). Empty architecturally remodelled shells are virtually non-existent (Laidre 2010). These architecturally remodelled shells are thus highly valuable resources for terrestrial hermit crabs, indeed differentially valuable relative to the unremodelled shells used by marine hermit crabs (Laidre 2019a). Furthermore, architecturally remodelled shells are reused by terrestrial hermit crabs across generations (Laidre 2019b), and these valuable resources can only be acquired after a conspecific is forcibly evicted or dies (Valdes and Laidre 2019). For terrestrial hermit crabs, therefore, individuals must specifically interact socially with conspecifics if they are to capitalise on opportunities for remodelled shells (Laidre 2018b). In contrast, while marine hermit crabs do engage in fights with conspecifics for unremodelled shells (Briffa et al., 1998; Elwood & Briffa, 2001; Briffa & Elwood, 2004; Briffa, 2006; Briffa & Williams, 2006; Arnott & Elwood, 2007; Briffa & Dallaway, 2007; Briffa & Fortescue, 2017), marine hermit crabs can acquire unremodelled shells in the wild directly from predated snails (McLean, 1974; Rittschof, 1980; Wilber & Herrnkind, 1984; McGuire & Williams, 2010; Laidre, 2011;

Laidre & Trinh, 2014; Valdes & Laidre, 2018), which substantially reduces marine hermit crabs' need to interact with conspecifics (Valdes & Laidre, 2019).

Given the more stringent social conditions experienced by terrestrial hermit crabs, it is possible that threat displays in terrestrial hermit crabs may have become irrelevant, both for signallers and receivers: receivers who were to heed these displays, by fleeing from signallers, would never acquire a remodelled shell or rise in the 'housing market' (Laidre and Vermeij 2012), thus being far less likely to survive and reproduce (Laidre 2012a). Indeed, given the extremely high resource value of remodelled shells, a "desperado effect" (Grafen 1987; Elias et al. 2010) may have favoured receivers that neglected threat displays and pursued remodelled shells at all costs, immediately escalating any conflicts. Consequently, signallers who continued using these displays would have found them ineffective at keeping conspecifics away, potentially abandoning these displays altogether. We therefore hypothesized that the transition from the 'less social' marine hermit crabs to the 'more social' terrestrial hermit crabs may have led to a complete evolutionary loss of threat display. Yet if such a loss has occurred, would this loss be attributable to the social environment (terrestrial hermit crabs having transitioned from less to more social) or to the physical environment (terrestrial hermit crabs having transitioned from sea to land)?

Critically, while all terrestrial hermit crab species live on land, not all are more social. Within the family Coenobitidae (to which all species of terrestrial hermit crab belong), there exists one species, the coconut crab (*Birgus latro*), which remains less social (Helfman, 1977; Laidre, 2018c). This species likewise made the evolutionary transition from living in the sea to living on land, and furthermore this species is evolutionarily ancestral to all other terrestrial hermit crab species (Bracken-Grissom et al., 2013). Yet unlike the more social terrestrial hermit crab species within the genus *Coenobita* (all of which use remodelled shells), *Birgus latro* does not use shells at all during its adult life (Laidre, 2018c). Indeed, other than a brief mating season, *Birgus latro* has no need whatsoever to interact with conspecifics, with individuals living alone in deep underground burrows and generally avoiding conspecifics aboveground (Helfman, 1977; Laidre, 2018a), emerging from their burrows only to forage (Kessler, 2005; Krieger et al., 2016; Laidre, 2017). *Birgus latro* can thus help test what ultimate factors might have led to the hypothesized evolutionary loss of threat display in terrestrial hermit crabs. If evolutionary loss of threat display occurred merely due to the transition in physical environment (from sea to land), then *Birgus latro* should no longer display, because it too lives on land. But alternatively, if evolutionary loss of threat display occurred due to the transition in social environment (from less social to more social), then *Birgus latro* should still display, because it is not more social.

Here we test whether a transition in sociality has resulted in the evolutionary loss of threat display, including both a loss in the production of displays and in the responsiveness to displays. First, to test the hypothesized evolutionary loss of threat display, we synthesised literature and observations on the presence versus absence of threat display in less social and more social species, mapping this information onto a phylogenetic tree. If the transition in sociality (not the transition in physical environments from sea to land) was ultimately responsible for a production loss, then we predicted the following: (i) threat displays would represent an ancestral state in the phylogeny, with all less social species (marine and terrestrial) performing threat displays; and (ii) only the highly derived and more social terrestrial hermit crab species, which use architecturally remodelled shells, would not perform threat displays.

Next, we contrasted natural interactions in the wild within a less social species versus within a more social species. If evolutionary loss has occurred, then we predicted the following: (iii) the more social species would not perform threat displays despite having more frequent social encounters and despite still being physically capable of performing display-like motions on land in its natural environment. Finally, following our phylogenetic comparisons and natural observations, we then experimentally 'reanimated' threat display in the more social species, using postured models to assess whether live receivers retained any responsiveness to threat display. Continued responsiveness, even after production loss, to 'ghosts of communication past' has been found in some species (e.g., sceloporus lizards: Quinn & Hews, 2000; Wiens, 2000). Yet if receivers have instead entirely lost their responsiveness to threat display, then we predicted that (iv) receivers would not differentiate between displaying versus non-displaying models. Furthermore, if this loss in responsiveness was specifically due to a 'desperado effect', reflected in the extreme need within the more social species for individuals to acquire conspecific-derived shells to reproduce, then we predicted that (v) small individuals would be the most likely to approach models, regardless of the model's size. This is because small individuals cannot reach the size threshold necessary to reproduce without first acquiring a bigger remodelled shell (Laidre, 2018a), which makes their need for these resources the greatest.

Together our phylogenetic comparisons, observations, and experiments offer insight into how and why evolutionary loss of threat display occurred in more social species within the hermit crab lineage.

Methods

Evolutionary comparison of species across phylogeny

Among hermit crabs (Crustacea, Decapoda, Anomura), threat displays occur when the chelipeds are thrust outward in a visual display specifically directed toward a facing recipient (shown in Figure 2 of Laidre, 2009). We compiled all available knowledge — including published literature dating back to the 1960s, personal observations of species we ourselves observed for at least several months, and personal communications from other long-term researchers (Table A1 in the Appendix) — to determine whether threat displays were present versus absent in different species of hermit crab. We then mapped this information onto a phylogenetic tree (Figure 1), which derived from Laidre (2019a) and was based on molecular data from Bracken-Grissom et al. (2013). Using the phylogeny, we examined the pattern of present-day species that do versus do not display. We used the most conservative evolutionary assumption (Harvey & Pagel, 1991), about the fewest possible transition states in threat display, to determine whether it was likely that threat display was lost evolutionarily in only particular species.

Our comparisons across the phylogenetic clade of hermit crabs spanned 3 families (Coenobitidae, Diogenidae, and Paguridae), 9 genera, and a total of 11 species. In particular, only three of the more social terrestrial hermit crab species (*Coenobita compressus*, *Coenobita perlatus*, and *Coenobita clypeatus*) have been positioned on the established molecular phylogeny, where they cluster closely together and are known to be highly derived (Bracken-Grissom et al., 2013; Laidre, 2019a). We focused on comparing these three species to their closest phylogenetic relatives, including (i) the less social marine hermit crab species, which branched off ancestrally and which all use unremodelled shells (N = 7 species in total: *Pagurus bernhardus*, *Paguristes cadenati*, *Isocheles pilosus*, *Clibanarius albidigitus*, *Calcinus obscurus*, *Petrochirus diogenes*, and *Dardanus insignis*); and (ii) the only other terrestrial hermit crab species that has been positioned on the molecular phylogeny (the coconut crab, *Birgus latro*), which is ancestral to all other terrestrial hermit crab species (Bracken-Grissom et al., 2013) and is not more social.

Two focal species in the wild: study sites

In addition to our broader phylogenetic comparisons (detailed above), we also collected quantitative data from the wild that specifically contrasted two focal species from the phylogeny, one of which was a less social marine hermit crab (*Pagurus bernhardus*) and the other of which was a more social terrestrial hermit crab (*Coenobita compressus*). Both these species were studied in their natural habitats in the wild at locations where they occur in abundance. *P. bernhardus* was studied during January 2018 in tide pools along the rocky coastal beach of Ballywalter, Co. Down, N. Ireland (54°33′33.1″ N, 5°28′35.8″ W). *C. compressus* was studied during January to March 2018 at the beach-forest interface of Osa Peninsula, Costa Rica (8°23′40″ N, 83°20′10″ W). For each species, observations were undertaken by the same individual (CD) during daylight and at low tide.

Natural interactions in the wild: a less social vs. a more social species

For each species, we calculated the density of individuals, their rate of encounter, and their rate of threat display per encounter. Critically, the rate of encounter directly reflects each species' relative level of sociality, based on the degree to which individuals actively initiate interactions with conspecifics. Density, in contrast, partly reflects spatial constraints, with stronger spatial constraints in the less social marine species (which is constrained to living within rocky tide pools at low tide) and with weak to non-existent spatial constraints in the more social terrestrial species (which occupies open sandy beaches without barriers). To quantify density, a rectangular quadrat (20 × 23 cm) was randomly tossed within the natural habitat of each species and then the number of individuals within the quadrat was counted (N = 37 quadrat samples for both species). Quadrat sampling was undertaken at the same time and place as observation of natural behaviour, but was conducted outside of actual observation to avoid disrupting the crabs' behaviour. Prior to the start of observations, any major obstructions (e.g., seaweed or debris floating on top of tide pools) was removed, so that individuals could be readily observed. We then waited several minutes before proceeding with observations, using binoculars to carry out observations from several meters away.

To quantify natural display behaviour, we employed focal animal sampling. For each focal sample a single, randomly selected individual was monitored continuously for a set length of time. Focal samples for *P. bernhardus*, which is restricted to tide pools, lasted for 10-min intervals. Focal samples for *C. compressus*, which can move vast distances over land without spatial constraints (Laidre, 2013a), lasted for only 5-min intervals (since following *C. compressus* individuals beyond this length of time would have required the observer to physically move, thus disturbing the focal crab's behaviour). To control for the difference in focal time lengths between species, we quantified rates, specifically rates of encounter and rates of display per encounter. During focal animal sampling, an encounter was defined as occurring whenever a focal crab or a conspecific actively approached within one shell length from an original distance of at least three shell lengths apart. For each encounter, both interacting crabs' behaviours were recorded based on an established ethogram that was made from years of prior observation (Table A2 in the Appendix), and which included whether or not either crab performed a threat display (see above). During focal sampling, if a threat display was performed, then any behaviours that followed were also recorded up until the two crabs separated by three or more shell lengths. For each species, N = 61 different, randomly chosen individuals were focal sampled.

Reanimated displays in the more social species: model design

The less social species (*P. bernhardus*) is known to respond robustly and differentially to models of dead conspecifics postured in threat displays versus not (Hazlett, 1968; Laidre, 2007; Laidre & Elwood, 2008; Laidre, 2009). To test whether such responsiveness to threat displays has been lost in the more social species, we prepared the same types of models using dead *C. compressus* specimens, which had been preserved by freezing soon after natural death. Specimens were used only if they were fully intact, still possessing all limbs and with no damage to the rest of the body. Each specimen's sex was recorded and its claw length and shield length were measured using electronic callipers to the nearest 0.01 mm (see Laidre, 2019a); then each specimen was size-matched to an empty, architecturally remodelled *Nerita scabricosta* shell based on shell diameter (Laidre, 2012b; see Table A3 in the Appendix for specimen and shell measurements). Size matching was determined by the crab's body fitting fully inside the shell, such that the claws could be in their natural position (flush with the aperture) when fully withdrawn.

To assess whether live crabs would differentiate between threat displays versus not, the models were secured in three different poses using Loctite® control gel glue: (A) withdrawn, (B) neutral and (C) threat (Figure 2). Poses were randomly allocated across specimens. For the withdrawn pose, each specimen was fully retracted into its shell, with the larger left chelae filling and sitting flush with the aperture (Figure 2A). For the neutral pose, each specimen's abdomen was inside the shell, the top of the aperture came midway up the shield, and the chelae and walking legs were out of the shell but carried ventrally, contacting the ground and with the chela closed (Figure 2B). For the threat pose, each specimen's abdomen was likewise inside the shell, the top of the aperture came midway up the shield, and the legs were out and touching the ground, but for this pose both chelae were raised, as high as physically possible, facing forward and opened (Figure 2C), thereby matching the form of the threat display posture that is highly conserved across other species. A total of N = 30 models were made (N = 10 for each of the three pose types). Within each pose type, we had a full range of sizes, spanning 20 mm to 38 mm in shell diameter, with equal size distributions across poses (Table A3 in the Appendix).

Reanimated displays in the more social species: model presentations

Stationary models

To test live crabs' reactions to models in the more social species, one randomly selected model was placed on the beach in the centre of a 30 × 30 cm quadrat, outlined in the sand with dowel imprints. To control for model direction, the orientation of the model within the quadrat (N, S, E or W) was randomised. A video camera mounted on a tripod above the quadrat was used to record each experiment. The tripod was placed on the forest side of the quadrat, with the camera directly overhead of the model, capturing the entire quadrat from above within its frame.

To quantify responsiveness, we measured the latency between the time the first crab made contact with the model and the time this same crab had originally entered the experimental quadrat (only the times of the crab that first made contact with the model were considered). Once contact was made, the interaction was recorded until one of the following occurred: (a) the crab left the quadrat, (b) the crab interacted with the model for 5 min alone (or with just one additional crab being present), or (c) a third crab entered the quadrat. These parameters ensured that the original crab was not lost track of, within a crowd of three or more crabs, by the end of the interaction. At the conclusion of the experiment, we measured the original crab's shell diameter to compare the shell size of crabs that first contacted models from each different pose.

To quantify the extent to which different model poses collectively attracted or repulsed live crabs, a separate set of experiments was conducted in which each model was again placed individually in the centre of the quadrat, but was then left unmonitored for 5 min. After 5 min the total number of crabs that had accumulated within the quadrat was counted to test whether there was any difference between model poses.

Dynamic models

Live individuals performing threat displays typically move, rarely being completely stationary, and furthermore specifically direct their displays at the recipient. Hence, models used in interactive experiments should ideally be tested not just when stationary but also when dynamically moving (see Laidre & Vehrencamp, 2008). We therefore also conducted another set of experiments with the more social species, in which the very same models (both those in a neutral and in a threat pose) were dynamically moved. If movement is integral to a posture being perceived as a threat display, then live crabs should differentiate between dynamically-moving models in a threat pose versus dynamically-moving models in a neutral pose.

To create dynamic movement, we mounted models onto a 10 cm wooden dowel using small magnets (5 mm diameter × 3 mm height). One magnet was glued to the top of the dowel and the other magnet was glued onto the underside of the model's shell with Loctite® control gel glue (Figure 2D). The dowel was then inserted into the beach sand into the centre of a 30 × 30 cm quadrat, such that the base of the model's shell touched the ground. The two magnets created a pivot point, which enabled the model to be dynamically moved and turned toward an approaching live crab (see Videos 1 and 2 at 10. 6084/m9.figshare.12871157 for exemplars). To control the model's movement, approximately 1 m of clear fishing line was attached to either side of the model's backmost ambulatory legs (both left and right). The other ends of the fishing line were controlled by the experimenter (CD) who sat motionless 1 m from the quadrat. The quadrat in which the model was set was identical to that of the stationary model experiments (above), except with an interior 15 × 15 cm quadrat that was also marked in the sand (to denote the midway point between the outer quadrat and the location of the model at the centre of the quadrat). When the first crab approached to within 15 cm of the model, the experimenter gently pulled the ends of the fishing line, moving the model so that it oriented directly toward the approaching live crab. A camera mounted on a tripod and placed on the forest side of the quadrat, recorded all interactions involving dynamic models from above. From the videos, we quantified the first crab's latency to contact the model. We defined latency as the time from when this first crab had entered the outer quadrat up until when it first contacted the model. In cases where this first crab did not contact the model within 30 s, then the latency was capped at 30 s (this cap was set since all models in the stationary experiments had been contacted by 30 s).

As a control for the dynamically-moving models, we created an identical setup, but without any attached model. This allowed us to assess any possible effects that the setup itself (magnets, wooden dowel, fishing line, and the experimenter's subtle movement from 1 m away) might have had on live crabs' responses. No difference was observed in any crab's behaviour, approach speed, or direction in response to the aforementioned factors, suggesting that it was exclusively the models and their movement (and not the rest of the apparatus or the experimenter's movement) that influenced live crabs' responses.

Ethical note

No hermit crabs were killed to make the models. Only individuals that had died naturally and had subsequently been preserved were used.

Statistical analyses of observational and experimental data

To test for differences in natural behaviour between the less social species and the more social species, we used t-tests to compare density, encounter rate, and display rate per encounter between the two species. The data for density and for encounter rate were log transformed (to make the data normally distributed) and those two analyses were therefore conducted on the transformed data. All figures in the manuscript graph the original, untransformed data. To test for differences in responses to reanimated models in the more social species, we ran two different ANOVA models. For experiments that only involved stationary models, we ran an ANOVA model that included the following factors: model pose (with three categories: withdrawn, neutral, and threat) and relative size (i.e., model's shell diameter minus live crab's shell diameter), allowing us to test whether these factors predicted either the first individual's latency to contact the model or the total number of individuals that accumulated around the model. For experiments with dynamically-moving models, we ran a separate ANOVA model, which included the following factors: model pose (with two categories: neutral and threat); movement (with two categories: dynamic and stationary); the interaction between model pose and movement; and relative size, allowing us to test whether these factors predicted latency to contact. In addition, we ran an ANOVA model to test whether the size (shell diameter) of live crabs that chose to interact with the models varied across different model poses. This ANOVA model included model pose (with two categories: neutral and threat) and movement (with two categories dynamic and stationary), allowing us to test whether these factors predicted the size (shell diameter) of live crabs. Finally, we also used a Pearson correlation test to test for a correlation between the size (shell diameter) of live crabs and the size (shell diameter) of the models that they made contact with. The Bonferroni method was applied when multiple tests were conducted to control the overall alpha level at 0.05. All analyses were performed in JMP® Pro version 12.1.0.

Results

Evolutionary comparison of species across phylogeny

Comparison of species across the phylogeny (Figure 1; Table A1 in the Appendix) revealed an overall pattern of widespread presence of threat display in the less social species (both marine and terrestrial), suggesting that threat display was the ancestral state in hermit crabs. Furthermore, threat display was found to be absent only in the more social terrestrial hermit crab species (*Coenobita* spp.), suggesting an evolutionary loss of threat display occurred in these highly derived species. Notably, this evolutionary loss of threat display could not be attributed merely to a sea-to-land transition: one species (*Birgus latro*), which likewise transitioned to living on land, but which is not more social, nevertheless still performs threat display. Of the factors we considered, the evolutionary loss of threat display was thus associated exclusively with the transition from less-to-more social species, occurring only within more social terrestrial hermit crab species (*Coenobita compressus*, *Coenobita perlatus*, and *Coenobita clypeatus*).

Natural interactions in the wild: a less social vs. a more social species

Contrasts of the two focal species revealed that the more social species was found at a significantly lower density than the less social species (t-test: $t = 9.49$, $df = 56.87$, $p < 0.0001$; Mean ± SE for density for less social: 4.19 ± 0.50; for more social: 0.41 ± 0.10;

Figure 3A). However, despite its lower density, the more social species showed a significantly higher encounter rate per minute (t-test: $t = 7.91$, $df = 118.52$, $p < 0.0001$; Mean ± SE for encounter rate for less social: 0.28 ± 0.03; for more social: 0.74 ± 0.07; Figure 3B), consistent with its greater level of social interaction. Surprisingly, this higher encounter rate was associated with a substantially lower rate of threat display per encounter (t-test: $t = 5.21$, $df = 60.06$, $p < 0.0001$; Mean ± SE for rate of display per encounter for less social: 0.24 ± 0.05; for more social: 0.00 ± 0.00; Figure 3C). Indeed, the rate of displaying by the more social species was essentially negligible, with just one apparent[1] display ever being performed and by only a single individual in a single interaction. Even when we conservatively included claw strikes (which involve a similar motion, but are not displays, since they involve physically knocking an individual away), the display rate remained significantly lower in the more social compared to the less social species (t-test: $t = 4.47$, $df = 67.60$, $p < 0.0001$).

Notably, despite the negligible rate of displaying by the more social species, individuals of this species nevertheless readily produced display-like motions in their natural environment on land. Indeed, during hundreds of live crabs' interactions with one another and with models, we observed 'piggybacking' (i.e., hopping onto the back of another's shell). This movement inherently requires the piggybacking crab to lift up its claws in a display-like motion (Video 3 at 10.6084/m9.figshare.12871157), but one that differs from displaying in that: (*i*) it is performed completely outside of the recipient's

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[1] We term this an 'apparent' display because the interaction was so brief that we could not determine if the claws were actually raised to a height reflective of a real threat display. We therefore classified it as 'apparent' to be conservative. It was the sole instance we observed of any behaviour that even approximated a display.

field of view (effectively ‘behind its back’) and (*ii*) it is always immediately followed by tactile assessment of the recipient’s shell. Thus, the more social species, despite not displaying, was clearly not physically constrained or incapable of doing so.

Reanimated displays in the more social species: response to models

Individuals of the more social species showed no difference in response toward stationary models from the three different poses (Figure 4): there was no difference across stationary model poses in either the latency individuals took to contact the models (ANOVA: $F_{3,26} = 0.97$, $p = 0.42$; Figure 4A) or in the number of individuals that accumulated around the models (ANOVA: $F_{3,26} = 1.50$, $p = 0.24$; Figure 4B). The absence of any difference in response, especially to models in a threat display, suggests that threat display has lost its meaning in the more social species. When we added movement to the models, individuals took longer to contact (ANOVA: $F_{4,45} = 5.62$, $p = 0.0009$; Figure 5), suggesting they were responding more cautiously. This greater caution in response to moving models applied both to models in neutral pose (Figure 5A) and to models in threat pose (Figure 5B). Critically though, movement (i.e., dynamic vs. stationary) was the sole factor that significantly predicted latency to contact (ANOVA: $F_{1,45} = 21.82$, $p < 0.0001$). No significant interaction existed between movement and pose (ANOVA: $F_{1,45} = 0.38$, $p = 0.54$). Indeed, individuals showed similar responsiveness to dynamic threat versus dynamic neutral models (Figure 5A, 5B).

The size (shell diameter) of live crabs remained relatively constant across both dynamic and stationary model poses (ANOVA: $F_{2,47} = 1.31$, $p = 0.28$; Figure A1 in the Appendix). Interestingly, the individuals that contacted stationary models did so rapidly across all model poses, always contacting in 20 s or less. While there was no correlation between the size of the model and the size of the individual that contacted it ($F_{1,28} = 0.13$, $p = 0.72$; Figure 6A), individuals that made contact were consistently smaller than the models, on average less than half the size of the models (paired t-test spanning all model poses: $t = 16.84$, $df = 29$, $p < 0.0001$; Figure 6B). Individuals of the more social species, particularly small individuals, thus showed a strong motivation to be near bigger conspecifics and their bigger architecturally remodelled shells, regardless of the conspecific model's pose.

Discussion

Few empirical cases are known in which there has been a complete evolutionarily loss in both production of and responsiveness to threat displays (Andersson 1980; Bradbury and Vehrencamp 2011). Theory suggests that responsiveness, in particular, should generally be maintained for threat displays, only ceasing if it becomes costlier on average to respond than to ignore them (Maynard Smith and Harper 2003). In the present study, we found evidence of an evolutionary loss of threat display. In particular, our phylogenetic comparisons suggest that an evolutionary loss of threat display occurred only in the highly derived, more social terrestrial hermit crab species, with this loss specifically associated with the transition from less social to more social hermit crabs. Our finer-grained contrast between two focal species in the wild (one less social and the other more social) likewise supported these phylogenetic comparisons: the more social species, despite having overall higher levels of social interaction, did not perform threat display in these interactions. The loss of threat display among more social species cannot be attributed to the terrestrial environment imposing physical restrictions on displaying: another terrestrial species that is not more social (*Birgus latro*) continues to perform threat displays on land. Moreover, individuals from the more social of our two focal species regularly performed a similar motion on land, just in a non-display context. Indeed, even if there were an increase in the physiological cost of performing threat displays on land (for which there is no evidence: Vermeij 2017), this would at best explain loss in production, not the loss in responsiveness that we found from our reanimated model experiments on the more social species. Furthermore, differences in predation pressures between sea and land cannot explain this loss of threat display: on land, predation pressures are relaxed (Vermeij 1993), and the architecturally remodelled shells used on land are safely outside the bite force of predators (Laidre et al. 2012); so such weak predation pressure should, if anything, have enabled more rather than less time to be devoted to displaying on land. The loss of threat display is thus consistent only with a transition in sociality, in which the more social terrestrial hermit crabs have ceased producing and responding to threat displays due to the necessity of acquiring vital resources from conspecifics, in the form of architecturally remodelled shells.

Ritualised threat displays involving the claws are ubiquitous across most marine crustaceans (Hazlett 1972), suggesting that the presence of threat display was likely the ancestral state not just among hermit crabs, but among crustaceans more generally. Future phylogenetic comparisons of threat display across the even broader clade of crustaceans as a whole could thus be useful in testing whether any other crustacean species may have also lost threat displays. Furthermore, more detailed examination of the presence versus absence of threat display across a greater number of species of hermit crab, each with a known position on the molecular phylogeny, could also be fruitful. Notably, there are additional species of less social marine hermit crab that are known to perform threat displays frequently (see Hazlett 1966a, b, 1972, 1975, 1981; Table A1 in the Appendix), but most of these species have still not yet been formally positioned on the molecular phylogeny (Bracken-Grissom et al. 2013), so could not be used for comparison. Likewise, while only three species of more social terrestrial hermit crab have been positioned on the molecular phylogeny (Bracken-Grissom et al. 2013; Laidre 2019a), there are additional more social terrestrial hermit crab species that have not yet been positioned on the molecular phylogeny, including *Coenobita brevimanus* and *Coenobita rugosus*, which show the same consistent pattern: an absence of threat display (Table A1 in the Appendix). At least a dozen more social terrestrial hermit crab species are also known to exist (Burggren and McMahon 1988; Greenaway 2003), and all appear to use architecturally remodelled shells (Vermeij 1993; Laidre 2019c). Future studies should therefore make detailed observations in the wild of these additional species and position them onto the molecular phylogeny, since this will help further test the association between a loss of threat display and the use of highly valuable, architecturally remodelled shells on land.

In general, shelters become more valuable resources based on increased investment in architectural construction costs (Hansell 2005; Laidre 2018a). If shelters are rare to begin with, require tremendous initial investment in their original construction or their subsequent modification, and also continue to persist for extended periods, then their resource value must be considerable, ultimately making them highly sought after among conspecifics (Strassman and Queller 2014). Among more social terrestrial hermit crabs, architecturally remodelled shells meet all these criteria (Laidre 2019a): not only do the thinned walls of remodelled shells still provide more than adequate protection against terrestrial predators (Laidre et al. 2012), their carved out internal structure makes them lighter in weight for carrying and locomotion (Laidre 2012b), and their greater internal capacity provides more volume for storing water (to avoid desiccation), as well as greater space for growth and fecundity. Without a remodelled shell, terrestrial hermit crabs cannot survive or reproduce (Laidre 2012a), so the resource value of these shells likely overrides any potential cost of not responding to threat display. Indeed, individuals in the evolutionary past who were dissuaded from interacting with conspecifics, simply because they heeded threat displays and retreated, would never have acquired the remodelled shells essential to reproductive success. In contrast, those “desperados” (Grafen 1987) that disregarded threat displays, initiating frequent encounters with conspecifics, would have had the greatest chance of being part of social vacancy chains (Laidre 2019b), thereby moving up in the housing market and acquiring a large enough remodelled shell to reproduce.

Small individuals in particular (Morrell et al. 2005), with the most to gain and the least to lose from approaching conspecifics with bigger remodelled shells, may have been central to the initial breakdown of threat display efficacy in more social terrestrial hermit crabs. Notably, in our study, individuals who were the first to contact the reanimated models always had relatively smaller shell diameters, consistent with their overriding motivation to take risks to acquire bigger remodelled shells. These results support the “desperado effect” (Grafen 1987; Elias et al. 2010), in which the high resource value of architecturally remodelled shells caused the smallest individuals—those most desperate for a chance to reproduce—to seek out these valuable resources and escalate conflicts at all costs. These “desperado” hermit crabs draw a natural parallel to “consumer vulnerability” within human societies (Hill and Sharma 2020). Indeed, as James Baldwin aptly pointed out (Baldwin 1963; quoted in the Introduction to our paper), such desperation may drive individuals to take dangerous actions. Future studies of more social terrestrial hermit crabs should thus compare those individuals that first contact threatening models (or other dangerous stimuli) with those individuals who never make contact, to determine if ‘first contacters’ are indeed smaller or otherwise more desperate.

When displays are lost in one modality, they may sometimes be replaced by equivalently-functioning displays in another modality (Stevens 2013). Such cross-modal replacement or switching has in some cases been selected for (Endler 1992; Badyaev et al. 2002), including to reduce eavesdropping by conspecifics (e.g., Oliveira et al. 1998), to avoid detection from predators or parasites (e.g., Jakobsson et al. 1995; Gray et al. 2014; Martins et al. 2015), or when one channel of communication becomes too noisy (e.g., Pruett et al. 2016). However, in each of these instances, the intended receiver still benefits from responding to the display. In the case of more social terrestrial hermit crabs, threat display has become irrelevant, since the act of responding now imposes an unbearable cost: missed social opportunities for acquiring vital shell resources from conspecifics. We thus would not predict that ancestral threat displays (visual-based ones involving the claw) would ever have been replaced by another non-visual modality after they were lost. Indeed, if they had been replaced, then individual distances (Hazlett 1975) should still be maintained, yet the more social terrestrial hermit crabs instead have heightened rates of social interaction with one another compared to the less social species. It seems, therefore, that regardless of modality, the same evolutionary logic applies: responding to threat display in the more social species is no longer beneficial to receivers.

Once responsiveness to threat display is lost, pure physical defence likely becomes of overriding importance, potentially favouring specialized morphology (Emlen 2014). It is notable, therefore, that more social terrestrial hermit crab species show a consistent claw morphology involving an enlarged left claw, which is shaped like a 'pseudo-operculum' (Grubb 1971; Burggren and McMahon 1988) and which effectively serves as a tightly-fitting 'door', closely matching the aperture of their architecturally remodelled shells (see Figure 2A) and thus blocking access to this valuable resource. While less social species, like *P. bernhardus*, also have asymmetrical claws, the claws of these less social species do not precisely match the opening to their shells, and individuals with relatively larger claws instead end up performing more threat display (Arnott and Elwood 2010). Thus, claws might have been repurposed in more social terrestrial hermit crab species to function as well-fitted 'doors', which not only reduce the chances of being evicted from one's home but also aid in water retention on land (de Wilde 1973). Indeed, in terrestrial environments, both social competition from conspecifics and desiccation pose major overlapping risks to survival (Burggren and McMahon 1988; Greenaway 2003). Notably though, the risk of desiccation on land does not stop individuals from exposing themselves to the elements as they swap shells (Laidre 2019b) or from frequently 'piggybacking' on conspecifics' shells, a motion that is very similar to threat displays; so clearly desiccation risk was not nearly as important as social competition in driving the loss of threat display. Future systematic measurements, comparing claw morphology and shape (e.g. Spani et al. 2020 in brachyuran crabs), but focusing specifically on less and more social hermit crab species, with reference to their differing shells, could test this ‘adaptive repurposing’ hypothesis that claws function as doors to prevent social eviction. Such measurements could perhaps also motivate further experiments investigating whether other features of claws (e.g., colour or size) provide finer-grained information about owners’ resource-holding potential, which individuals might use while assessing and attempting to evict others.

Enhanced defence implies a decreased probability of resources becoming available and thus an increased length of time that individuals must wait to acquire these resources. If individuals from more social species were to risk playing this ‘waiting game’ away from fellow conspecifics, then once a vacancy arose, either through eviction or death of conspecifics (Valdes and Laidre 2019), such individuals might miss out on the rapid social chain-of-succession that ensues around vacancies in architecturally remodelled shells (Laidre 2014, 2019b; Bates and Laidre 2018; Valdes and Laidre 2019). Selection should thus favour individuals within these more social species to interact frequently with conspecifics in fission-fusion social groupings (Couzin and Laidre 2009; Steele and Laidre 2019), while exhibiting at least some degree of social tolerance as they opportunistically await potential vacancies. Such social tolerance could itself create new opportunities for eavesdropping and social information transmission (Laidre 2013b; Ward and Webster 2016) and even for cooperation, with more social terrestrial hermit crabs forming opportunistic ‘coalitions’, in which smaller individuals team up to cooperatively evict bigger individuals (Laidre 2018b). Ultimately though, each crab is still a ‘rugged individualist’ (Laidre 2010), in close competition with others in its social milieu for the very same architecturally remodelled shell resources. Thus ‘social hermit’ groupings, while not involving threat displays, nevertheless exist on a knife edge between conflict and cooperation, with the tension between these opposing forces (Dunbar 1998; Lihoreau et al. 2012) potentially fuelling more sophisticated social information gathering and cognitive abilities (Krieger et al. 2020), especially relative to less social hermit crab species.

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Figures

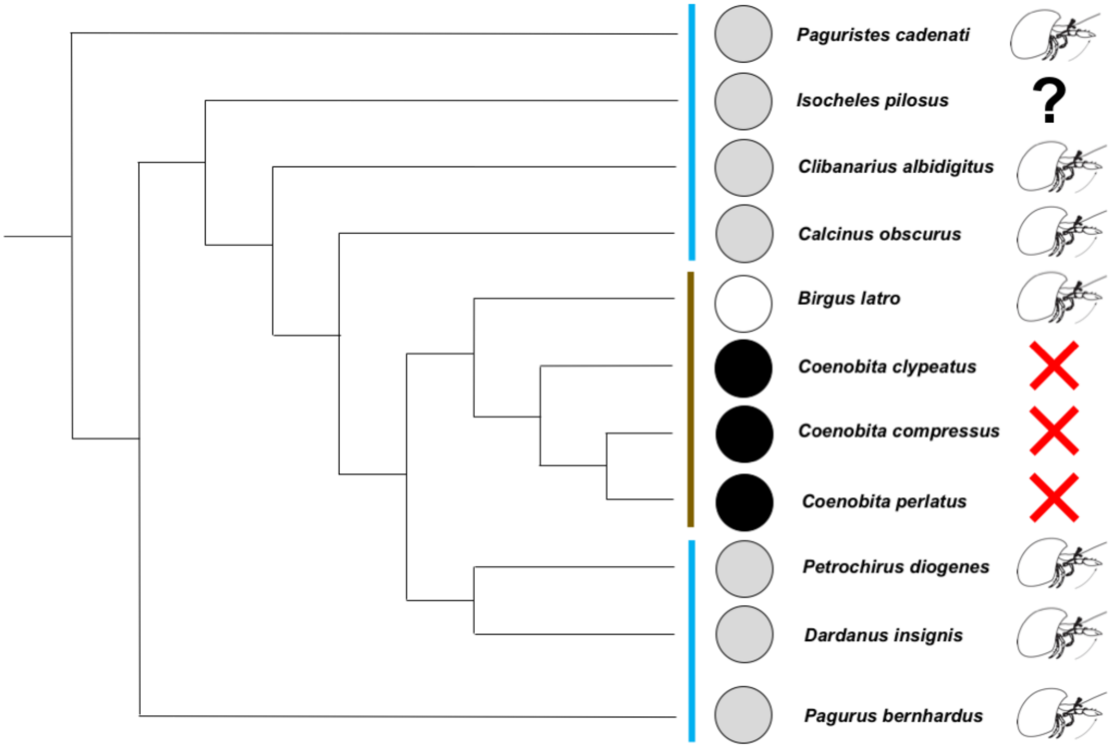

Figure 1. Evolutionary loss of threat display across a phylogenetic tree of hermit crabs (tree modified from Laidre, 2019a). The eleven closely-related hermit crab species are arrayed based on their evolutionary relatedness from molecular data (Bracken-Grissom et al., 2013). Presence versus absence of threat display within each species was then mapped onto the phylogeny based on a synthesis of literature and personal observations on each species (Table A1 in the Appendix). Presence is designated by the hermit crab icon in a threat display posture; absence is designated by the red 'x'; and uncertainty about presence or absence is designated by '?'. Note that species are either marine or terrestrial (blue line = marine species; brown line = terrestrial species) and circles designate the type of shell used by each species, which impacts their level of sociality (white circle = no shell, which is only found in a single 'less social' terrestrial species; grey circles = unremodelled shells, which are used by 'less social' marine species; and black circles = architecturally remodelled shells, which are used by 'more social' terrestrial species in which individuals are highly dependent on conspecifics for shells).

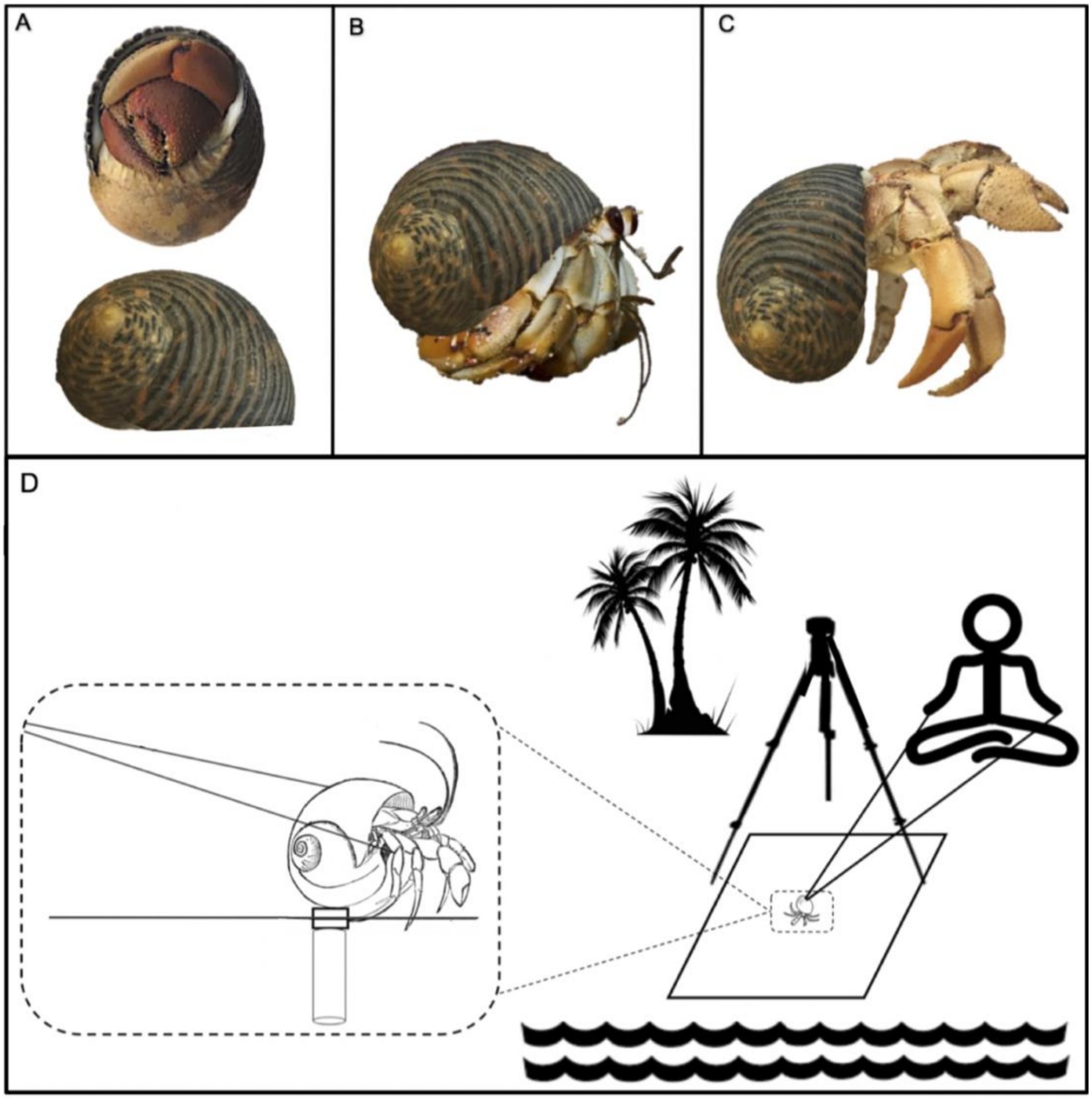

Figure 2. Reanimated models of the more social species (*Coenobita compressus*) in three different poses: (A) withdrawn, (B) neutral, and (C) threat. (D) Experimental setup for making models move dynamically. Models were mounted onto a wooden dowel, anchored in the sand, with magnets on top of the dowel and at the base of the model's shell, so that the models could be rotated around a pivot point and oriented to directly face approaching live crabs. Model movement was achieved via subtle manoeuvring from a distance using clear fishing lines attached to the model's back legs.

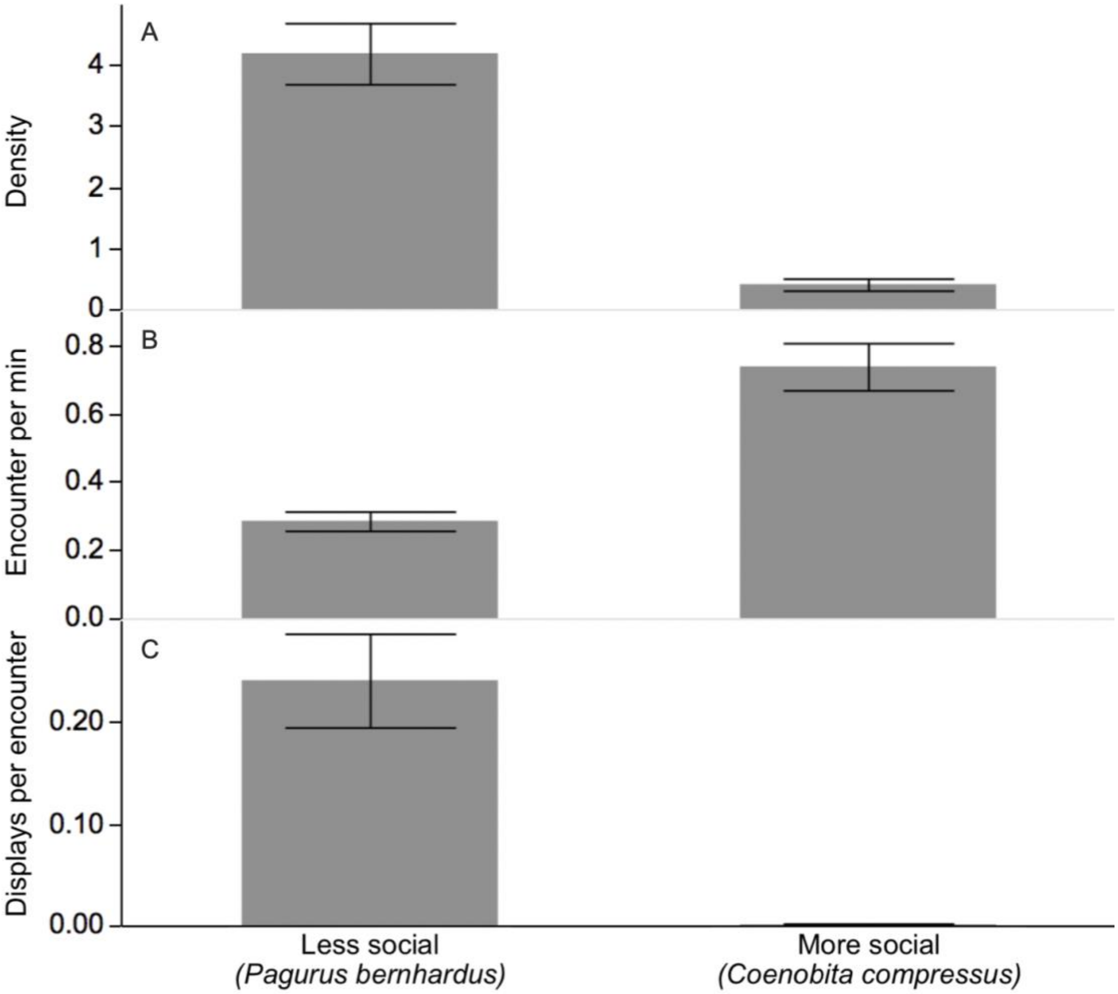

Figure 3. Less social marine (*Pagurus bernhardus*) and more social terrestrial (*Coenobita compressus*) hermit crabs: (A) density in the field (number of individuals per quadrat), (B) encounter rate (social encounters per min), and (C) threat displays (per encounter). Mean ± SE.

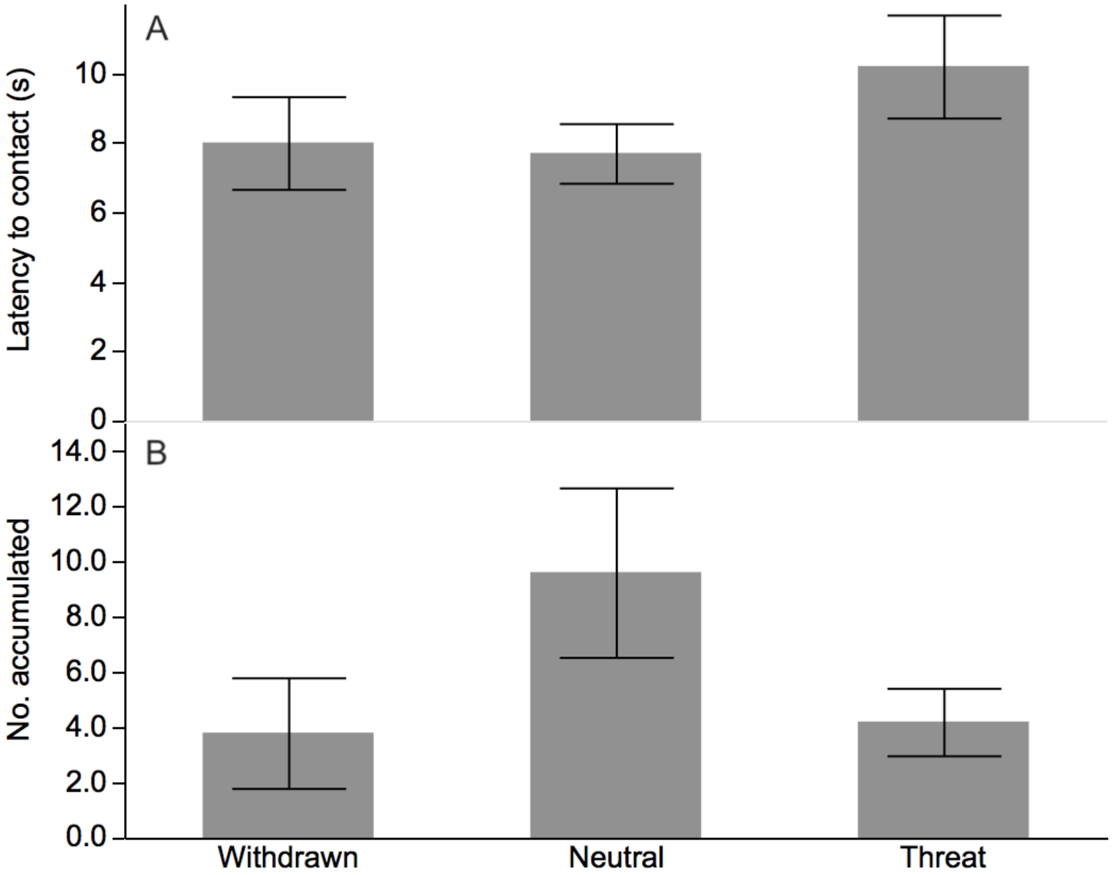

Figure 4. In the more social species, response of individuals to stationary models in each of the three poses: (A) latency of first individual to contact model (in s) and (B) total number of individuals that accumulated around model (during 5 min). Mean ± SE.

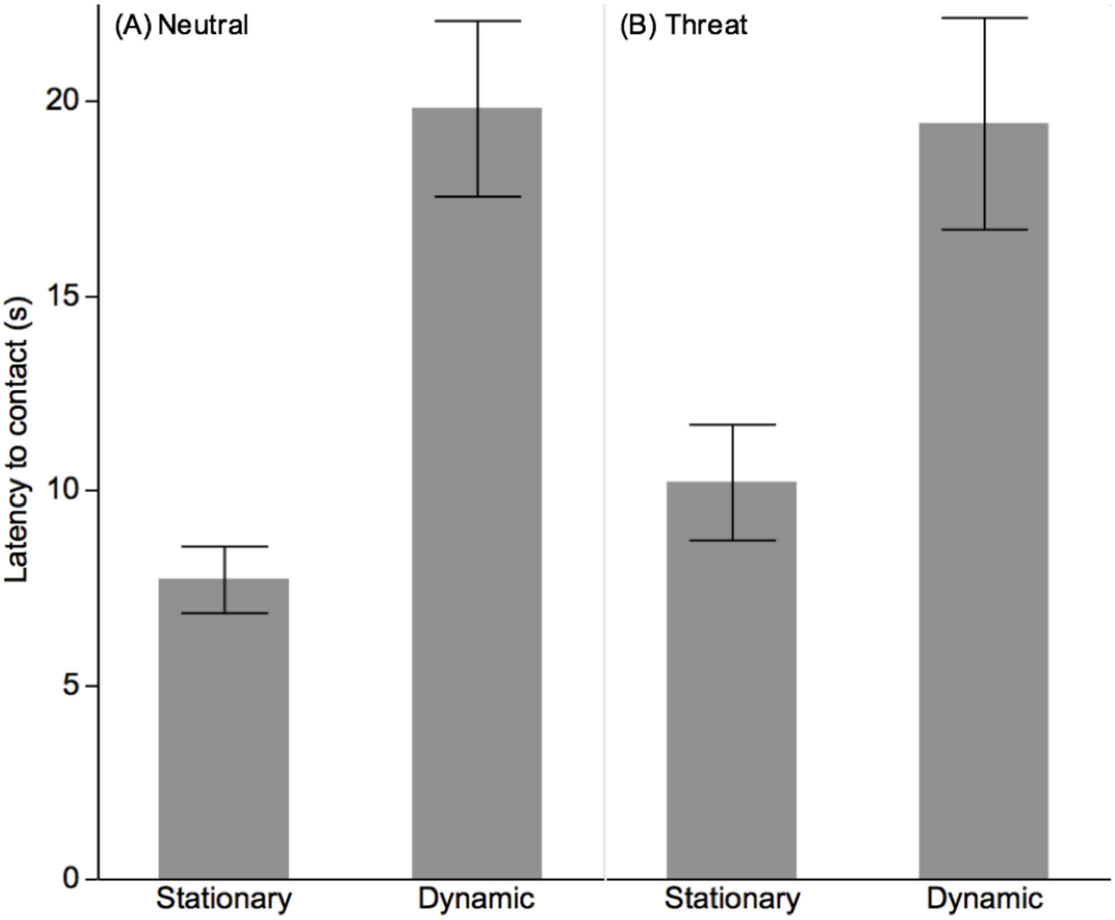

Figure 5. In the more social species, latency (in s) of first individual to contact stationary versus dynamically-moving models in (A) neutral pose and (B) threat pose. Mean ± SE.

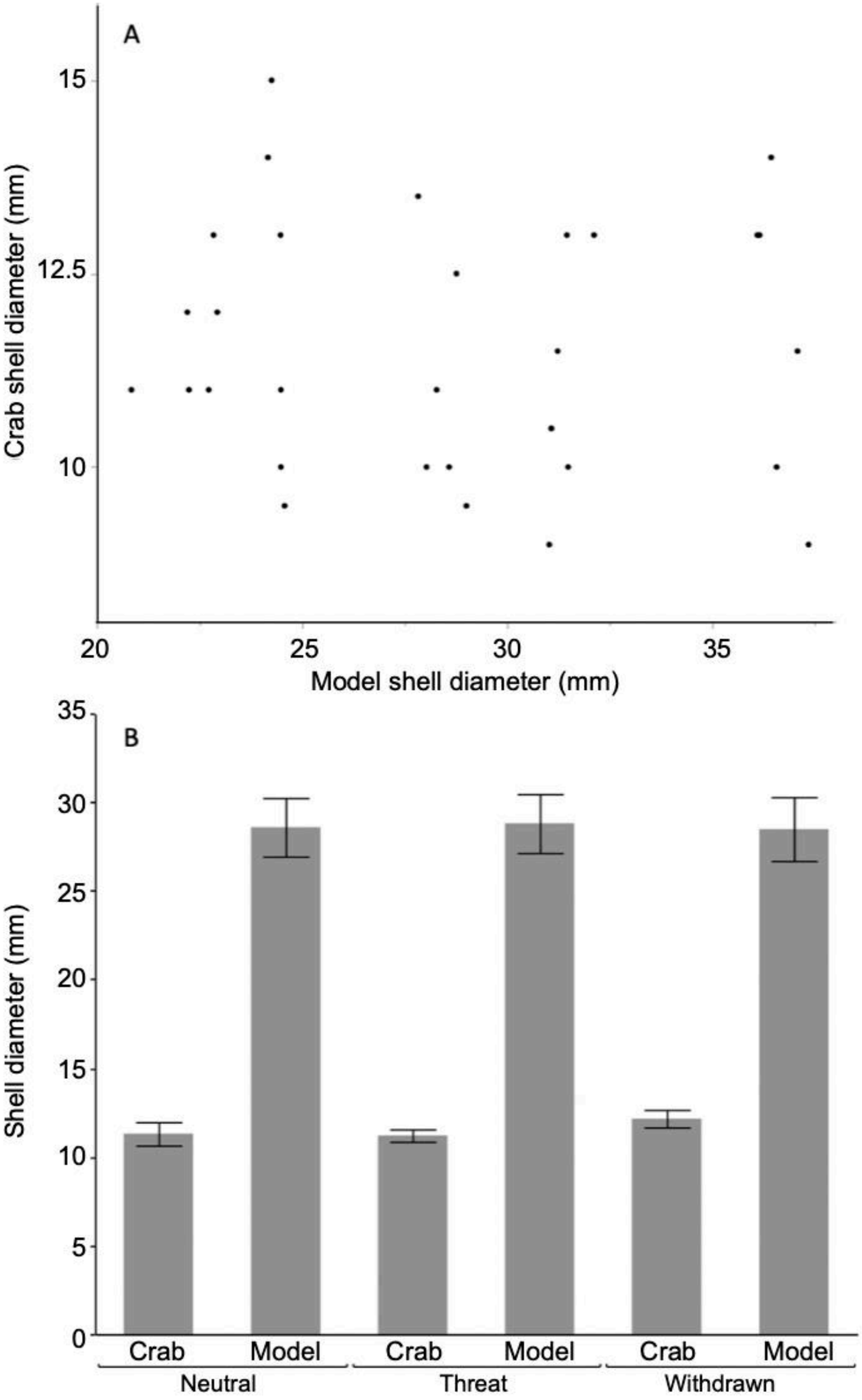

Figure 6. In the more social species, shell diameter (in mm) of live crabs relative to the stationary models they contacted, for (A) all model poses together and (B) each of the three model poses (neutral, threat, and withdrawn) separately. Mean ± SE.

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Appendix

Tables

Table A1. Synthesis of literature, personal observations from the authors, and personal communications from other researchers about the presence or absence of threat display in each species (see phylogeny in Figure 1).

Species	Threat display (present or absent)	Reference
Paguristes cadenati	Present	Hazlett 1966b, including on other *Paguristes* spp.
Isocheles pilosus	?	No available references or observations
Clibanarius albidigitus	Present	Hazlett 1966a, b, 1972, including on other *Clibanarius* spp.; Laidre personal observation
Calcinus obscurus	Present	Hazlett 1966a, b, 1972, including on other *Calcinus* spp.; Laidre personal observation
Birgus latro	Present	Helfman 1977; Burggren and McMahon 1988; Laidre personal observation
Coenobita clypeatus	Absent	de Wilde 1973; Laidre personal observation
Coenobita compressus	Absent	Laidre 2010; Laidre personal observation; Doherty personal observation
Coenobita perlatus	Absent	Grubb 1971; Laidre personal observation
Petrochirus diogenes	Present	Hazlett 1972; Laidre personal observation
Dardanus insignis	Present	Hazlett 1966a; Hazlett personal communication
Pagurus bernhardus	Present	Hazlett 1966b, including on other *Pagurus* spp.; Hazlett 1968; Elwood et al. 2006; Laidre 2007; Arnott and Elwood 2007; Laidre and Elwood 2008; Laidre 2009; Arnott and Elwood 2010; Laidre personal observation; Doherty personal observation; Elwood personal communication
Coenobita brevimanus	Absent	Grubb 1971; Laidre personal observation
Coenobita rugosus	Absent	Grubb 1971; Laidre personal observation

Table A2. Interacting crabs' behaviours were recorded based on an established ethogram.

Behaviour	**Description**
Display	A threat in which chelae are raised outward towards the opposing crab
Grapple	One or both individuals physically hold and wrangle one another, occasionally one individual strikes the other with a leg
Piggybacking	One individual climbs onto the dorsal side of the shell of a conspecific
Claw strike	Rapid movement of a claw away from the individual's own body and toward the other crab, with contact
Shell fight	Repeated rapping of one's shell against that of the other crab (this only happens in marine hermit crabs, not terrestrial hermit crabs)
Eviction	Forcible removal of an individual from its shell
Shell swap	Moving into the shell of another individual

Table A3. Measurements (in mm) of models made from dead *Coenobita compressus* specimens.

Pose	Shield length	Claw length	Sex	Shell diameter
Withdrawn	8.74	9.93	Male	27.83
Withdrawn	10.67	12.20	Male	37.34
Withdrawn	9.52	11.30	Female	32.12
Withdrawn	8.14	9.18	Female	24.16
Withdrawn	8.09	8.94	Male	24.47
Withdrawn	10.27	10.84	Female	31.45
Withdrawn	7.00	7.90	Male	20.84
Withdrawn	10.71	11.47	Male	36.09
Withdrawn	8.57	9.28	Male	28.28
Withdrawn	7.65	8.20	Female	22.24
AVERAGE	**8.94**	**9.92**		**28.48**
Neutral	10.04	11.16	Female	31.48
Neutral	13.23	14.74	Male	36.43
Neutral	9.35	10.08	Female	28.03
Neutral	8.69	9.92	Female	24.57
Neutral	10.77	11.80	Male	36.15
Neutral	10.12	11.15	Female	31.02
Neutral	7.60	8.42	Male	22.72
Neutral	7.24	8.86	Female	22.20
Neutral	9.18	10.55	Female	24.25
Neutral	10.98	11.42	Female	29.00
AVERAGE	**9.72**	**10.81**		**28.59**
Threat	8.62	10.70	Female	31.07
Threat	9.04	10.29	Female	31.22
Threat	8.24	9.53	Female	22.84
Threat	8.73	10.04	Male	28.58
Threat	9.70	11.20	Male	37.07
Threat	8.80	9.89	Female	22.93
Threat	8.90	10.64	Female	24.48
Threat	9.29	11.26	Female	24.48
Threat	9.43	10.95	Female	28.76
Threat	12.14	13.32	Male	36.56
AVERAGE	**9.29**	**10.78**		**28.8**

Figures

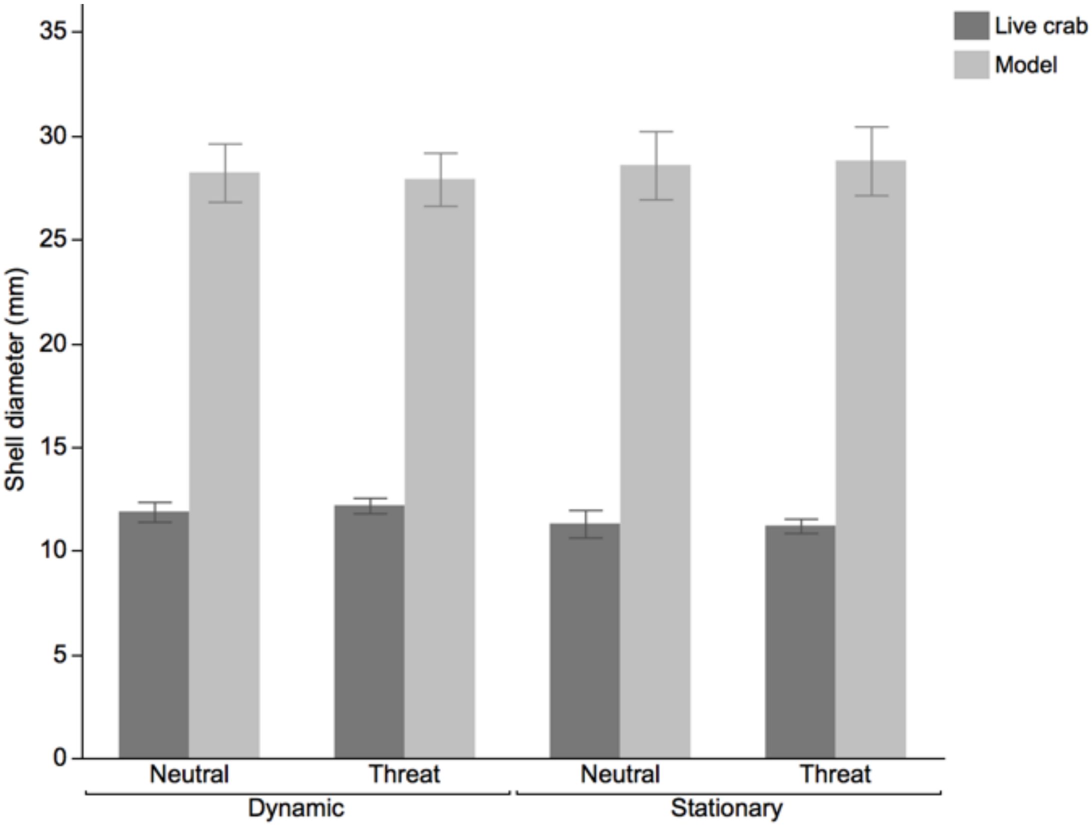

Figure A1. In the more social species, shell diameter (mm) of both live crabs and models across dynamic and stationary experiments with neutral or threat pose. Mean ± SE.

Videos

Video 1. Live crab of the more social species (*Coenobita compressus*) interacting with dynamically-moving model in neutral pose. The video can be viewed at 10.6084/m9.figshare.12871157

Video 2. Live crab of the more social species (*Coenobita compressus*) interacting with dynamically-moving model in threat pose. The video can be viewed at 10.6084/m9.figshare.12871157

Video 3. Live crab of the more social species (*Coenobita compressus*) performing display-like motion while ‘piggybacking’ on another shell. The video can be viewed at 10.6084/m9.figshare.12871157

CHAPTER 2

Doors to the homes:
signal potential of red colouration of claws in social hermit crabs

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Abstract

Red colouration on a signaller's body may be an informative signal in many animals. For species that inhabit architecture (e.g., burrows, nests, or other structures), certain parts of the body are more exposed than others, potentially serving as superior platforms for signalling via colouration. Yet whether animals differentially advertise red colouration on body parts that are more versus less exposed from their architecture remains to be tested. Here we systematically quantified red coloration in social hermit crabs (*Coenobita compressus*), which inhabit architecturally remodelled shells and which have claws that visibly block the shell entrance, like doors to their home. We hypothesised that red colouration of claws may be a signal of resource-holding potential (RHP). Consistent with this RHP signalling hypothesis, we found that within the same individuals' bodies, exposed claws showed significantly greater red colouration than unexposed carapaces. Furthermore, larger body size predicted greater red colouration, specifically among males. These results were not explained by competing hypotheses (e.g., interspecific signalling, camouflage, or UV protection). Red claw coloration may therefore function as a signal to conspecifics, though experiments are still needed to test recipient responses. Broadly, relative to surrounding architecture, exposed body surfaces offer rich potential as signalling platforms for colouration.

Keywords: red colouration, claws, architecture, shells, signal, RHP

Introduction

Animal signals are acts or structures produced by signallers, that convey information [1]. For signals to convey information about the signaller itself, the signal must correlate with an underlying trait of the signaller, that is of interest to receivers [2, 3]. Often, substantial variation exists in many traits within a population, but only signals have been specifically selected over evolutionary time to convey information about traits. Even when signals convey information imperfectly, they can still be useful, especially when combined with other information sources. While signals from many modalities can be informative, for species with vision, colour may be of great significance [4].

Red colouration, in particular, may be a potentially relevant signal in multiple contexts. For example, in fighting contexts, red has been found to be an indicator of signallers' resource-holding potential (RHP) (e.g., in red-shouldered widowbirds, *Euplectes axillaris*, red colouration of epaulets signals competitive ability [5, 6]). Many examples of red colour signals also exist in sexual selection, as indicators of mate quality (e.g., in zebra finches red colouration of beaks determines sexual attractiveness [7]). Other correlates of red colouration include immune function and antioxidant activity [8, 9, 10] as well as UV protection [11, 12]. One reason red colouration is thought to be a potentially useful signal across many taxa is that certain pigments which generate red colouration (e.g., carotenoids) cannot be synthesised *de novo* by animals [13] and must instead be obtained from food in the external environment [14, 15]. Therefore, individuals with a differential ability to acquire these pigments (e.g., through more efficient discovery or a greater capacity to dominate at resource patches) will display more red. Critically though, conveying this information effectively may depend on the precise placement of red colouration on the signaller's body.

Generally, it is physically impossible for organisms to display all areas of their body at once. Thus, while some species exhibit full-body red colouration (e.g., male cardinals), most animals with red colouration only have specific areas of their bodies on which red is more concentrated (e.g., the face of mandrills, the epaulets of red-winged blackbirds, and the dewlaps of Anolis lizards). Interestingly, organisms that inhabit architecture (e.g., burrows, nests, or other built structures) only have certain parts of their bodies that are regularly exposed [16, 17], typically at the architecture's entrance (e.g., mantis shrimp [18], phragmotic-headed ants [19], woodpeckers [20], and marten [21]). Such partial exposure often occurs when owners are protecting their architectural structures from intruders, with the owner keeping the majority of its body inside the structure for protection [16]. Exposed body surfaces of owners, relative to their architecture, may make ideal platforms for signalling via colouration. Yet, whether animals differentially advertise red colouration on body parts that are more versus less exposed from their architecture remains to be tested.

The organisms with perhaps the most intimate connection to the architecture they inhabit are hermit crabs [22]. These animals' bodies are mostly covered by transportable gastropod shells [23], except for their anterior appendages, especially claws, which represent a first line of defence of shells [24, 25]. Interestingly, for highly social terrestrial hermit crabs (*Coenobita* spp.), the evolutionary transition to living on land [26] was accompanied by dramatic changes in both sociality [27, 28, 29, 30] and claw morphology [31]. These social hermit crabs no longer produce threat displays with their claws [32]. Instead, their enlarged left claw now fits the shell entrance, essentially functioning as a ‘door’ or ‘pseudo-operculum’ [31-34], which is visible to conspecifics and blocks potential evictors [30]. Within one of these social hermit crab species (*Coenobita compressus*) the level of red colouration of claws varies greatly between individuals in the wild [35] (Fig. 1a). Yet no studies have systematically quantified colouration to test possible functional explanations. We hypothesised that red colouration on exposed body parts may be a potential signal, with the level of red providing information about RHP.

To test the hypothesis that red colouration serves as a signal of RHP, we systematically measured colour variation between different parts of the body for individuals spanning a range of sizes and both sexes. If the RHP signalling hypothesis is true, then exposed areas should differentially advertise red colouration compared to unexposed areas of the same individuals’ bodies. Furthermore, if red colouration is a signal of RHP, then variation in red should correlate with body size, such that bigger individuals are more red. Critically, the sex that differentially benefits from attaining larger size (which is males in *C. compressus* [36, 37]) should be more likely to show a relationship between red colouration and body size. We therefore examined between-sex variation, predicting that males would show a stronger relationship than females between red colouration and body size. We also evaluated within-sex variation (based on residuals in exposed surface area, i.e., claw area, relative to body size), determining whether males with greater exposed surface area, relative to body size, were more red. If variation in red colouration is not a signal and is unrelated to RHP, then the above predictions should not follow. Broadly, we considered the extent to which any alternative hypotheses, adaptive or non-adaptive, may explain the observed patterns in colouration.

Methods

Sample collection and study site

C. compressus specimens were collected in the wild from a long-term study population [38] along the beach-forest interface of Osa Peninsula, Costa Rica (8°23′40″ N, 83°20′10″ W). Individuals of all sizes across the population were collected. Collection was entirely blind with respect to colour and sex. The sole criteria for inclusion were that an individual must have all its appendages intact and not be moulting. Once the sample (N = 103 individuals) was collected, all individuals were then systematically measured. To test if body parts that are exposed out of the shell architecture could act as signalling platforms, a series of systematic morphological and colour measurements (see below) were taken on each individual. All measurements were made by the first author (CD) during February to March 2018. After measurements were completed, all collected individuals were then returned to the wild.

Morphological measurements

For each individual, we recorded sex (N = 47 females, N = 56 males) and made the following morphological measurements using electronic callipers to the nearest 0.01 mm: shield length (mm) [39], claw length (mm) [31], and claw width (mm) [31]. We also calculated exposed claw area (mm^2) as claw length x claw width. In addition, we measured posterior carapace length to the nearest 0.01 mm and body weight to the nearest 0.01g. However, because shield length is regarded as the most reliable metric of overall body size [39], and also because shield length correlated strongly with both posterior carapace length and body weight (Table S1), all our analyses of body size focus on shield length.

Colour measurements

We measured spectral reflectances (from 250 to 800 nm) using a solarization-resistant reflectance probe (QR400-7-SR reflection probe, Ocean Optics Inc., Dunedin, FL) coupled with a pulsed xenon source (Ocean Optics) and a JAZ spectrometer (JAZ-COMBO, Ocean Optics; Fig. 1b). Reflectance measurements were taken on two body parts for each individual (Fig. 1c): (1) the enlarged left claw (i.e., the body part that is most exposed and visible at the shell opening) and (2) the carapace (i.e., the body part that is concealed within the shell and only becomes visible after an individual is removed from its shell). Both body parts represent hardened areas of the same overall exoskeleton (as opposed to the soft fleshy tissue of the abdomen). Note, we did not make any colour comparisons with the smaller right claw or the walking legs, since these body parts were too small to enable spectrometer measures; and furthermore, they are neither fully concealed nor fully exposed, so would not have provided informative comparisons. Only the enlarged left claw and the carapace, which were possible to measure, could provide a direct and informative test of the RHP signalling hypothesis.

Reflectance measurements were calibrated using a Spectralon plastic standard that reflects nearly 100% of the light at all wavelengths from 200 to 800 nm (WS-1-SL Diffuse Reflectance Standard, Ocean Optics), which allows the spectrometer to calculate processed spectrum values (i.e., reflectance corrected using the white reference; for example see Fig. 1d). To control for variation caused by the angles of illumination or measurement, a reflection probe holder (RPH-1) was used to ensure the end of the reflectance probe was always placed at the same distance from the measured surface and held at a consistent 45° angle to the surface. This arrangement, which uses an angle of collection that is not equal to the angle of incident light, measures diffuse reflectance (which is relatively angle-independent), and avoids detection of specularly reflected light [40].

For each body part, we quantified red colouration using the following formula [41] (Fig. 1d):

$$\frac{\textbf{(average red – average green)}}{\textbf{(average red + average green)}}$$

This formula calculates chromaticity (i.e., average red – average green) while controlling for brightness (i.e., average red + average green), and uses measurements in the 500-600 nm wavelength range to denote the green spectrum and measurements in the 600-700 nm wavelength range to denote the red spectrum.

Final sample

Of the original sample (N = 103 collected individuals), a subset were excluded from the analyses of colour for the following reasons: N = 1 individual had an abdominal abnormality, which was only detectable after it had been removed from its shell; N = 21 individuals were too small to accommodate the spectrometer to take colour measurements; N = 9 individuals were large enough to take colour measurements, but ultimately their spectrometer files could not be opened or were somehow corrupted.

Hence, analyses of colour were performed on a final sample of N = 72 individuals (N = 28 females and N = 44 males).

Statistical analyses

To examine whether red colouration could function as a signal, we conducted a series of analyses that tested each of the predictions of the RHP signalling hypothesis (see Introduction). To test whether colouration differed between exposed versus unexposed body parts, we used a paired t-test to contrast red colouration of the claw (exposed) versus the carapace (unexposed) of the same individuals. To test whether colouration was related to overall body size, we conducted a linear regression of red colouration of claws and of carapaces against shield length. We conducted regressions across both sexes, as well as for females and for males separately. Finally, to test if colouration was related to the size of the exposed claw area, relative to body size, we conducted a post-hoc linear regression of red colouration of claws against the residuals of exposed claw area relative to shield length. All analyses were performed in JMP® Pro 16.0.0.

Results

Consistent with the RHP signalling hypothesis, within-subject contrasts revealed a significant difference in red colouration between exposed vs unexposed body parts (i.e., claw vs carapace, Fig. 2). In particular, claws showed significantly greater red colouration than carapaces (paired t-test: $t = 7.55$, $df = 71$, $p < 0.0001$). Further supporting the RHP signalling hypothesis, larger body size significantly predicted increased red colouration exclusively for exposed claws (linear regression: $F_{1,70} = 6.61$, p

= 0.012, r^2: 0.086, Fig. 3a) and not for unexposed carapaces (linear regression: $F_{1,70}$ = 0.34, p = 0.56, Fig. 4a). When males and females were examined separately, this relationship did not hold for both sexes: for males, larger body size significantly predicted increased red colouration of exposed claws (linear regression: $F_{1,42}$ = 5.94, p = 0.019, r^2: 0.12, Fig. 3b), but for females, this was not the case (linear regression: $F_{1,26}$ = 0.68, p = 0.42, Fig. 3c). For both sexes, red colouration of unexposed carapaces did not significantly correlate with body size (linear regression, males: $F_{1,42}$ = 0.37, p = 0.55, Fig. 4b; females: $F_{1,26}$ = 0.01, p = 0.92, Fig. 4c).

Exposed claw area strongly correlated with body size (Table S1). However, among males, red colouration of claws did not correlate with variation in exposed claw area relative to body size (linear regression: $F_{1,42}$ = 0.02, p = 0.89; Fig. 5). Thus, males with proportionately more exposed surface area did not show greater red colouration.

Discussion

Our systematic measurements of colouration and morphology among social hermit crabs revealed a stark difference in the level of red colouration between exposed and unexposed areas of the body, relative to architecture. In particular, exposed claws exhibited substantially greater red colouration than unexposed carapaces, suggesting that red colouration could be a signal. Moreover, in males, red colouration of claws correlated with body size, suggesting that the level of red colouration in claws could be a signal of RHP. While the relationship between red colouration of claws and body size is relatively weak, red colouration could still provide valuable information for receivers, supplementing other sources of information about RHP, like visual motion [42], olfaction

[43], and tactile feedback [44]. Notably, one reason the relationship between colour and body size may have been weak is because measurement of colouration was impossible for the smallest individuals sampled (20.4 % of the original sample of N = 103 individuals; see Table S1, Fig. S1). Individuals of this small size, which were too small to accommodate the spectrometer, tend to exhibit little if any red colouration ([35]; ML & CD personal observation). Thus, the relationship we found between red colouration and body size might well have been stronger had it been possible to include the smallest individuals. Only one of the predictions of the RHP signalling hypothesis was not supported in the current study: that there would be a relationship between the residuals of exposed claw area and red colouration of claws for males. Such a relationship may have been impossible given the extremely tight correlation between exposed claw area and body size ($r^2 > 0.9$), which greatly restricted the range of residuals. Regardless, exposed areas could effectively advertise important information about RHP, and our results suggest that further tests of such possible signalling platforms on the body, in reference to architecture, are merited.

Further study of the pattern of red colouration we found will also be vital for testing potential alternative explanations that do not invoke intraspecific signalling. These alternative explanations (see Table 1), which cannot all be eliminated at present, include both adaptive and non-adaptive explanations. For example, one adaptive explanation is that red colouration of claws is used for interspecific signalling to predators. However, predation on land is relaxed for terrestrial hermit crabs [45] and, furthermore, the architecturally remodelled shells used by our study species are above the bite force of their predators [46]. Hence, explanations relating to interspecific signalling (e.g., aposematism [47, 48]), as well as camouflage against predators [41, 49-51], are unlikely. Another adaptive explanation for the greater red colouration of claws is that red colouration is used for UV protection of exposed areas [52]. However, the study species carries its claws ventrally [23] in the shade of both its body and shell while locomoting [53], so the claws are the least exposed to the sun; and furthermore, individuals move to forested areas [38] and beneath leaves [54] during the day. Hence, explanations relating to UV protection are also unlikely. In contrast, non-adaptive explanations for the difference in red colouration between exposed claws and covered carapaces remain possible. For example, perhaps direct environmental impacts and relative exposure to external elements (e.g., weather, sand abrasion, salinity, or sunlight) causes the different colouration of claws compared to carapaces, especially if such impacts accumulate over a crab's lifetime. Or, theoretically, differences in red colouration between claws and carapaces might arise as an incidental by-product of some other trait that is directly selected for besides colour (e.g., morphological structures, such as integument thickness [55]). More studies are needed to determine the plausibility of alternative adaptive and non-adaptive explanations and the extent to which they can better explain patterns of red colouration compared to the RHP signalling hypothesis that was the focus of the present study.

In addition to testing alternative hypotheses, more detailed tests of the RHP signalling hypothesis would also be informative. If this hypothesis is true, then multiple finer-grained measures of RHP should correlate even more strongly with the level of red colouration in claws. For example, muscles both in the claw and the abdomen are undoubtedly critical for obtaining and retaining shells [30], thereby allowing individuals to successfully rise and maintain their positions in the housing market [56]. Future studies could therefore measure both claw pinching force and physical resistance to eviction, testing how well red colouration predicts individual's ability to evict others and withstand eviction. Furthermore, physiological studies could quantify the density of muscle fibres within both claws and abdomens, testing how well such internal musculature measures [57] correlate with red claw colouration. Ultimately, if further correlations exist between a variety of measures of RHP and red colouration, then this would bolster the RHP signalling hypothesis.

A key criterion for a signal is that recipients must be able to perceive and hence respond to the signal [1-3]. Are recipients able to perceive red colouration in claws? Interestingly, laboratory experiments in terrestrial hermit crabs have revealed that individuals can differentiate artificial red colouration from blue and green colouration [58]. However, the response to natural colour variation in claws has yet to be tested. Future experiments could exploit such natural variation by using postured or withdrawn models of dead crabs [32], thereby testing recipient responses in the wild, particularly when other factors (e.g., claw size and shell quality) are held constant. Experiments might also be able to manipulate claw colour itself, thereby directly testing whether recipients' attempts at evicting a target change in response to altered colour. Critically, if the level of red colouration of claws is indeed an effective signal, then recipients should mount fewer attempts at evicting the signaller and give up earlier for signallers whose claw colouration is more red. Beyond signalling RHP, it is also possible that red claw coloration could simultaneously be used in sexual signalling [36, 37], in which case tests of female responses to males would be informative. Recent discoveries in birds revealing that colour perception can be categorical, with discrete thresholds, rather than operating along a continuum [59] raises many further questions about the use and effectiveness of red colouration as a signal across taxa.

To fully elucidate the function of red colouration, it may also be critical to gain a deeper understanding of mechanism. Mechanistically, red colouration is often generated using pigments obtained from food [13], most notably carotenoids such as astaxanthins for crustaceans [60]. Presently, it remains unknown precisely which compounds in the diets of terrestrial hermit crabs might contribute to their red colouration. Yet, interestingly, *C. compressus*, in particular, is a highly opportunistic omnivore, with one of the most diverse diets of any crustacean [61]. If specific dietary components required to achieve red colouration are hard to obtain in this species' environment, then variation in individuals' ability to find and gain access to such foods could provide a mechanistic basis for the RHP signalling hypothesis for red colouration. Determining what, if any, components of diet contribute to the accrual and retention of red colouration in this species may require experiments with controlled feeding regimens. By simultaneously monitoring individuals' colouration longitudinally, both within and across moults, it may even be possible to reveal how individuals allocate colour differentially to certain body parts. Such feeding experiments could also be supplemented with nutritional analyses that isolate the exact chemical composition of a range of natural foods in the wild. Ultimately, by understanding red colouration at the proximate level, including what compounds are involved, how limited those compounds are in nature, and how individuals incorporate these compounds, we can further inform our understanding of potential functions of red colouration.

To summarise, here we tested the hypothesis that red colouration in claws serves as a signal of RHP. Several key predictions of this RHP signalling hypothesis have been supported by our systematic measurements of colour and morphology in social hermit crabs. Furthermore, various competing hypotheses (Table 1) can be logically excluded. Future studies, especially behavioural experiments on the responses of recipients to colour variation, can further test the RHP signalling hypothesis, as well as other hypotheses. Broadly, we suggest that studies of other animals, particularly those inhabiting architectural structures [16], consider exposed body parts, relative to architecture, as potential signalling platforms.

Acknowledgements

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Tables

Table 1. Competing hypotheses for pattern of red colouration.

	Explanation	*Supported?*
Adaptive		
Intraspecific signal	Selected to convey information to conspecifics (e.g., signaller's RHP)	**Yes**
Interspecific signal	Selected to convey information to heterospecifics (e.g., signaller's toxicity)	**Unlikely**
Camouflage	Selected to help individual evade predators by blending with background	**Unlikely**
UV protection	Selected to absorb sunlight at damaging wavelengths	**Unlikely**
Non-adaptive		
Direct environmental impact of exposure	Due to greater exposure to external elements (e.g., weather, sand abrasion, salinity, or sunlight) outside of architecture	**Unclear**
By-product of selection for another trait	Selection on a trait other than red colouration incidentally gives rise to this colour pattern	**Unclear**

Figures

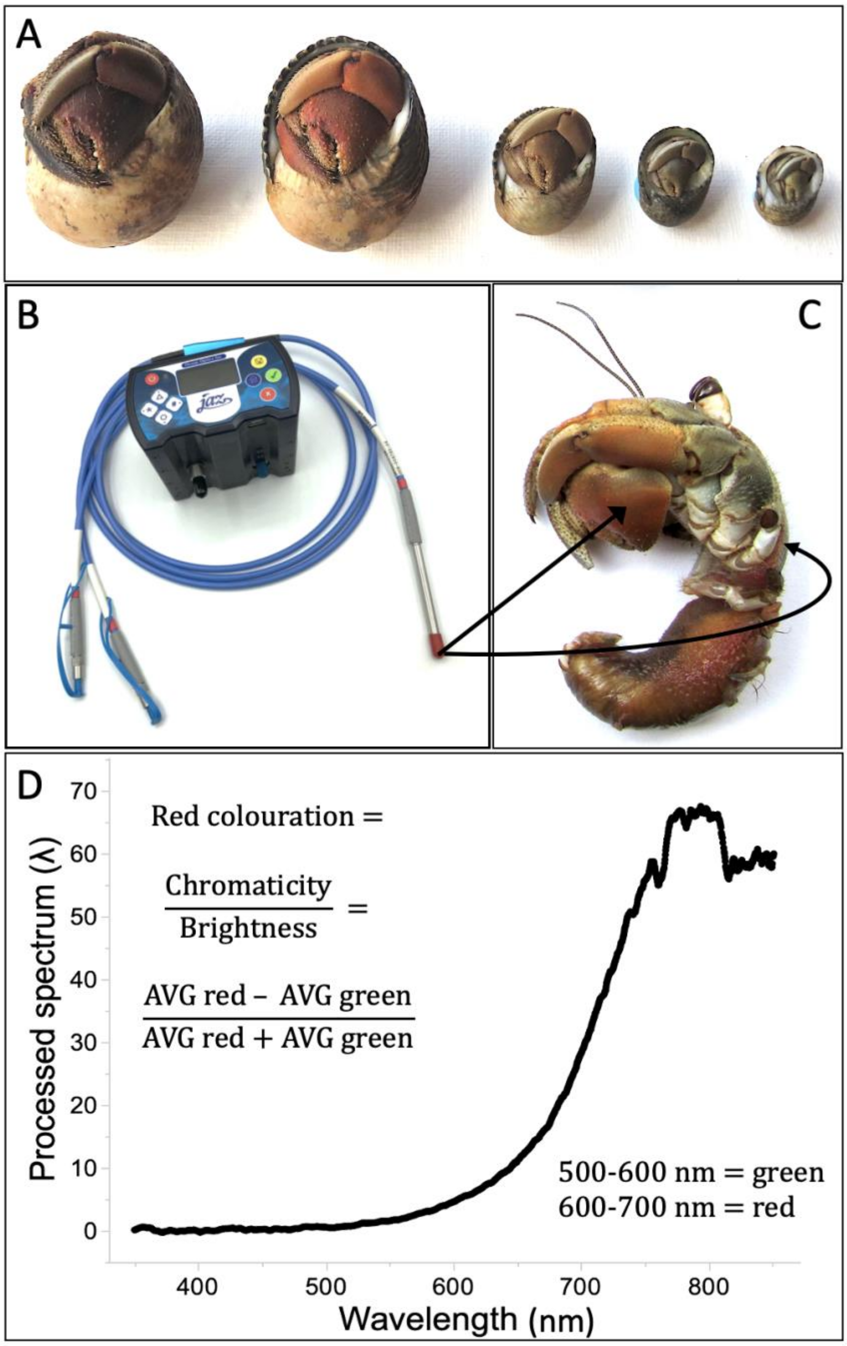

Figure 1. Measurements of body colour, in relation to shell architecture, within the social hermit crab (*Coenobita compressus*). (A) Photograph of colour variation across individuals (arrayed largest to smallest from left to right). Note, only part of each individual's body, particularly its enlarged left claw, is exposed out of the shell architecture, being visible as a 'door to the home'. (B) Reflectance was measured using a Jaz spectrometer. (C) Colour measurements focused on two areas of crabs' bodies: exposed claws (arrow on left) and unexposed carapaces (arrow on right). Individual pictured has been removed from its shell to show both areas. (D) Example of a reflectance curve for the claw of a male, including the formula used to calculate red colouration. (Photos for A and C: Mark Laidre, Photo for B: Elliott Steele).

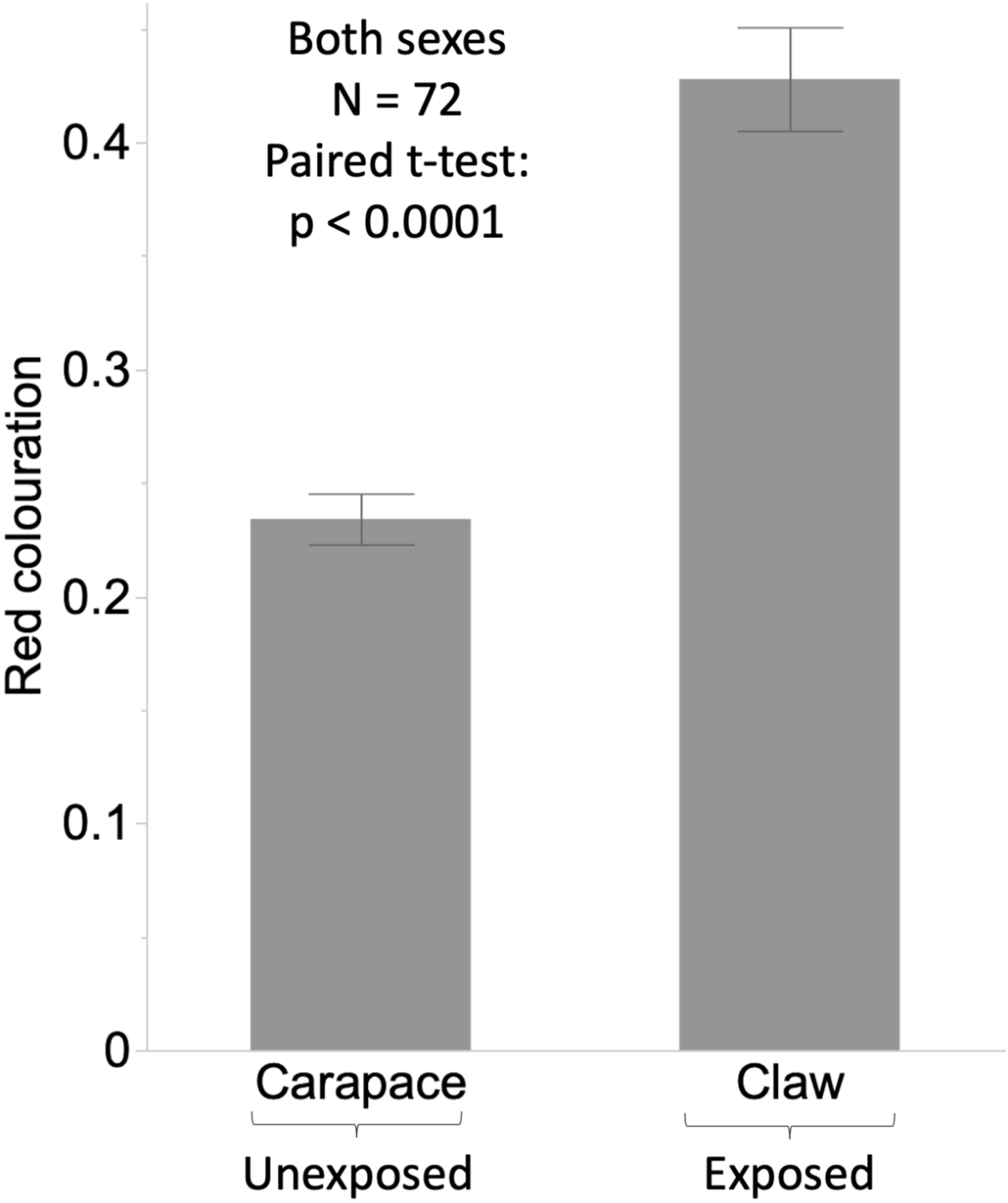

Figure 2. Red colouration (Mean ± SE) of exposed claws versus unexposed carapaces. Paired t-test and p-value for within-subjects contrast, including both sexes.

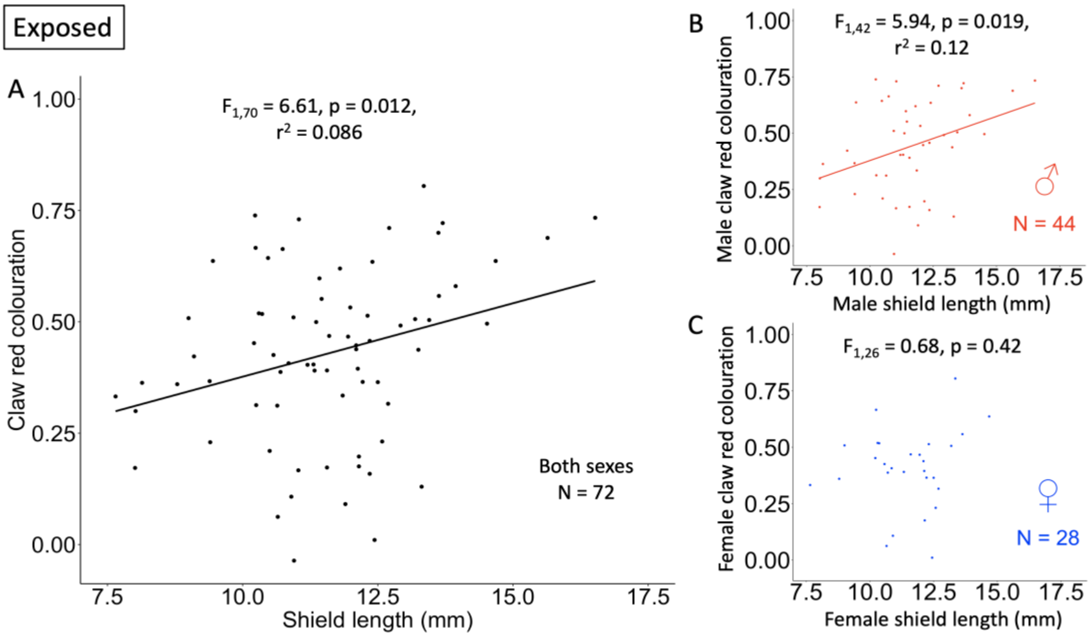

Figure 3. Linear regression of red colouration of exposed claws against overall body size (shield length in mm), including (A) both sexes (shown in black), (B) males only (shown in red), and (C) females only (shown in blue). Trendline shown when relationship was significant.

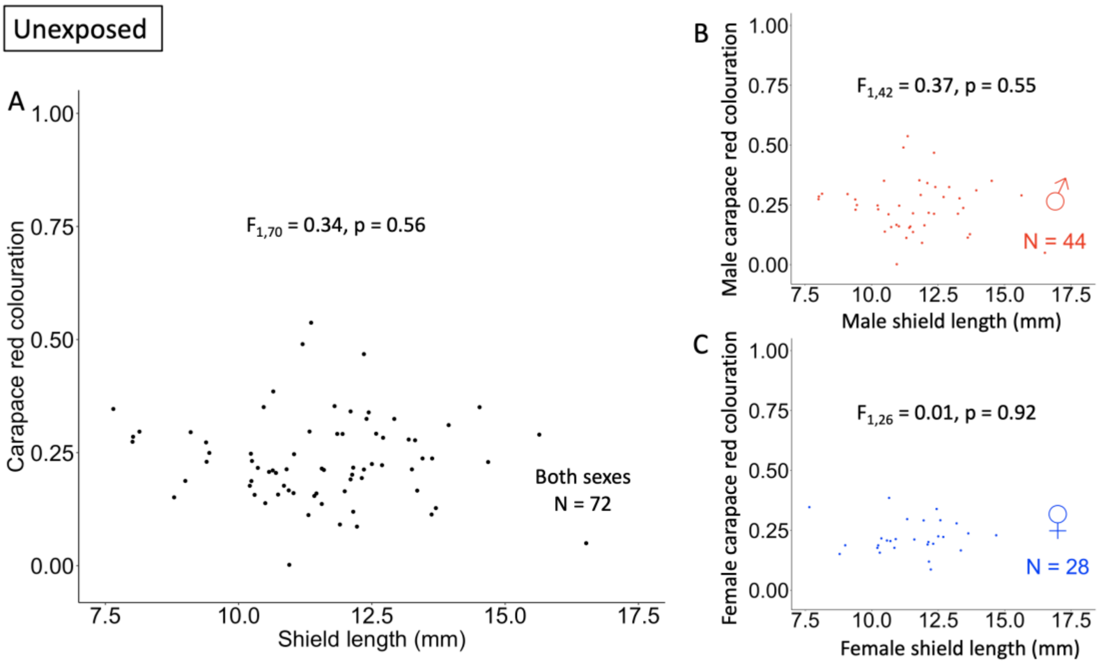

Figure 4. Linear regression of red colouration of unexposed carapaces against overall body size (shield length in mm), including (A) both sexes (shown in black), (B) males only (shown in red), and (C) females only (shown in blue).

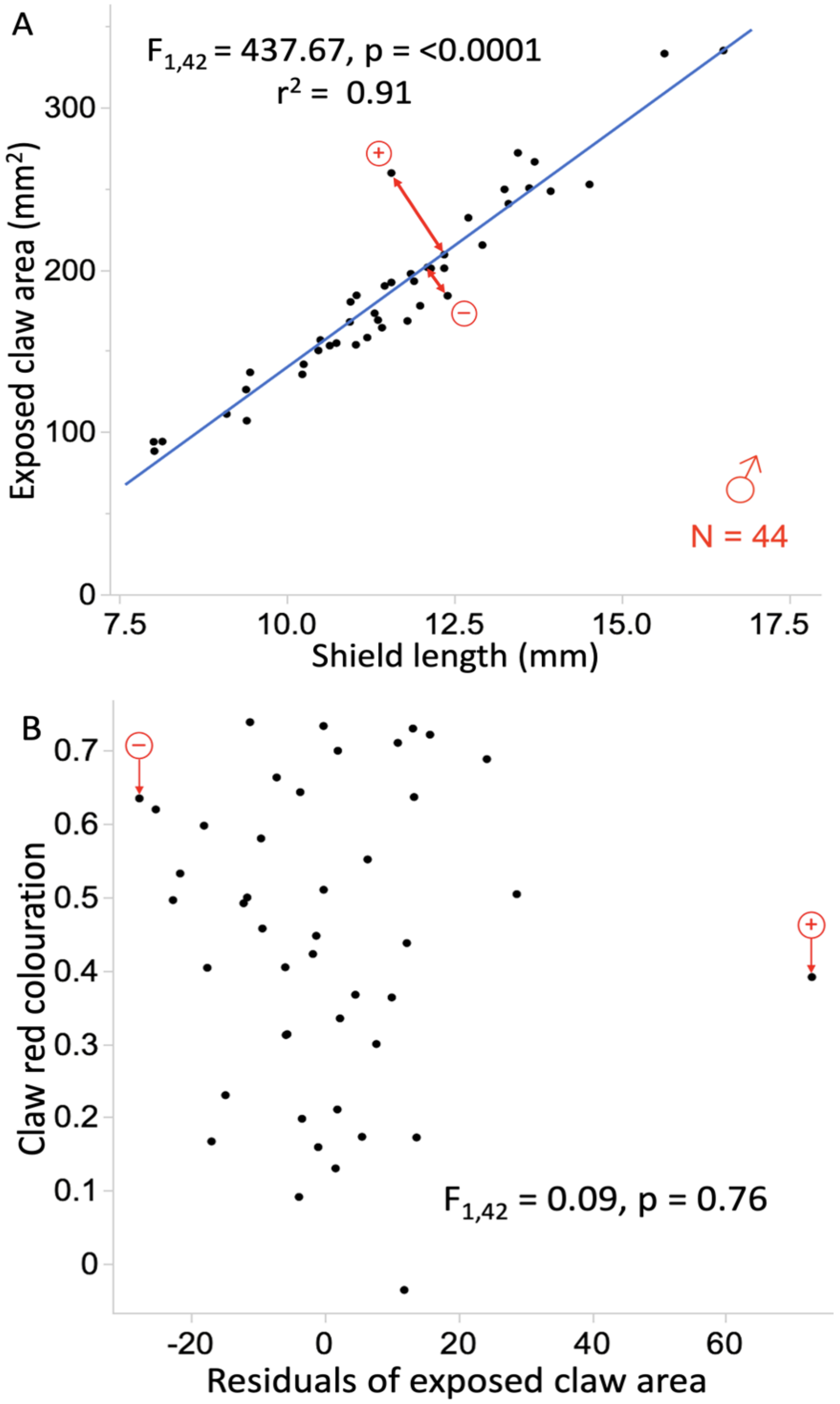

Figure 5. (A) Linear regression of exposed claw area (mm^2) against overall body size (shield length in mm) for males. Red arrows show residuals (positive and negative) for difference from the predicted line. (B) Linear regression of red colouration of exposed claws against residuals of exposed claw area. Related data points highlighted in (A) and (B) for reference.

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CHAPTER 3

Individualism versus collective movement during travel

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Abstract

Collective movement may emerge if coordinating one's movement with others produces a greater benefit to oneself than can be achieved alone. Experimentally, the capacity to manoeuvre simulated groups in the wild could enable powerful tests of the impact of collective movement on individual decisions. Yet such experiments are currently lacking due to the inherent difficulty of controlling whole collectives. Here we used a novel technique of experimentally simulating the movement of collectives of social hermit crabs (*Coenobita compressus*) in the wild. Using large architectural arrays of shells dragged across the beach, we generated synchronous collective movement and systematically varied the simulated collective's travel direction as well as the context (i.e., danger level). With drone video from above, we then tested whether focal individuals were biased in their movement by the collective. We found that, despite considerable engagement with the collective, individuals' direction was not significantly biased. Instead, individuals expressed substantial variability across all stimulus directions and contexts. Notably, individuals typically achieved shorter displacements in the presence of the collective versus in the presence of the control stimulus, suggesting an impact of traffic. The absence of a directional bias in individual movement due to the collective suggests that social hermit crabs are individualists, which move with a high level of opportunistic independence, likely thanks to the personal architecture and armour they carry in the form of a protective shell. Future studies can manipulate this level of armour to test its role in autonomy of movement, including the consequences of shell architecture for social decisions. Our novel experimental approach can be used to ask many further questions about how and why collective and individual movement interact.

Keywords: collective movement, individualism, architecture, personal armour, shells, social hermit crabs, traffic

Introduction

Collective movement is a widespread phenomenon, seen across many taxa, where groups of animals move as a single coordinated whole [1, 2]. Such instances include swarming insects, shoaling fish, flocking birds, and herds of migrating mammals. This collective behaviour is an emergent property of groups, which arises from simple, local movement rules operating at the individual level [1-3]. Selection acts on individuals to behave in ways that increase their personal fitness, with the benefits of collective behaviour typically occurring through resource acquisition (e.g., foraging in vortex-forming spadefoot toad tadpoles [4]), access to social information (e.g., habitat copying in kittiwakes [5]), or protection from predators (e.g., group defence in spiny lobsters [6]). When moving as part of a group produces a greater fitness benefit to the individual than can be achieved alone, selection will favour individuals that coordinate their activity with others, with such coordination giving rise to collective behaviour [7, 8].

In the last decade, while empirical research in the field of collective behaviour has been steadily accumulating [9], substantial advancements have occurred through theoretical work, most notably using models of computer-simulated groups [10]. Exciting strides have also been made in developing novel lab-based experimental approaches to gather finer-grained detail about individuals' movement decisions in response to others [11]. In the wild, a majority of studies of collective movement to date have focused on movements of whole, naturally behaving groups, where all or many group members are tracked [e.g., 12]. These studies have analysed the movement of individuals relative to their neighbours to infer decisions at the individual level [13, 14]. However, no studies, to our knowledge, have tested how individuals in the wild respond to experimentally-simulated group movement. Such a novel experimental approach in the wild might enable definitive tests of the causes and consequences of collective movement, linking individual decisions to group behaviour.

For example, by experimentally simulating a group of 'stand-in' conspecifics that are fully controllable and manipulatable, it would be possible to test responses of live individuals to simulated group movement. Indeed, total control of the group would allow us to examine the extent to which single individuals use social information to guide themselves, as well as how and why their social bias might differ across contexts. Some individuals' motivations to move with the group might change, for instance, depending on that individual's perceived level of threat (e.g., due to the safety in numbers inherent in selfish herding [15]). Importantly, control over the entire group would enable collective group movement to become a repeatable, standardised factor in field experiments that test single focal individuals.

Highly social terrestrial hermit crabs (*Coenobita compressus*) offer a simple, yet powerful system for studying fundamental questions about collective influence on individual decisions. Multiple crabs have been observed moving over short distances in unison, both when collectively attracted to conspecific death sites [16] and while returning to the forest at midday when beach temperatures become too hot [17]. Furthermore, these social hermit crabs are dependent upon one another for an extremely limiting resource: architecturally remodelled shells [18-20]. Without a large enough remodelled shell, an individual is unable to grow to the size necessary to reproduce, making shells pivotal to fitness [21]. At the same time, individuals must avoid being evicted by others, who may seek their own current shell. Individual crabs are highly mobile [22], carrying their shell with them as a transportable, protective home as they locomote [23]. And because only a small portion of an owner's body protrudes from its shell [24], the shell is typically all that can be seen as individuals traverse the beach landscape. Prior work has therefore successfully used shells as stand-ins for conspecifics [25], both in localised groups [26], which were collectively jostled with variable levels of commotion, and in stationary shell arrays [27], involving various fine-grained social structures. These experimental studies using shells as stand-ins have revealed that individuals are highly attracted to simulated collectives that remain in the same localised spot [17, 25-27]. However, to date, no studies have attempted to simulate coordinated, directional group travel using synchronously moving shells that replicate collective movement across the beach landscape. Such experiments could test if the synchronised movement of multiple crabs, which naturally occurs in the field, is an incidental product of entirely separate yet overlapping individual decisions; or else is an emergent property of socially-influenced decisions.

Here we take this novel approach of experimentally simulating collective movement to test the impact on individuals' movement decisions in the field. We examined whether free-roaming individuals were biased in their direction of movement due to a simulated collective, which was moved synchronously in pre-determined directions. One hypothesis is that moving with a collective confers benefits via selfish herding, which could also facilitate the transfer of social information and the acquisition of resource, including shells. If this hypothesis is true, then individuals should be highly biased by the collective, showing greater uniformity in their movement direction. Notably though, the shell that each live individual carries is also a form of personal armour and architecture [28], which offers more than adequate protection from predators [29] and which may therefore enable a sort of 'rugged individualism' [17]. Thus, as an alternative hypothesis, personal protection could render social conformity in movement unnecessary, in which case, individuals should not be biased by the collective and should instead exhibit large variation in direction, indicative of their greater freedom of individual movement.

In addition to testing these two competing hypotheses, we further investigated the potential benefits of moving with the collective across different levels of perceived risk, by experimentally testing whether increased danger (via handling of individuals) reduced their variability in direction. If personal protection is more than sufficient in the face of such danger, then even after handling, individuals should still exhibit high levels of variation in direction. Finally, even if individuals are indeed free to move in an unbiased direction of their choosing, their movement may nevertheless still be impacted by the collective due to 'traffic' [2]—since even with high autonomy, manoeuvring through a crowd could impede how far an individual can travel. We therefore tested whether an individual's displacement (linear distance moved), was impacted by the presence of the simulated collective.

Methods

Study site

Social hermit crabs (*Coenobita compressus*) were studied in Osa Peninsula, Costa Rica, at a long-term field site (Osa Conservation's Piro Biological Station), where the population has been under study since 2008 [17]. Experiments were carried out from

January to March 2019 at the beach-forest interface (Fig. 1A), an area where ‘fission-fusion’ social groupings [30] continuously form and dissolve [31] and where free-roaming individuals regularly travel [17]. All studies were undertaken during daylight hours (06:30 to 11:30 h) during periods of peak social activity.

We conducted two separate sets of experiments, both involving a similar stimulus design (below). First, to determine whether free-roaming individuals were biased in their movement decisions by a collective, we performed a set of free-roam experiments (see ‘Experiment 1: Free-roam’). The free-roam experiments were conducted directly on the beach (Fig. 1B; 8°23’39.5” N, 83°20’10.2” W). Second, to determine whether an increase in danger influenced the relative independence versus social bias in individual movement, we performed a set of handled experiments (see ‘Experiment 2: Handled’). The handled experiments were conducted on a platform (Fig. 1C; 8°23'33.2" N, 83°19'50.6" W), which was immediately adjacent to the beach and situated within the range of the crabs’ normal daily movements. All reported compass bearings are relative to magnetic North (0º) unless otherwise specified.

Stimulus design

As conspecific ‘stand-ins’, we used N = 60 *Nerita scabricosta* shells (*C. compressus*’ preferred shell species [23]), spanning a natural range of sizes (9 – 32 mm) within this population (see Table A1 and Fig. A1 in the Appendix). To create a group of these stand-ins that we could manoeuvre as a collective, each shell was affixed using epoxy to one of four strands of clear fishing line, which were each 4 m long. These lines were spaced approximately 30 cm apart on a long wooden dowel (Fig. 2A, B; Fig. 3A, B). An equal number of shells (N = 15 shells per line) were distributed randomly along the 2 m of each fishing line furthest from the dowel. To allow the experimenter to manoeuvre the stimuli, without disturbing live crabs' behaviour, another fishing line (4 m in length) was attached to the top of the dowel. With this line, the entire apparatus could be pulled by the experimenter from a distance, thereby simulating synchronised movement of the entire collective. To control for any influence the apparatus might have on focal individuals (other than that produced by the movement of the shell 'stand-ins'), the entire apparatus—dowels and fishing lines—was replicated, just without any attached shells, for use as a control (Fig. 2C, 3C).

Experiment 1: Free-roam

To test whether the movement of the collective influenced free-roaming individuals' travel direction, the stimuli were pulled across the beach at a uniform speed (1 m per min), within the natural range of the walking speed of social hermit crabs [17, 22, 23]. Each trial lasted 1 min. A total of N = 80 free-roam trials were conducted, N = 40 experimental (with the full collective, represented by all the shells) and N = 40 controls (with only the raw materials, but no shell collective). For each of the N = 80 trials, the movement of a single free-roaming focal individual was recorded.

It is not uncommon to see multiple crabs moving parallel to (or perpendicular to) the shore, since many individuals will often be collectively attracted to eviction sites, injured conspecifics, or food items, with all the attracted individuals travelling in a roughly parallel formation [16, 17]. For each trial in the free-roam experiments, the stimuli were pulled parallel to the shore (Fig. 1B), either to the right (116.1°) or to the left

(296.1º). We did not pull the stimuli perpendicular to the shore, given the substantial slope from the forest down to the ocean, which would have confounded any such comparisons. Condition (experimental or control) and stimulus direction (right or left) were selected randomly, with balanced sample sizes (N = 20 for each). To ensure there was a free-roaming focal individual, whose movement we could measure in response to the stimulus, a trial was only carried out when at least one live crab was walking within approximately 30 cm of the stationary stimulus. Then pulling was initiated.

To avoid disturbing live individuals by moving through or near the vicinity, we gathered overhead video footage of all experiments using a drone (Phantom advanced model GL300C). Drone video recorded all interactions between the focal individual and the simulated collective while the drone hovered at a height of approximately 2 m above the beach. At this height, there was no disturbance to natural behaviour or movement of the crabs, and the drone remained positioned overhead for at least 1 min prior to the start of a trial. Minor adjustments to position were then made between trials due to drone drift (i.e., slight movement of the drone due to wind).

To randomly select focal individuals for video coding, we first split an image of the starting frame of each video file into a 4 x 4 matrix, with N = 16 equally-sized sections, and then used a random number generator to choose one section (repeating this step if no crabs were present in the selected section). Second, we numbered all individuals in the selected section and again used a random number generator to select the individual.

To calculate bearings relative to magnetic North for the direction each focal crab moved, we first measured the angle of divergence (º) between the stimulus trajectory and the focal crabs' trajectory. Focal crab trajectory—a proxy for the overall direction of the crab's movement—was measured by drawing a straight line from the start-to-end position of that individual (see Fig. A2 and Vid. 1 in the Appendix for further explanation). Stimulus trajectory was measured in the same manner, using the shell closest to the focal at the beginning of the trial. Using Google Maps and the IGIS Map bearing angle calculator, we calculated the bearing of our stimuli (right and left) relative to true North (right: 114°, left: 294°). To determine bearings for our stimuli relative to magnetic North, we then used the Enhanced Magnetic Model (EMM) magnetic field calculator, provided by NOAA, to calculate the relevant declination (-2.1º) for our coordinates on the dates the experiments were carried out, subtracting this value from true North. Thus, for the free-roam experiments, the bearing of a stimulus moving to the right, relative to magnetic North, was 116.1º, and the bearing of a stimulus moving to the left, relative to magnetic North, was 296.1º. Lastly, bearings for focal crabs' directions, relative to magnetic North, could then be calculated using the new bearings of the stimuli and the angle of divergence between stimulus and crab trajectories.

To gauge the level of interaction that focal individuals had with the collective, we recorded whether or not individuals initiated contact with shells in the experimental condition. An individual was classed as having initiated contact if it climbed onto a shell or touched a shell with its claws (Vid. 2 in the Appendix). Additionally, we noted whether individuals were bumped by passing shells. An individual was classed as having been bumped if a moving shell hit it while the individual was withdrawn, stationary, or facing away from the moving shell (Vid. 3 in the Appendix).

To assess whether drone drift during experiments was a problem, we examined a random sample (N = 20) of the videos, both control (N = 10) and experimental (N = 10). We took N = 40 images from these 20 videos (i.e., two images from each video: one at the start of the 1-min trial and one at the end of the 1-min trial) and used a system wherein we marked the same two distinguishable fixed points on the landscape in each pair of images. We then overlaid the images in each pair, allowing us to see any longitudinal or latitudinal movement as well as any potential rotation of the drone. Nineteen of the N = 20 pairs of images showed virtually identical overlap of the markers, with just one image showing a minor gap between 1 of the 2 landmarks, suggesting slight rotation of the drone. We were therefore confident that drone drift was not an issue in our analyses.

All videos were coded by CD. To measure inter-observer reliability for the angle of divergence (º) between stimulus trajectory and focal crabs' trajectory (see Fig. A2 in the Appendix), a random sample of videos (N = 41 total, N = 22 of experimental and N = 19 of control) were also coded by a second observer (MP) who was naïve to the competing hypotheses. There was strong inter-observer reliability in the measurements ($F_{1,39} = 142.8$, $p < 0.0001$; $r^2 = 0.79$). Indeed, excluding a single outlier, the r^2 value was 0.995 ($F_{1,38} = 7233.6$, $p < 0.0001$). And the vast majority (N = 35) of the angles measured by both observers fell within 10º of each other.

Experiment 2: Handled

To investigate whether danger levels may mediate the impact a collective has on individual movement, we ran another set of experiments, in which focal crabs were handled prior to testing. Unlike the free-roam experiments, where individuals only interacted with conspecifics in the wild, in these handled experiments, individuals were picked up by the experimenter—a strong negative stimulus—immediately before being tested. Furthermore, we carried out the handled experiments on an artificial beach (Fig. 1A, C), involving a flat platform, which eliminated the slope of the natural beach, enabled us to precisely measure each focal individual's displacement (below), and ensured no other free-roaming individuals were present besides the single focal individual. The artificial beach consisted of a 4 x 4 m tarpaulin, topped with a layer of natural sand collected from the adjacent beach. The artificial beach thus afforded a high level of control, while still involving semi-naturalistic field conditions. The same experimental and control stimuli (see section on 'Stimulus design') were used to test focal individuals' responses in both the free-roam and the handled experiments.

Individuals in the handled experiments were collected from the wild, on the beach adjacent to the platform, shortly before the start of the experiment. A focal individual was then placed under an opaque cup in the centre of the stimulus (Fig. 3), where it remained for 1 min before being released. This 1-min buffer allowed the experimenters to leave the vicinity and get in position to manoeuvre the stimulus. The cup containing the focal individual had fishing line attached and was removed via a pulley system. At the same time, the stimulus, either experimental (N = 80 trials) or control (N = 80 trials), was pulled at a speed of 1 m per min for 1 min. Both the stimulus type (control or experimental) and direction (forest = 27°, ocean = 207°, left = 297° or right = 117°) were randomly selected prior to the start of the trial. The handled experiments were not videoed, since measurements could be directly taken in situ. At the end of each 1-min trial, the compass bearing was taken of the focal individual, based on a straight line from its start-to-end position. Also, to test whether the simulated collective affected the focal individual's travel distance, we measured the focal individual's displacement (cm) as the same straight line from its start-to-end position. Note that degrees for left and right are slightly different between the handled versus the free-roam experiments. Left and right were defined as parallel to the shoreline, which differed marginally between the two experimental sites (Fig. 1A).

Statistical analyses

To assess variability in direction of focal individuals, we calculated circular variance for each condition (control versus experimental) and analysed data separately for each stimulus direction. Circular variance ranges from 0 to 1 (with 0 meaning no variance, i.e., all individuals go in exactly the same direction, and with 1 meaning maximum dispersion in all directions, such that a mean angle cannot be described). We considered the level of variation in individual direction to be indicative of bias, with less variation signifying stronger bias. Hence, if little or no bias occurred due to the collective, then variation in individual direction should remain high across all conditions and stimulus directions.

To test for directed orientation (i.e., whether a true mean or median direction existed) within each condition, we used the Rayleigh test for any conditions that had a von Mises distribution (the equivalent of a normal distribution for circular data). For conditions with a distribution other than von Mises, we used the Hodges-Ajne test (hereafter referred to as an omnibus test). Significant p-values for the Raleigh or omnibus tests, respectively, indicate that a true mean or median exists [32]. Data for these tests were analysed separately for each different stimulus direction.

To test for differences in displacement (i.e., the absolute distance individuals moved during the trials), we ran an ANOVA model, which included the following factors: condition (with two categories: control and experimental); stimulus direction (with four categories: right, left, forest, and ocean); and the interaction between condition and stimulus direction. We used an orthogonal contrast test to specifically examine the impact of condition (i.e., control versus experimental) on displacement.

All circular statistics were calculated in R version 1.3.1056, with the exception of the omnibus tests, which were carried out in MATLAB R2020a. All analyses of displacement and inter-observer reliability were performed in JMP® Pro 15.0.0.

Ethics approval and consent to participate.

All experiments were approved by the Costa Rican Ministerio de Ambiente y Energía (MINAE).

Results

Experiment 1: Free-roam

Direction

The direction of individuals was highly variable across all conditions (Fig. 4), with circular variance ranging from 0.49 - 0.73. Neither of the two experimental conditions showed a significant orientation, and only one of two control conditions did (control to the right, Rayleigh: $\bar{x}$ = 19.03°, $\bar{r}$ = 0.51, p = 0.0039; Table 1). Thus, the direction of free-roaming individuals was not significantly biased by the movement of the collective.

Crab-stimulus interactions

Despite the absence of a significant bias in direction, focal individuals frequently initiated contact with one or more shells from the collective (60% of N = 40 experimental trials). Less frequently were individuals passively bumped by shells from the collective (20% of N = 40 experimental trials). Notably, individuals never remained withdrawn in their shell for the entire experiment. Rather, all focal individuals emerged from their shells to perceive the collective and also actively moved at some point during the experiment. Thus, although individuals' movement direction was not significantly changed, they still showed considerable engagement with the collective.

Experiment 2: Handled

Direction

Similar to the free-roam experiments, the direction of individuals in the handled experiments was variable, with circular variance ranging from 0.26 - 0.72 (Fig. 5). Only one of the four experimental conditions showed a significant orientation (experimental to the ocean, Omnibus: $\tilde{x}$ = 196°, $\bar{r}$ = 0.73, p = 0.0022). Thus, in general, the direction of handled individuals was not significantly biased by the movement of the collective. Indeed, if anything, the presence of the collective often increased variability in individuals' directions relative to the control (Table 2).

Surprisingly, three of the four control conditions showed a significant orientation (control to the right, Rayleigh: $\bar{x} = 174.11$, $\bar{r} = 0.74$, $p < 0.0001$; control to the left, Raleigh: $\bar{x} = 167.99°$, $\bar{r} = 0.57$, $p < 0.0001$; control to the forest, Omnibus: $\tilde{x} = 195°$, $\bar{r} = 0.66$, $p = 0.012$; Table 2); and the fourth control showed a similar trend in orientation, though was not significant (control to the ocean, Rayleigh: $\bar{x} = 162.45$, $\bar{r} = 0.36$, $p = 0.053$). Interestingly, of the four conditions with a significant orientation (three controls and one experimental), all their true mean or median directions fell within a narrow range (167° – 196°), close to that of the ocean (207°) (Fig. 5). It is notable that the only experimental condition that showed a significant orientation had its stimulus move in that same direction, towards the ocean.

Displacement

The displacement of handled individuals was significantly predicted by the model comprised of condition, stimulus direction, and their interaction (Two-way ANOVA: $F_{7,152} = 2.92$, $p = 0.0067$; Fig. 6). Consistent with the traffic hypothesis, individuals' movement was reduced in the presence of a collective, with individuals achieving shorter displacements in experimental versus control conditions (orthogonal contrast: $F_{1,152} = 10.79$, $p = 0.0013$). While stimulus direction alone did not predict displacement ($F_{3,152} = 1.12$, $p = 0.34$), the interaction between stimulus direction and condition was marginally significant ($F_{3,152} = 2.80$, $p = 0.042$). In particular, three of the four stimulus directions (right, left, and forest) showed a pattern of shorter displacement in experimental versus control conditions (Fig. 6). The only stimulus direction that contradicted this trend was in the same direction (ocean) that crabs had previously shown a tendency to move (see above section on direction).

Discussion

This study pioneered a novel technique of simulating collective group movement in the wild within a model system. Surprisingly, individuals' directions were not significantly biased by the collective, despite strong uniformity in the collective's movement. Our experiments instead revealed considerable variance in individuals' directions across conditions and contexts. Individuals only conformed to the direction of the collective when the experimental stimulus was moving in the direction of the ocean, the same direction crabs were inclined to move in control conditions. Thus, we can conclude that travelling collectives do not significantly influence individual's directional decisions in either context tested (free-roam or handled). Instead, social hermit crabs move with a high level of independence, with each crab, in effect, being a 'rugged individualist' [17].

Many animals live in groups as a collective, but largely travel alone as individuals [7, 8]. In social hermit crabs, for example, lone individuals are highly attracted to localised stationary groups of conspecifics [17, 25-27, 31]. These social groups represent sites where coalitions [33], social evictions [25], and hence valuable shell-exchange opportunities occur [34]. Social evictions and shell exchanges are unlikely to occur though if individuals are actively travelling, which may explain why the collective of travelling shells in our experiments had little impact on individuals' movement directions. In stark contrast, when the same shells are jostled at fixed sites, then free-roaming individuals are strongly attracted and use the commotion to orient toward established groups at stable locations [26]. Free-roaming individuals may therefore have less incentive to ‘go with the flow’ (i.e., travel along the path of a collective headed in a uniform direction), particularly if by going in their own independent direction (which may even be against the flow) the individual can reap better opportunities elsewhere. Thus, social hermit crabs can attend strongly to social cues and join stationary social groups, yet lack the tendency to follow synchronised groups travelling in a coordinated direction. Such collective, synchronised travel may be less relevant in species where the benefits of sociality are experienced at specific locations in space and time, rather than on the move.

Future experiments could try simulating ever more realistic stand-ins (e.g., by adding olfactory cues [16]; or additional visual cues, such as reanimated models [21] or 3D printed replicas of crabs and shells [35]), and perhaps the level of social bias in response to collective movement might increase. Likewise, many variables of the collective can be experimentally altered (e.g., its speed and the relative synchronisation of movement), with some movements (e.g., less-than-perfect synchrony) potentially better mimicking natural movements observed in the field. Increasing the realism of the movement of the collective in such ways, might increase bias in individual responses. However, our findings of a high level of independence in individual movement direction are consistent with the personal armour and architecture hypothesis, namely, that shells nullify the risk of predation. This armour hypothesis could be further tested by enhancing or reducing the size or quality of individuals’ shells (e.g., [36]). If greater protection confers greater autonomy, then individuals placed in ill-fitting or damaged shells should show an increased bias to move with the collective. Such a bias could arise both due to the individual desperately seeking out shell opportunities as well as gaining safety in numbers. Understanding how an individual's personal safety shapes its movement patterns may extend to numerous other armoured species [37, 38], many of which are solitary or only occasionally move in collectives. The same logic of personal safety may apply to species that grow large enough such that predation becomes irrelevant [39]. Additionally, many invasive species experience enemy release when they reach a new habitat [40]. If perceived vulnerability changes movement decisions, then once species experience enemy release, they may no longer need to move as a collective. Understanding such transitions from collective to independent movement could aid in management of invasive species.

Interestingly, despite individuals' independence in direction, our findings suggest that being surrounded by a gauntlet of collectively moving shells can constrain individual displacement. Reduced displacement could occur for multiple reasons: (1) individuals may be side-tracked if assessing passing shells; (2) individuals may be disoriented by all the surrounding movement; or (3) individuals may need to pause on their route to wait for gaps in traffic. Future experiments could tease apart these non-mutually exclusive explanations. If shell assessment is a main driver of decreased displacement, then time spent assessing shells should correlate negatively with displacement. If disorientation explains reduced displacement, then individuals may either freeze amid the collective or they may move with greater tortuosity during experimental versus control conditions. If traffic is to blame, then forward movement of focal individuals should be most likely when there are gaps in traffic and not when an individual's route is obstructed by a shell. This traffic hypothesis could be further tested by increasing the size of gaps between shells within the collective, determining if forward movement, and ultimately displacement, thereby increases.

The experimental capacity to control many aspects of a collective offers great power for testing causation between group and individual movement. Future experiments can test what properties of the collective influence individuals' zones of attraction, repulsion, and orientation, all properties that determine an individual's alignment or lack thereof with group members [41]. For instance, individuals may be more attracted to similarly sized or slightly larger individuals, as this size-specific attraction could put them in prime positions for taking advantage of shell vacancies [34]. Hence, whether biases arise in individuals' directional movements could depend both on the size of shells in the collective and the size of the focal individual. Additionally, in further iterations we could test if such bias is impacted by the focal individual initiating contact versus being bumped by members of the collective, as well as the influence of general background densities of conspecifics. A wide variety of experimentally-generated, emergent patterns of the collective could be used to further test possible consequences for individual movement. Thus, our study system and experimental technique might serve as a valuable wild counterpart to laboratory experiments and theoretical simulations on collective movement.

Aside from the collective itself, another major variable that could be experimentally manipulated to assess its effects on individual movement is the environment. In this study, although we manipulated external danger (via handling), we did not focus on the physical environment. Yet, local topography could be important [42]. Indeed, we saw hints of the importance of environment in our handled experiments, with orientation consistently being ocean-bound. Beyond moving back and forth from the beach [22], where they socialise [17] and forage [43], to the shade of the forest, where they rest and shelter from the heat at mid-day [23], the patterns of microscale movements in *C. compressus* are largely unknown. A combination of marker-less video tracking and deep learning video analyses could be a valuable next step in garnering information on microscale movement in this species. Such monitoring would allow us to track many individuals' movements simultaneously, thereby shedding light on general patterns of movement within and between fission-fusion groupings, as well as how these movement patterns vary across different landscapes. The role of environmental topography on movement behaviour is vital to elucidate, as environments can change dramatically over space and time [10]. Thus, understanding such environmental influences will enhance predictions for animal movement models.

At the macroscale, migration is perhaps the most fascinating link between individual and collective movement [44, 45]. However, many questions regarding social bias in migration remain [reviewed in 46]. For example, a major outstanding question is the extent to which mass migrations involve innate pre-set migratory routes [e.g., 47, 48] versus widely shared social information [e.g., 44, 49], the latter of which could help fine-tune movements, particularly for novice individuals. Interestingly, the focal species of this study (*Coenobita compressus*) has a sister species (*Coenobita clypeatus*), which carries out a synchronous annual migration that can surpass 5 km [50]. This migration moves from inland areas, often atop mountains, down to the sea, where females release their eggs [51]. The number of potential routes from land to sea are staggering due to the vast number of watersheds, which likely makes fully pre-programmed routes impractical.

Social information might be highly valuable in this context. Thus, even if individual crabs are fully protected by the armour and architecture of their shells, and hence capable of independent movement, these annual migration events might provide a biological context in which social bias is more likely to manifest.

Conclusions

We conclude that collective, synchronised travel may be less relevant in species like social hermit crabs, where the benefits of sociality are experienced at specific locations in space and time, rather than on the move. Furthermore, personal architecture and armour, in the form of the protective shells carried by individuals, appear to enable individuals to have a high level of independence in their movement decisions, especially in their direction of travel. Yet even with this autonomy of movement, the simulated collective still impacted how far individuals were able to travel, likely based on the constraints of traffic or other mechanisms. Future experiments can utilise this novel technique—simulating collective group movement in the wild—to test how and why a range of other variables might impact individuals' decisions, including collective-level variables (e.g., the relative speed and synchrony of traffic), as well as individual-level variables (e.g., the individual's shell architecture), and surrounding environmental variables (e.g., landscape features and migration contexts).

Acknowledgements

We thank all members of the Laidre lab, including Nick Funnell, Jakob Krieger, Elliott Steele, and Sarah Smith, as well as Osa Conservation staff, including Marina Garrido, for assistance in the field. We thank Jeff Kerby for teaching the Laidre lab to use drones.

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Tables

Table 1. Movement patterns of free-roaming crabs exposed to control vs experimental stimuli. Results include: Circular variance, a measure of circular spread of the data points; mean/median bearing direction reported in degrees (°) across all individuals; Rayleigh test for significance of mean direction (R), or omnibus test for significance of median direction (O); Data separated by stimulus direction (Right = 116.1°, Left = 296.1°). Significant values are in bold.

	CONDITION	**SAMPLE SIZE**	**CIRCULAR VARIANCE (1-$\bar{r}$)**	**DEGREES (º)** MEAN ($\bar{x}$) / MEDIAN ($\tilde{x}$)	**RAYLEIGH (R)/ OMNIBUS (O) P VALUE**
RIGHT	Control	20	0.49	$\bar{x}$: 19.03	**(R): 0.0039**
	Experimental	20	0.73	$\tilde{x}$: 116.1	(O): 0.59
LEFT	Control	20	0.70	$\bar{x}$: 40.33	(R): 0.17
	Experimental	20	0.64	$\bar{x}$: 3.93	(R): 0.076

Table 2. Movement patterns of handled crabs exposed to control vs experimental stimuli. Results include: Circular variance, a measure of circular spread of the data points; mean/median bearing direction reported in degrees (°) across all individuals; Rayleigh test for significance of mean direction (R), or omnibus test for significance of median direction (O); Data separated by stimulus direction (Right = 117°, Left = 297°, Forest = 27°, Ocean = 207°). Significant values are in bold.

	CONDITION	**SAMPLE SIZE**	**CIRCULAR VARIANCE** $(1-\bar{r})$	**DEGREES (º)** MEAN ($\bar{x}$) / MEDIAN ($\tilde{x}$)	**RAYLEIGH (R)/ OMNIBUS (O) P VALUE**
RIGHT	Control	22	0.26	$\bar{x}$: 174.11	**(R): <0.0001**
	Experimental	18	0.66	$\bar{x}$: 159.21	(R): 0.12
LEFT	Control	21	0.43	$\bar{x}$: 167.99	**(R): <0.0001**
	Experimental	19	0.72	$\bar{x}$: 166.36	(R): 0.23
FOREST	Control	15	0.34	$\tilde{x}$: 195	**(O): 0.012**
	Experimental	25	0.67	$\bar{x}$: 204.13	(R): 0.068
OCEAN	Control	22	0.64	$\bar{x}$: 162.45	(R): 0.053
	Experimental	18	0.27	$\tilde{x}$: 196	**(O): 0.0022**

Figures

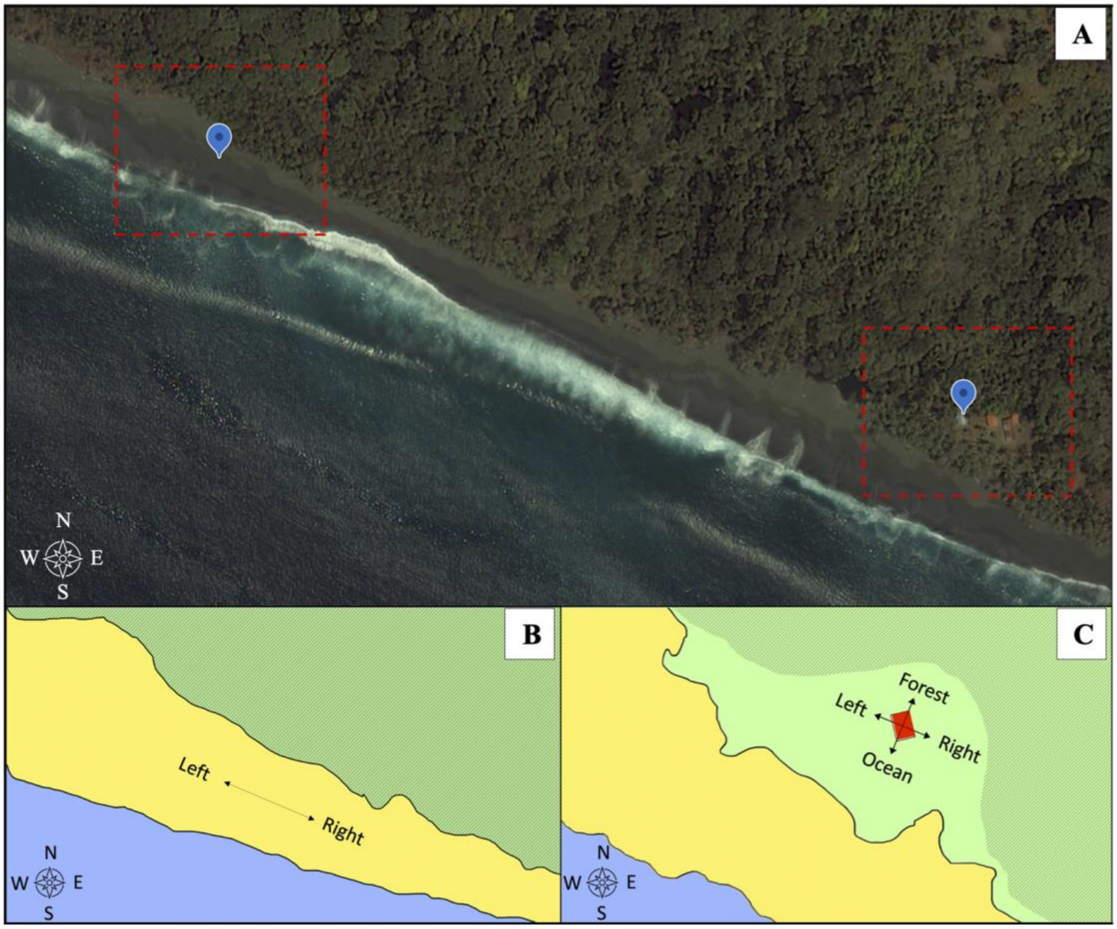

Figure 1. Study site and experimental areas. (**A**) Satellite view of study site: a section of Piro beach, Osa Peninsula, Costa Rica. Dashed red squares indicate areas where experiments were carried out and schematic versions are shown below in (**B**) and (**C**) (Satellite image: created using Google Earth Version 9, https://earth. google.com/). (**B**) Overhead view of the section of the beach where free-roam experiments were carried out. Arrows denoting left and right correspond to stimulus directions during free-roam experiments. (**C**) Overhead view of the beach-forest interface where the handled experiments were carried out. Arrows denoting left, right, forest, and ocean correspond to stimulus directions during handled experiments. The solid red box represents the platform on which the artificial beach was created. For (**B**) and (**C**), environment is color coded: blue = ocean, yellow = beach sand, dark green = rainforest, light green = open grassy area with sparse trees. Compass in the bottom left of each panel shows cardinal directions.

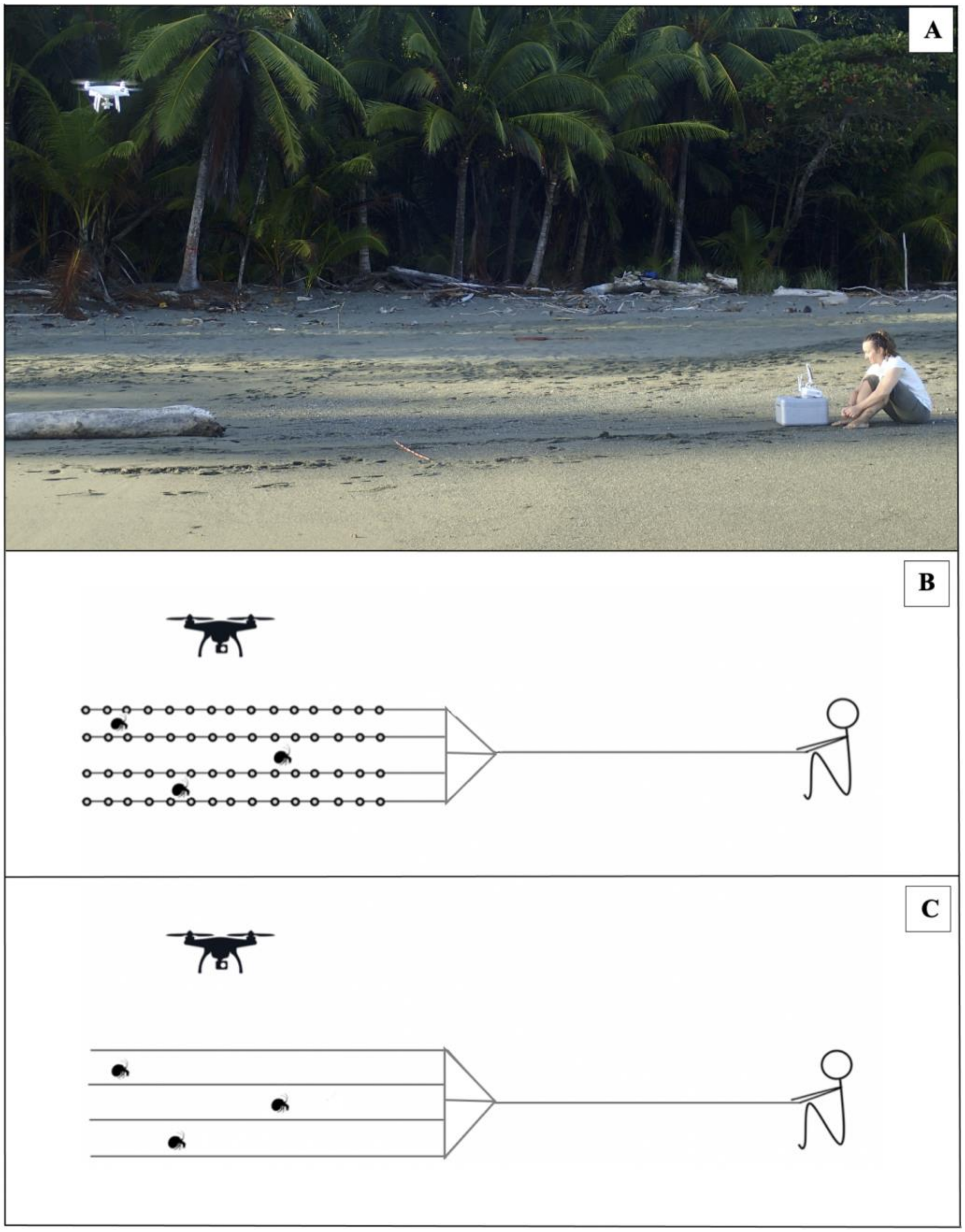

Figure 2. Free-roam experiments: stimuli and experimental design. (**A**) Photograph of a free-roam experiment in progress, with a drone hovering above and one of the authors (CD) pulling the simulated collective (Photo: Jakob Krieger). Schematics of stimuli are shown in B and C, with N = 3 free-roaming crabs also pictured. (**B**) Experimental stimuli: consisting of N = 60 shells arranged in four lines of fifteen shells each, attached to clear fishing line and fixed to a wooden dowel. (**C**) Control stimuli: four empty lines of clear fishing line, fixed to a wooden dowel. An experimenter moved the stimuli from a distance, by pulling another clear fishing line along an open strip of sandy beach in the presence of free roaming crabs. Each experiment was video recorded from above by an overhead drone.

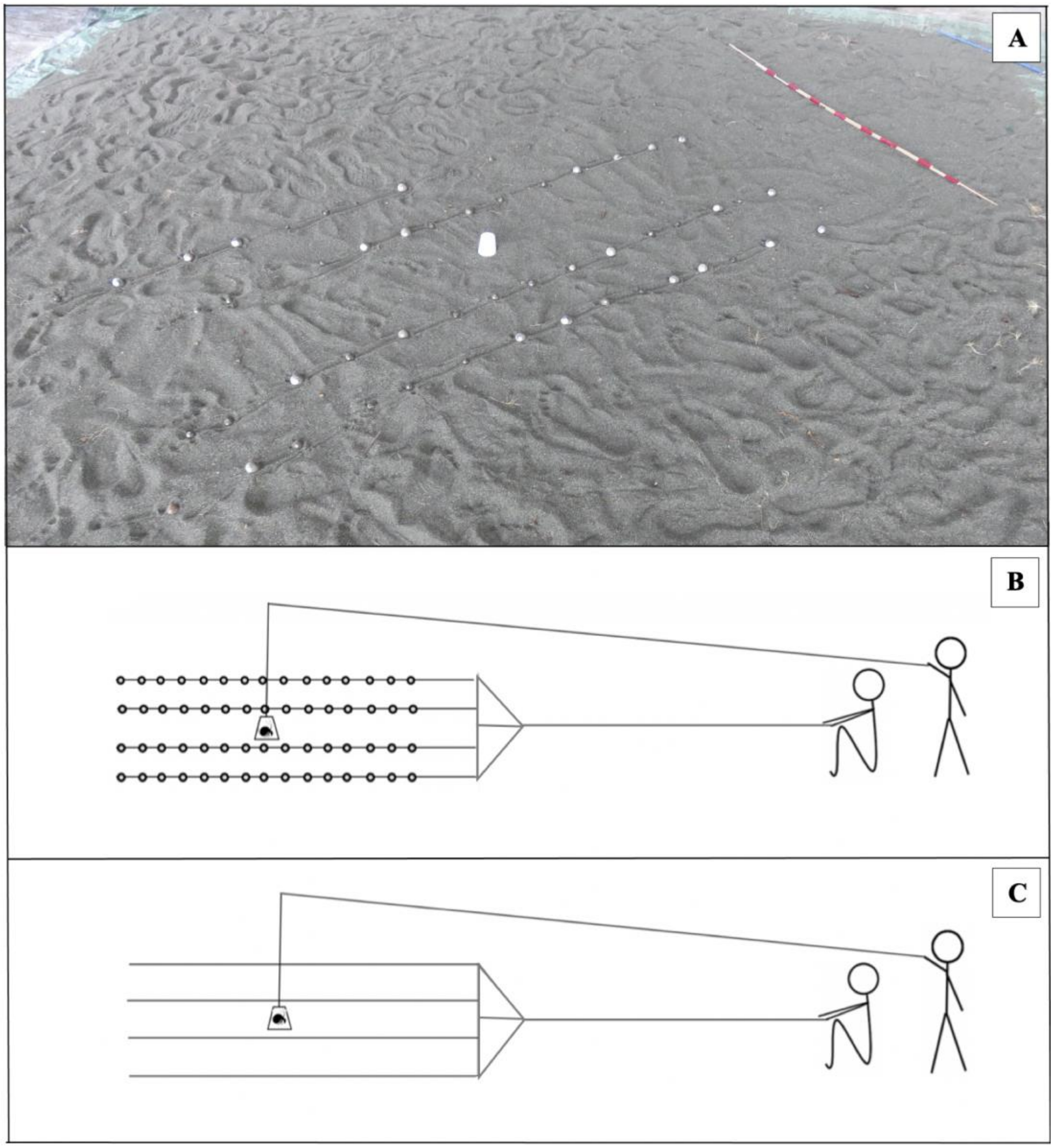

Figure 3. Handled experiments: stimuli and experimental design. (**A**) Photograph of the artificial beach created on a platform adjacent to the natural beach (Photo: Mark Laidre). Photo shows experimental stimulus and an opaque plastic cup in the center, under which a focal crab was placed prior to the start of each experiment. Schematics of stimuli are shown in (**B**) and (**C**). (**B**) Experimental stimuli: consisting of 60 shells arranged in four lines of fifteen, attached to clear fishing line and fixed to a wooden dowel. (**C**) Control stimuli: four empty lines of clear fishing line, fixed to a wooden dowel. The cup was removed by one experimenter from a distance via an attached clear fishing line on a pulley system; the stimulus was then maneuvered by a second experimenter, also from a distance, via another clear fishing line.

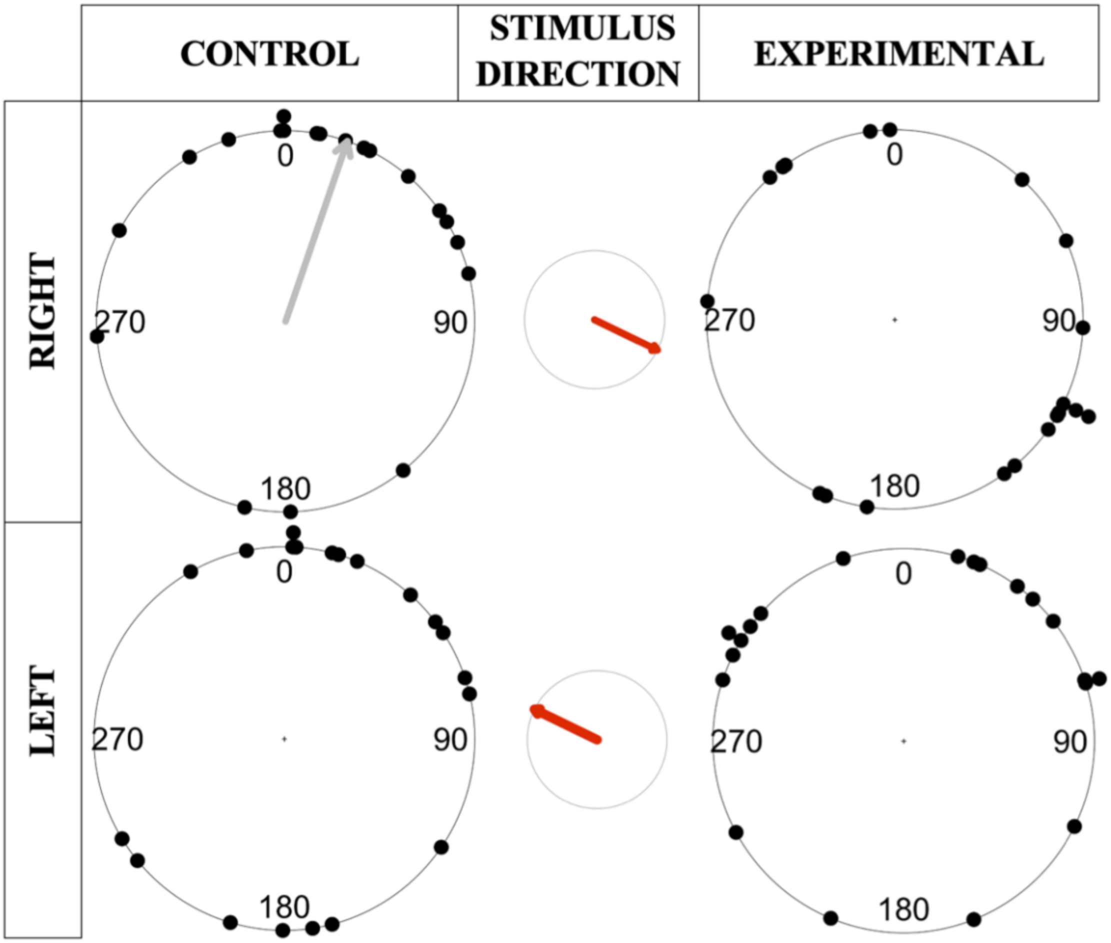

Figure 4. Circular plots of the directions free-roam crabs moved in control vs experimental conditions. Plots display the compass bearing direction of individual focal crabs (each black dot represents a single crab). Data are separated by condition (control or experimental) and stimulus direction (left or right). The red arrow in the center circle displays the stimulus direction. Grey arrow shows mean direction when a significant orientation existed (see Table 1).

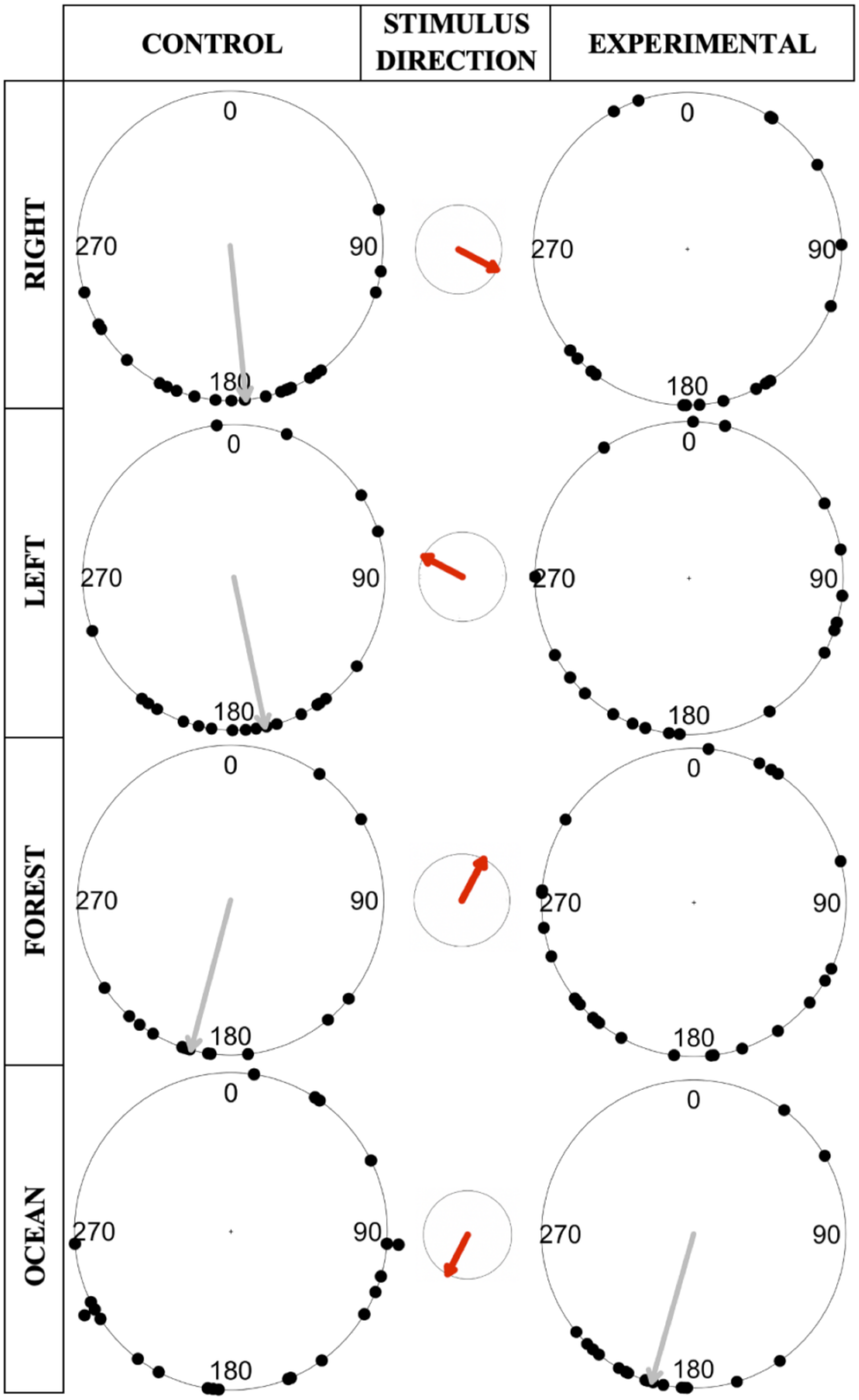

Figure 5. Circular plots of the directions handled crabs moved in control vs experimental conditions. Plots display the compass bearing direction of individual focal crabs (each black dot represents a single crab). Data are separated by condition (control or experimental) and stimulus direction (left, right, forest, or ocean). The red arrow in the center circle displays the stimulus direction. Grey arrows show mean/median directions when a significant orientation existed (see Table 2).

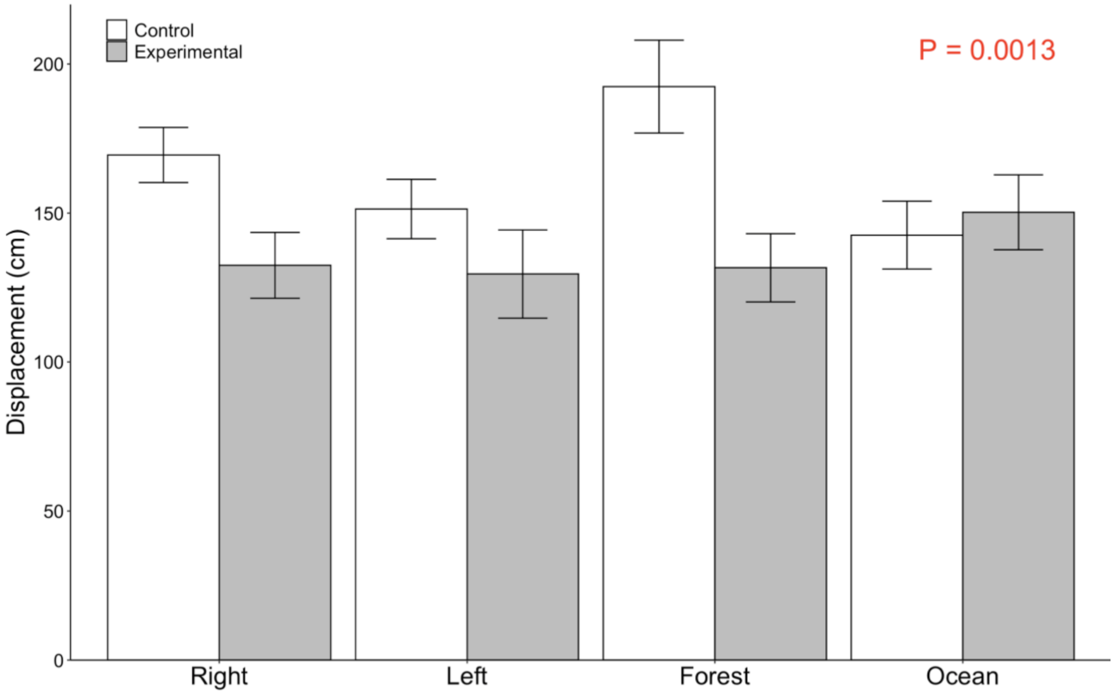

Figure 6. Displacement of handled crabs in control vs experimental conditions. Displacement (Mean ± SE in cm) is shown by condition (control or experimental) and stimulus direction (left, right, forest, or ocean). P-value indicates orthogonal contrast of control versus experimental.

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Appendix

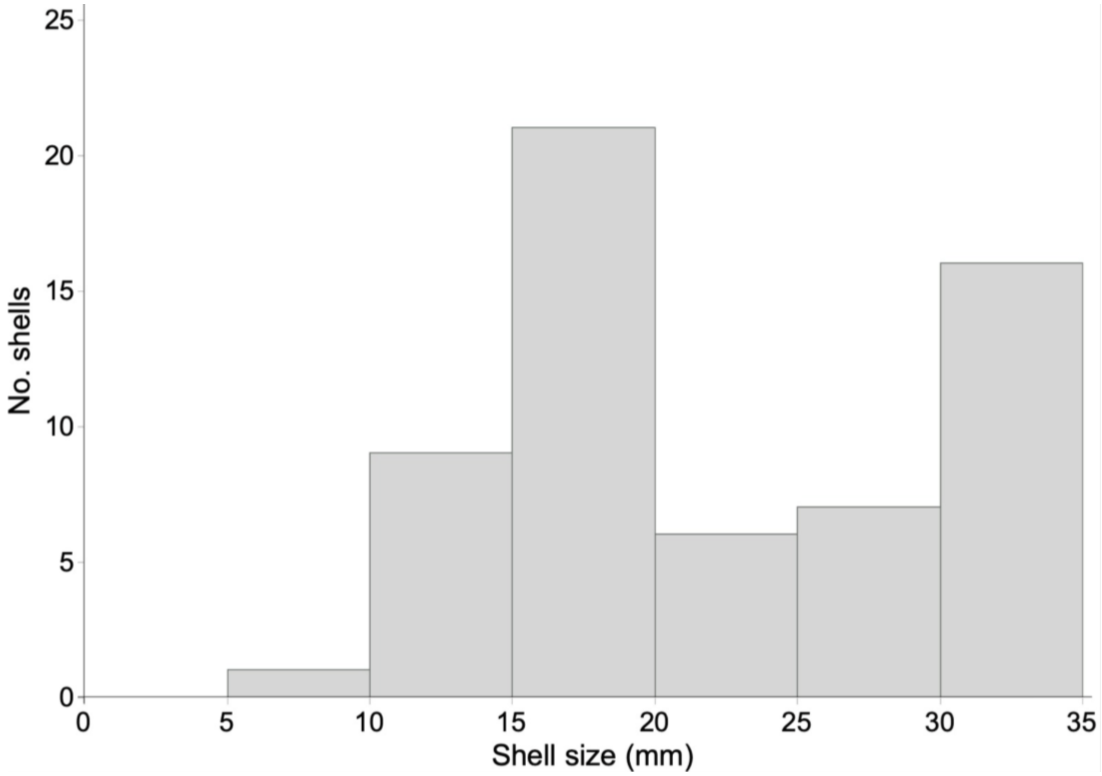

Fig. A1. Shell-size distribution (in 5 mm bins of shell diameter) for experimental stimulus.

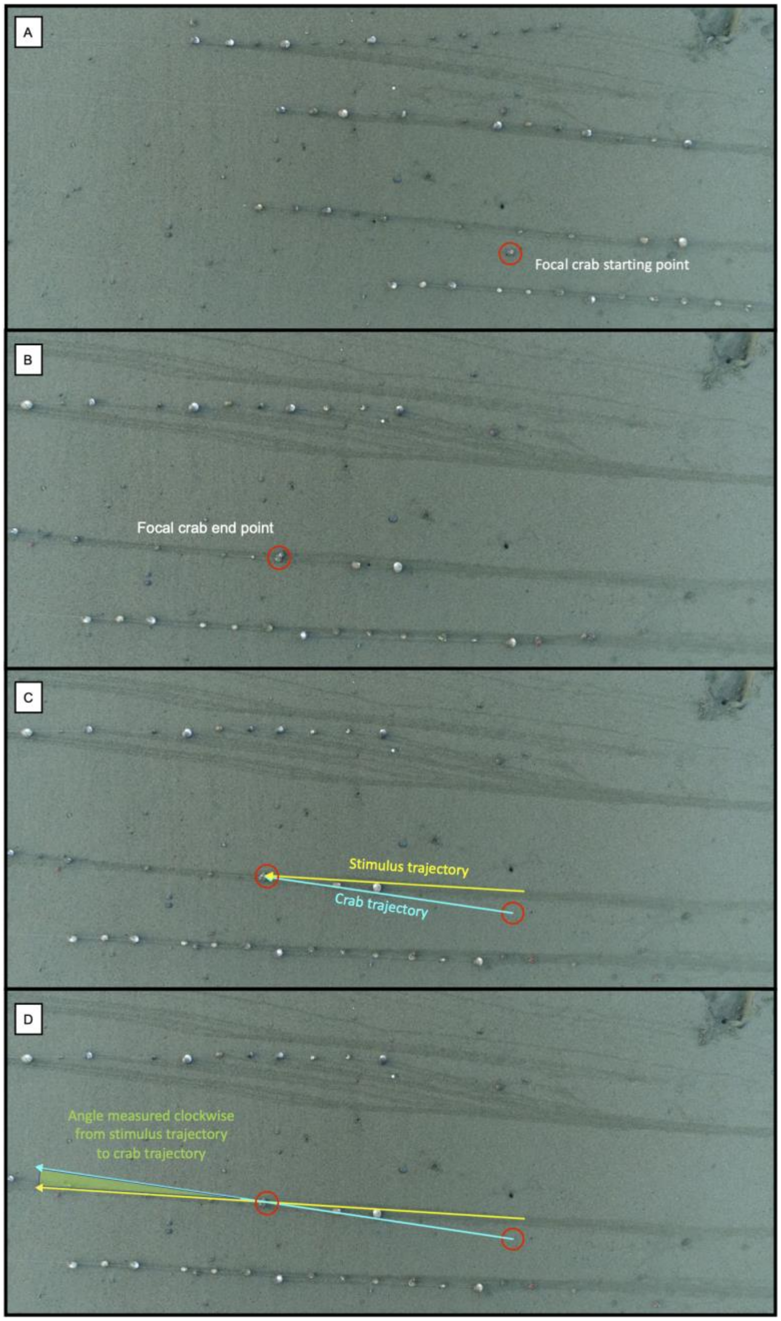

Fig. A2. Method of calculating angle of divergence (in degrees) between stimulus trajectory and focal crab trajectory. Focal crab trajectory was taken as a straight line, drawn from the crab's starting point (red circle in panel A) to its end point (red circle in panel B). When the start and end points were connected (panel C), it showed the focal crab's trajectory (blue line) relative to the stimulus trajectory (yellow line). The angle between these lines (shaded area in panel D) was then measured in a clockwise direction from the stimulus trajectory to the focal crab's trajectory. For controls, the clear fishing lines were not always distinguishable in the video recordings, so the overhead drone was oriented such that the stimulus trajectory was always horizontal across the center of the video.

Table A1. Shell sizes (mm) arrayed for experimental stimulus. Fifteen shells per fishing line and four fishing lines in total, with shell sizes listed at their position along each line.

SHELL	**SHELL SIZE (MM)**			
	LINE 1	LINE 2	LINE 3	LINE 4
1	12	30.5	29.5	30
2	10	29.5	13.5	31.5
3	9	18	31	16.5
4	17	30	17.5	30
5	12	18	19.5	29
6	17.5	20	31	17
7	15	27.5	22.5	24
8	31	19	20.5	31
9	10	32	17.5	28
10	17	31	19	14
11	10	13.5	27	17
12	30.5	31	20	15
13	19	16	31	31.5
14	31	19	19.5	28
15	17	13	17	23

Videos

Video 1. Drone video from a free-roam experiment, showing a focal crab's start and end point, as well as the focal crab's trajectory relative to the stimulus trajectory. The video can be viewed at https://doi.org/ 10.1038/s41598-022-11469-1.

Video 2. Drone video from a free-roam experiment, showing a focal crab initiating contact with one of the passing shells that was part of the simulated collective. The video can be viewed at https://doi.org/ 10.1038/s41598-022-11469-1.

Video 3. Drone video from a free-roam experiment, showing a focal crab being bumped by one of the passing shells that was part of the simulated collective. The video can be viewed at https://doi.org/ 10.1038/s41598-022-11469-1.

CHAPTER 4

Experimentally-seeded social information in the wild: costs to bearers and benefits to receivers

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Doherty C.T.M. and Laidre M.E. Experimentally-seeded social information in the wild: costs to bearers and benefits to receivers.

Abstract

Conspecifics can provide social information about the presence or absence of certain features of the surrounding environment, such as predators or food resources. Attending to social information may therefore benefit receivers, and certain types of information may even be worth following. Yet, bearing social information may also be costly, particularly if social information increases the likelihood of close-range interaction with non-kin. Here, we experimentally-seeded social information in the wild onto focal individuals of the social hermit crab (*Coenobita compressus*), testing (1) the 'benefits to receivers' hypothesis, which predicts that receivers will use social information to orient towards valuable resources, and (2) the 'costs to bearers' hypothesis, which predicts that bearers of social information will experience direct or indirect costs due to interaction with receivers. Our results support both hypotheses. Naïve individuals followed focal individuals bearing chemical-based social information about a food resource more often than other, less attractive social information. Furthermore, bearers of social information about a food resource incurred direct costs (being flipped more frequently) and indirect costs (achieving shorter displacements) versus bearers of other, less attractive social information. We conclude that experimentally-seeded social information in the wild conferred both benefits to receivers and costs to bearers. The direct and indirect costs of bearing social information, revealed here, highlight the importance of considering costs to bearers more generally in studies of social information use.

Keywords: social information, costs, benefits, bearers, receivers, social hermit crabs

Introduction

A major goal of behavioural ecology is understanding how costs and benefits are distributed across individuals in variable social contexts. Social animals (Ward and Webster, 2016) provide rich opportunities for such research, since they often have access to social information (Sumpter, 2010). Social information is any information that individuals obtain from conspecifics (Danchin et al., 2004), and can take the form of signals (Otte, 1974; Maynard Smith and Harper, 2003; Searcy and Nowicki, 2005) or cues (Bradbury and Vehrencamp, 2011; Stevens, 2013). Importantly, much of social information is not active signalling, but rather passive cues given off by individuals when performing their normal activities. For such social information to be transmitted it requires both a bearer and a receiver. For the receiver, it may pay to attend to social information borne on the body or breath of conspecifics, as this can provide information about aspects of the environment, such as presence or absence of predators or food. A prime example is found in rats (Galef and Stein, 1985; Galef, 1993) and other mammals (Laidre, 2009), which smell the breath of conspecifics and thereby learn what foods are safe to eat. Thus, specific chemical cues, once paired with a conspecific, can generate social information and ultimately produce responses in receivers that are different from responses to the chemical cue or conspecific alone.

While receivers may occasionally incur costs by using social information, for example through competition (Kohles et al., 2022), copying other individual's mistakes (Smith et al., 1999), or through misinformation (Rieucau and Giraldeau, 2009), the majority of studies suggest that social information is beneficial. Social information can be particularly useful when searching for resources that are ephemeral and unpredictable over space and time, such as food patches (Torney et al., 2006; Kohles et al., 2022), or when avoiding predators (Tóth, 2021). One early hypothesis, the 'information centre hypothesis' (ICH; Ward and Zahavi, 1973), proposed the importance of following individuals that bear social information about foraging success. However, there have been few tests in systems in the wild that support this hypothesis (Brown, 1986; Wilkinson, 1992), and most studies have also been solely observational. Nevertheless, following may be the most basic and essential way that receivers can respond to social information, and many contexts exist where it may pay to follow a bearer of social information. For instance, bearers of social information may present opportunities for stealing leftovers of a resource that the bearer is still carrying (Davis and Dill, 2012); or the bearer may be returning to the resource (Wilkinson, 1992), effectively leading the way. Broadly, we have yet to disentangle when following may be beneficial for receivers of social information, and our understanding would be greatly advanced with experimental tests in wild populations.

Notably, because bearing social information can be a by-product of normal behaviour, it is often assumed that the cost of bearing social information is negligible. Yet, particularly if social information is borne on the body or breath of an individual, it may increase the risk of having leftover resources stolen. Furthermore, passive cues that are gathered by receivers via chemical or tactile modalities often necessitate close-proximity (e.g., Galef and Stein, 1985; Laidre, 2009; O'Mara et al., 2014), so potentially substantial costs to bearers could be associated with close-range physical encounters, especially with non-kin or strangers. Such costs might include increased exposure to pathogens (Lorch et al. 2011) and parasites (Lucatelli et al., 2021), being forced to circumvent conspecific traffic (Doherty and Laidre, 2022), and of course, the inherent increased risk of injury or aggression from receivers (Innocent et al. 2011). These potential costs to bearers of social information have rarely been tested experimentally, yet the nuanced ways bearers might incur costs merit further investigation.

Social hermit crabs (*Coenobita compressus*) frequently interact with non-kin in the wild (Doherty and Laidre, 2020), including in highly competitive (Laidre, 2018) as well as cooperative (Laidre, 2021) ways. One form of social interaction involves chemo-tactile sensing at close range via antennal contact (Fig 1a), which is a mechanism for gathering potentially useful social information about the environment from conspecifics. Importantly, one of the highly sought-after resources in this system are architecturally remodelled shells, which can also only be obtained from conspecifics during close-range interactions (Laidre, 2010, 2012, 2014). With any of these close-range interactions comes increased risk of eviction and even death, which means gathering social information may be highly costly. From an experimental perspective, seeding social information in this system could be achieved by dousing specific individuals in ecologically relevant chemicals, then monitoring ensuing social interactions and their consequences. For example, coconut milk signifies a valuable food resource (Laidre, 2013), and when placed on the surface of a conspecific effectively becomes social information with a positive valence. In contrast, water is, in effect, neutral. And finally, mammal urine signifies a potential predator, so when placed on a conspecific would provide social information with an ambivalent valence: such a predator cue denotes both the risk of being eaten by a predator as well as an opportunity, since if the predator kills another conspecific, it’s left behind shell becomes a valuable resource (Valdes and Laidre, 2019).

The inherently unpredictable nature of ambivalent information should make it less attractive to receivers than positive social information. By pairing each of these different chemical cues with conspecifics, experiments could effectively seed different types of social information, testing differential costs and benefits to bearers and receivers.

Here we experimentally-seeded chemical-based social information onto individuals in the wild and measured the impact this social information had on both bearers and receivers. We tested two hypotheses: (1) the ‘benefits to receivers’ hypothesis, which predicts that receivers will use social information to orient towards valuable resources; and (2) the ‘costs to bearers’ hypothesis, which predicts that bearers of social information will experience direct or indirect costs due to interaction with receivers. We used positive, neutral, and ambivalent chemical stimuli, thus creating different types of social information that should change these relative costs and benefits. In particular, for the ‘benefits to receivers’ hypothesis, naïve individuals should change course and follow focal individuals bearing positive social information more often than those bearing neutral or ambivalent social information. And for the ‘costs to bearers’ hypothesis, focal individuals bearing positive social information should be physically harmed more by receivers and achieve shorter displacements compared to focal individuals bearing neutral or ambivalent information. Broadly, our study suggests that experimentally-seeded social information in the wild can generate both benefits to receivers and costs to bearers.

Methods

Study site

We conducted observations and experiments on highly social terrestrial hermit crabs (*Coenobita compressus*) from February to March 2022. All observations and experiments were carried out in the wild at the beach-forest interface of a long-term study site (Laidre 2010) in Osa Peninsula, Costa Rica (8°23'55.6"N 83°20'52.8"W), where the species occurs naturally in abundance and displays high social activity levels. All data were collected by the same individual (CD) during daylight hours (05:00 -16:00).

Antennal contact during natural encounters

To quantify how frequently individuals were gathering chemo-tactile social information via antennal contact we carried out focal and behavioural sampling. For focal sampling, the observer stood stationary and used binoculars from > 3 m distance to observe specific, randomly selected focal individuals on surrounding beach. Each focal individual was observed for 5 min (with N = 20 focal individuals observed across 10 days). For behavioural sampling, a similar methodology was used, with each observation also lasting 5 min: instead of a specific focal individual being chosen, the observer sampled the entire surrounding area through binoculars for any instances of two individuals more than three body lengths apart, where one or both individuals were approaching the other head on, so that both individuals in the pair had equal opportunity to make antennal contact. Behavioural sampling was likewise carried out across 10 days (N = 20 5-min observations), yielding a cumulative 100 minutes of sampling. For both focal and behavioural sampling, we recorded instances in which one crab came within a body length of another crab, which itself originated more than three body lengths away (Fig. 1a). When two individuals came within a body length of each other, this represented an encounter, and we then recorded whether antennal contact (i.e., one or more of an individuals antennae makes contact with any part of the other individual, at any time during the encounter, regardless of who initiates contact) was made by just one individual, both individuals, or neither individual. We classified any contact by one or both individuals as antennal contact having been made (thus any reference to antennal contact which does not specify by ‘one’ or ‘both’ individuals will denote the two categories combined).

Overall attraction to chemical stimuli in dishes

Experimental setup

To determine levels of attraction by individuals to different chemical-based information, we gathered overhead video (N = 60 total) of free-roaming individuals in the wild around three types of chemicals (N = 20 per condition). Experimental areas were designated by drawing 65 cm diameter circles in the sand and placing shallow plastic 5 cm diameter circular dishes in the centre (Fig. 1b). To remove any barrier to access, the sides of the dishes were pressed into the sand, flush with the sand substrate. To gather overhead video of the experimental area, a video camera (Canon Vixia HF R72) was attached to a long pole driven into the sand. The experimental area was filmed for 10 min after setup, providing a baseline. Visual counts were made of the number of individuals present at the start of the trial before the addition of chemicals (at t = 0), with the overhead camera continuing to video for another 10 min. From the overhead videos, visual counts were again made of the number of individuals present in the experimental area at the end of the trial (t = 10; Fig. 1b). From the videos we also quantified latency for the first individual to contact each of the dishes after the addition of the chemical. Experiments were carried out in triplicates each day, sequentially and >1 metre apart, with the order of the conditions (see below) being randomised.

Three conditions: chemical stimuli

Three chemical stimuli were used: (1) coconut milk, which signifies a valuable resource (and therefore positive social information when paired with a conspecific); (2) water (from the adjacent lagoon that individuals regularly pass through), which served as neutral social information when paired with a conspecific; and (3) mammal urine, which signifies both a potential danger and a potential opportunity (and therefore represents ambivalent social information when paired with a conspecific). Mammal urine was collected from voluntary human donors, including the authors, and was collected in the same receptacle and at the same time each day, prior to its experimental use. These different chemical stimuli (coconut milk, water, and mammal urine) are all common and natural elements of the crabs' environment, and were chosen for their biological significance to the crabs (positive, neutral, and ambivalent, respectively). The neutral and ambivalent chemical stimuli were used as comparisons to the positive chemical stimulus. When these chemicals are paired with conspecifics (as residues on the bearer's body surface), then each, in effect, becomes a different type of social information, allowing us to test our core hypotheses.

Experimentally-seeded social information: focal individuals doused in chemicals

Experimental setup

To test the impact of chemical-based social information, we experimentally seeded these chemicals onto randomly selected focal individuals in the population (N = 20 individuals for each condition), then released them and recorded all subsequent interactions from a distance for 5 min using a handheld video camera (Canon Vixia HF R72). To quantify the impact of social information on both receivers and bearers, we recorded the number of encounters each focal crab had with conspecifics, as well as ensuing interactions that indicated a benefit to receivers (i.e., receivers following the bearer; Fig. 1c), or that indicated a cost to bearers (i.e., the bearer being flipped by receivers; Fig. 1c; see Table S1 in the Appendix for definitions of each behaviour). Only encounters with moving conspecifics were counted to clearly distinguish conspecifics from stationary object (e.g., pebbles) in the background.

Focal crab selection

For each day of experiments, three focal crabs were randomly selected from the population and then allocated randomly to each of the three experimental conditions. Crabs were only included as focal individuals if they had all appendages intact and were occupying the most common (*Nerita* spp.) shell. Across the three conditions, there was no difference in the size of focal individuals (One-way ANOVA: $F_{2,57} = 0.037$, $p = 0.96$; positive: 11.48 ± 0.33 mm shell diameter; neutral: 11.33 ± 0.45 mm; and ambivalent: 11.45 ± 0.47 mm).

Application of chemicals

For each day, the order of conditions was randomised within each triplicate of experiments. At the start of each experiment the focal crab, experimenter's hands, and forceps were washed and dried, removing any potentially confounding chemical information. To enable identification of focal crabs in the video, they were then marked with a small square of high-vis Duct tape on the dorsal side of their shells. To seed the social information onto them, each focal crab was placed in a holding container and doused with 9 ml of the relevant chemical stimulus, using a pipette (Fig. 1c), so that the entire external surface of the crab and its shell were covered with the chemical cue. The crab was then removed using forceps and held until dripping of any excess chemical ceased, so that only a thin trace remained on the surface for detection by receivers. The focal crab was then carried with the forceps to a randomised drop point within the experimental area on the beach, and placed on the sand, where their start position was marked by the insertion of a vertical wooden dowel. The number of conspecifics within a 30 cm radius of the start position was recorded, and then the focal crab was videoed for 5 min. After 5 min, the end position of the crab was marked by the insertion of another vertical wooden dowel, the number of conspecifics within a 30 cm radius of the end point was recorded, and the crab was recollected. Upon recollection, the focal crab's marker was removed, and it was placed in a holding container until the day's experiments were completed, after which it was released. To test if there was a difference in how far focal crabs moved across different conditions, we measured the distance between their start and end positions (i.e., their displacement; Fig. 1c).

Statistical analyses

Antennal contact during natural encounters

To test for differences in the number of encounters that entailed antennal contacts by both individuals, one individual, or neither individual during focal sampling, we conducted a One-way ANOVA. For behavioural sampling, we used a Chi-square test to examine if observed occurrences of each of the three outcomes different from the assumption of an equal likelihood of all three possible outcomes.

Overall attraction to chemical stimuli

To test for differences in latency to contact stimuli across the three chemical conditions, we performed a One-way ANOVA. To test if the positive condition attracted individuals faster than the neutral or ambivalent conditions, we conducted post-hoc All-Pairs Tukey-Kramer tests, which also allowed us to explore any potential differences between the neutral and ambivalent conditions. Data for latency were square route transformed (to be normally distributed) and analyses were conducted on the transformed data. To compare differences in the number of individuals present in the experimental area from before-to-after the addition of each chemical stimulus, we performed a Kruskal-Wallace test. To test if the positive condition attracted more individuals than the neutral or ambivalent conditions, we conducted post-hoc All-Pairs Dunn tests, which also allowed us to explore any potential differences between the neutral and ambivalent conditions.

Experimentally-seeded social information on focal individuals

To test differences across the three social information conditions, we used Kruskal-Wallace tests to compare the number of encounters focal individuals had with conspecifics and the number of conspecifics surrounding the focal individual at the end of each experiment. For any variables that showed a significant difference across conditions, we then used post-hoc All-Pairs Dunn tests to determine if the positive condition differed from the neutral or ambivalent conditions and if any potential differences existed between the neutral and ambivalent conditions. To compare the proportion of encounters that led to receivers following the focal individual, we arcsine transformed these proportions and performed a One-way ANOVA. To compare how many times focal individuals were flipped by receivers, depending on social information condition, we used a generalized linear model, with a Poisson distribution and a Log link function. Lastly, to test differences across the three social information conditions in displacement achieved by individuals, we performed a One-Way ANOVA. A post-hoc All-Pairs Tukey-Kramer test was then conducted to determine if individuals in the positive condition achieved shorter displacements than individuals in the neutral or ambivalent conditions, and if any potential differences existed between the neutral and ambivalent conditions.

All videos were coded by the author and an independent observer, who was blind to the hypotheses and to the chemical conditions. To measure inter-observer reliability in the experimentally-seeded social information experiments for the number of encounters, follows, and flips (see Figure 1), a random sample of videos (N = 30 total, N = 10 for each condition) were coded. There was strong inter-observer reliability in the measurements ($r^2 > 0.75$) for all measures (encounters: $F_{1,28} = 94.2$, $p < 0.0001$, $r^2 = 0.77$;

follows: $F_{1,28} = 88.53$, $p < 0.0001$, $r^2 = 0.76$; flips: $F_{1,28} = 705.83$, $p < 0.0001$, $r^2 = 0.96$). Analyses were performed using JMP® Pro version 16.0.0. For post-hoc analyses, All-Pairs Tukey-Kramer tests controlled for the overall error rate, and All-Pairs Dunn tests used the Bonferroni adjustment.

Results

Antennal contact during natural encounters

Antennal contact occurred frequently in natural encounters (mean ± SE: 0.75 ± 0.1 per min across N = 20 focal individuals). During focal sampling, a significant difference existed in how often encounters involved antennal contact by both individuals, one individual, or neither individual (One-way ANOVA: $F_{2, 57} = 6.50$, $p = 0.0029$), with antennal contact by both individuals occurring most often (Figure 2a). Similarly, during behavioral sampling, a disproportionate percentage of natural encounters involved antennal contact by both individuals (61% of N = 117), significantly more than predicted by chance ($X^2 = 39.44$, df = 2, $p < 0.0001$, Figure 2b). Thus, antennal contact provided substantial opportunity for close-range social information exchange.

Overall attraction to chemical stimuli in dishes

Following the addition of the chemical stimuli, the change in number of individuals from start to end varied significantly across the three conditions (Kruskal-Wallis: $X^2 = 39.82$, df = 2, $p < 0.0001$; Fig. 3a). The number of individuals increased significantly more in the positive condition than in both the neutral condition (post-hoc Dunn test: $P < 0.05$) and ambivalent condition (post-hoc Dunn test: $P < 0.05$). The neutral and ambivalent conditions did not differ (post-hoc Dunn test: $P > 0.05$). Furthermore, latency to contact the stimulus differed significantly across conditions (ANOVA: $F_{2,57} = 9.43$, $p = 0.0003$; Fig. 3b). Individuals in the positive condition contacted the chemical stimulus quicker than in either the neutral condition (post-hoc Tukey-Kramer test: $P < 0.05$) or ambivalent condition (post-hoc Tukey-Kramer test: $P < 0.05$). The neutral and ambivalent conditions did not differ (post-hoc Tukey-Kramer test: $P > 0.05$). Thus, relative to the neutral and ambivalent conditions, the positive condition resulted in greater accumulation and attraction.

Experimentally-seeded social information: focal individuals doused in chemicals

The number of conspecific encounters did not significantly differ across the three conditions (Kruskal-Wallis: $X^2 = 0.46$, df = 2, $p = 0.80$; Figure 4a). Consistent with the benefit to receiver hypothesis, the proportion of follows per encounter differed across the three conditions (ANOVA: $F_{2,57} = 5.83$, $p = 0.005$; Figure 4b): individuals in the positive condition were followed significantly more than those in the neutral condition (post-hoc Dunn test: $P < 0.05$) or ambivalent condition (post-hoc Tukey-Kramer test: $P < 0.05$). The proportion of follows in neutral and ambivalent conditions did not differ (post-hoc Tukey-Kramer test: $P > 0.05$). Consistent with the cost to bearer hypothesis, the number of times focal individuals were flipped differed across the three conditions (GLM: $X^2 = 46.53$, df = 2, $p < 0.0001$). Individuals bearing positive social information were flipped an average of 1.2 times per trial (Figure 4c), comparatively more often than bearers of social information that was either neutral ($\bar{x} = 0.05$ flips per trial; Figure 4c) or ambivalent ($\bar{x} = 0.00$ flips per trial; Figure 4c). There was no significant difference across conditions in the number of conspecifics that surrounded focal individuals at the end of the experiments (Kruskal-Wallis: $X^2 = 1.19$, df = 2, p = 0.55; Figure 4d). Consistent with the cost to bearer hypothesis, displacement achieved by focal individuals differed across the three conditions (ANOVA: $F_{2,57} = 5.42$, p = 0.007; Figure 4e): individuals in the positive condition achieved significantly shorter displacement than individuals in the neutral condition (post-hoc Tukey-Kramer test: $P < 0.05$). Displacement of individuals in the ambivalent condition though was not significantly different from those in the positive condition (post-hoc Tukey-Kramer test: $P > 0.05$) or the neutral condition (post-hoc Tukey-Kramer test: $P > 0.05$). Thus, the predictions of the benefit to receiver and the cost to bearer hypotheses, were both supported.

Discussion

Experimentally-seeded social information elicited responses in receivers that suggested both a benefit to themselves and, simultaneously, a cost to bearers. Additionally, our observation of natural encounters suggested ample opportunity exists for social information exchange via antennal contact between individuals in the wild. Overall, our results support the ‘benefits to receivers’ hypothesis, as naïve individuals followed focal individuals bearing positive social information more often than those bearing ambivalent or neutral social information. And supporting the ‘costs to bearers’ hypothesis, focal individuals bearing positive social information incurred obvious direct costs, being significantly more likely to be flipped than those bearing ambivalent or neutral social information. Furthermore, bearers of positive social information also experienced indirect costs, as they achieved significantly shorter displacements than those bearing neutral social information. Thus, depending on the type of social information, receivers can benefit, and bearers can incur costs.

Costs to individuals bearing social information have been underexplored. Our study quantified both direct costs to the bearer (i.e., being flipped) as well as indirect costs (i.e., achieving reduced displacement). Yet, there are also likely to be other costs to bearers that deserve consideration. For instance, becoming a beacon of social information may have consequences akin to harassment (Sakurai and Kasuya 2008). Indeed, being flipped and thus unable to move freely, incurs a clear opportunity cost (McNamara and Houston 1992), reducing the time an individual can spend in search of further resources. Moreover, among social hermit crabs, an increased likelihood of being flipped inherently contributes to escalation towards potential eviction and even death (Laidre 2012), as flipping is a necessary precursor to these more deadly costs. After following, flipping by receivers may be necessary if they are to determine whether the bearer, not only knows the whereabouts of a valuable resource, but may be carrying some of the food resource on itself that can be taken and consumed. Interestingly, social information has been implicated (Barnard and Sibly 1981) in increasing rates of kleptoparasitism (reviewed in Giraldeau and Caraco 2000) via processes such as local enhancement. Though in cases where there is only a chemical residue and no actual physical resource, kleptoparasitism is impossible. Yet, even in the absence of a physical resource, bearers of residues may still be worth following as they may soon return to the source. However, if, and when the bearer will return to a resource is ambiguous, therefore, like most cues, is imperfectly correlated to conditions of interest to receivers. For this reason, social information is often most useful to the receiver when integrated with information gathered directly from the environment (Bradbury and Vehrencamp 2011; Danchin et al. 2004). It is worth noting that information and resources may not be all that is passed when bearers are followed or flipped. The longer exposure times that such interactions necessarily entail could also increase opportunities for parasite or pathogen transmission. Thus, further studies are needed to quantify the full costs to bearers of social information, with these costs potentially being a pervasive yet overlooked element across many social taxa.

Individuals may, in theory, be able to reduce costs of bearing social information by changing their behaviour (Sumpter 2010). Some direct costs, such as flipping, could be reduced by simply avoiding conspecifics, particularly when a bearer is covered in positive social information. However, an avoidance strategy did not appear successful in the present study, given there was no significant difference in conspecific encounter rate across the three social information conditions. It is possible that avoidance may simply not be achievable for individuals traversing a flat open environment, like the beach. Another strategy to reduce costs may be self-cleaning, a behaviour that is too fine-grained to quantify from our videos. Nevertheless, individuals might be able to rub off certain cues (eliminating them from their body), or even scent mask (by adding other cues, e.g., Clucas et al. 2008), thereby potentially reducing the detectability of disadvantageous chemical-based social information present on their body. Critically though, cleaning and masking likely trade-off with locomotion, reducing displacement and broader exploration of the environment. Furthermore, self-cleaning may be ineffective depending on properties of the chemical and the animal's morphological body shape. Few examples exist in the literature of individuals successfully disguising (Emery and Clayton 2006), concealing (Legg and Clayton 2014) or otherwise reducing (Davis and Dill 2012) social information, and even these examples concern visual cues. For chemical-based social information, some cost of bearing this information may be inevitable.

Interestingly, relative aspects of bearers and receivers may further alter dynamics (Parker 1974), including the costs and benefits of interactions between the two parties. Across all study systems, the relative size of individuals can have major impacts on the outcome of interactions (e.g., Bridge et al. 2000). Thus, whether a receiver flips a bearer of social information may depend not just on the valence of social information (positive, neutral, or ambivalent), but also on whether the receiver is larger or smaller relative to the bearer. Individuals can more easily flip conspecifics that are smaller than themselves, with ease of flipping being determined by the magnitude of this size differential. Furthermore, the size differential between bearer and receiver could also impact the ability (Stevens 2014) of a receiver to follow a bearer, with smaller receivers potentially being less capable of following a larger bearer that can move faster. Displacement could also be impacted by the relative size of bearers and receivers: larger bearers, relative to surrounding receivers, might be less impeded by 'traffic', so could potentially take a more direct route, over or through many conspecifics. Future experiments focusing on fine-scale size differences can test how relative size may create further nuanced differences in benefits to receivers and costs to bearers.

In addition to the relative size of individuals, where on the body of the bearer the social information is carried may further impact receivers' responses. Indeed, for chemical-based social information, in particular, the precise position on the body may change the meaning of the information. Bats have been shown to differentially learn food preferences from conspecifics, depending on where chemical-based social information about those foods are borne (i.e., breath versus fur; O’Mara et al. 2014). Using the same distinction in body position, individuals may be able to identify the most reliable bearers. In our study, we covered the entire surface of focal individuals, which often occurs naturally when individuals feed, especially on coconuts (Laidre 2013). However, there are also instances in which individuals may not become completely covered in residue and instead only a very limited portion of their body ever makes contact with a food resource. Thus, a food cue around the antenna and mouth would be the strongest evidence that a bearer recently ate a meal (Galef and Stein 1985; Laidre 2009; O’Mara et al. 2014), whereas the same cue detected elsewhere on an individual’s body could be interpreted differently, potentially having rubbed off by other means. Future experimental studies should measure receiver responses when social information is applied only on a conspecific’s anterior body parts (e.g., mouth and antenna) versus only on its posterior body part or even only the dorsal side of its shell. If receivers can differentiate between bearers who have directly fed on a valuable food resource versus those who have merely brushed up against the resource, then we would predict receivers to follow only the bearers with cues on their mouths.

Another avenue of great interest in the field of social information is understanding information, not just via primary bearers of social information, but also secondary bearers, which have made contact with primary bearers and thus have acquired some of the residual chemicals. In the context of chemical-based social information, it is important to determine whether initial receivers of this social information can subsequently become bearers, effectively propagating the social information more broadly (Tóth et al. 2020). Experiments on this question could quantify whether chemical-based social information diminishes in its potency with each step away from the original bearer and information source. For sound-based social information, its transmission, even if sparse or weak, can nevertheless generate larger-scale changes in the movements of many receivers (Couzin 2018), including more efficient convergence on stopover sites during migration (Larkin and Szafoni 2008). For chemical-based social information, further studies, especially in the wild, are needed to determine how far it can transmit across original and subsequent bearers, and the ultimate impacts over time of this information propagation.

In conclusion, our study has revealed that experimentally-seeded social information in the wild confers both benefits to receivers and costs to bearers. The direct and indirect costs of bearing social information, revealed here, highlight the importance of considering costs to bearers more generally in studies of social information use. Further, we have outlined how and why future studies should address whether bearers are able to reduce costs, the ways in which relative properties of bearers and receivers may impact their interactions, and the extent to which chemical-based social information propagates beyond the original bearer. Broadly, our study suggests that receivers and bearers may both be impacted by social information in the wild, just in different and nuanced ways.

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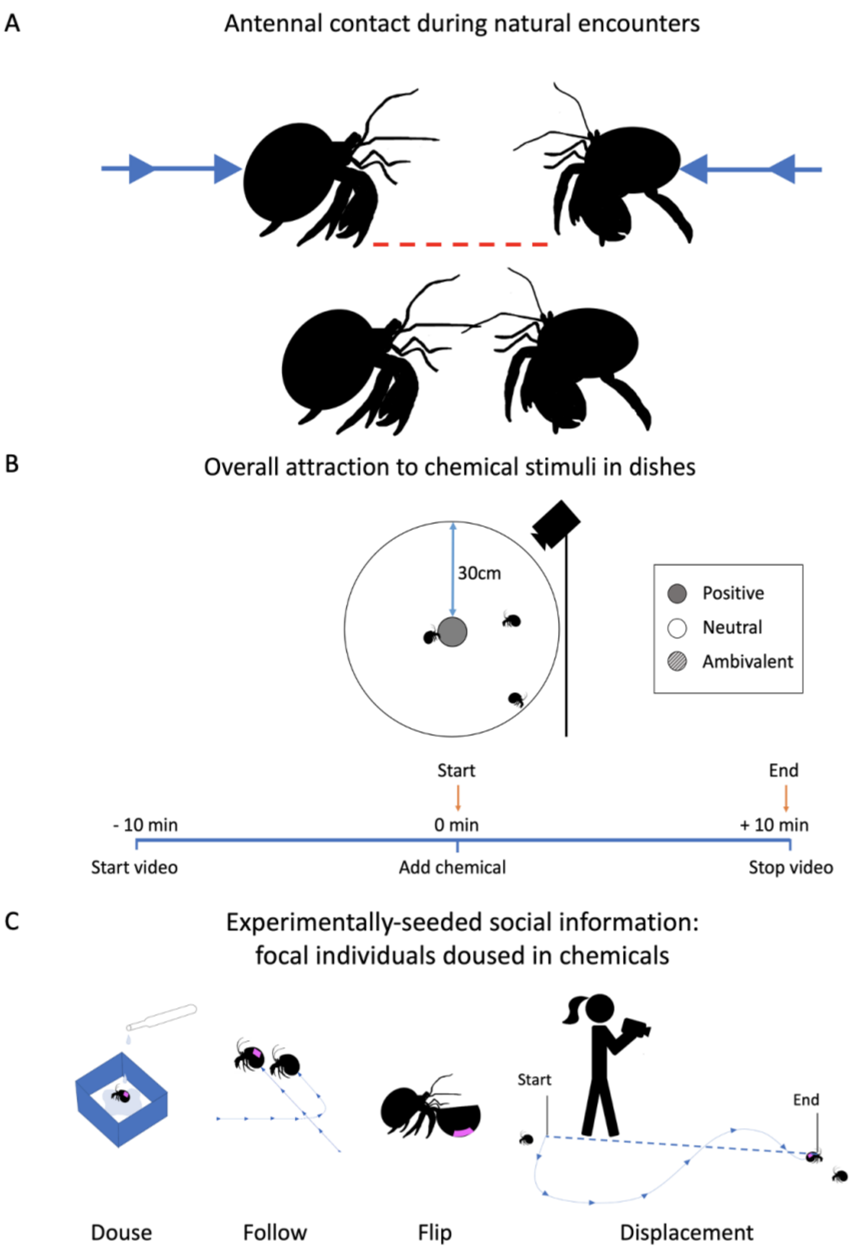

Figure 1. (A) Illustrations of ‘encounter’ and ‘antennal contact’. An encounter occurs when two individuals come within a body length of each other. Graphic illustrates antennal contact by both individuals. (B) Experimental setup for measuring overall attraction to chemical stimuli in dishes. Overhead video of free-roaming crabs was collected for 10 min before and 10 min after adding chemical stimuli to dishes. Chemical stimuli were coconut milk (positive), water (neutral), and mammal urine (ambivalent). (C) Experimental setup for experimentally seeding social information and recording subsequent conspecific encounters in the wild. Left to right: Focal individuals were doused in chemicals (positive, neutral, or ambivalent) before the start of each trial; a conspecific following a focal individual; a conspecific flipping a focal individual onto its back; trials were recorded by the experimenter and the focal crab’s displacement (linear distance between start and end point, shown by the dashed blue line) was measured.

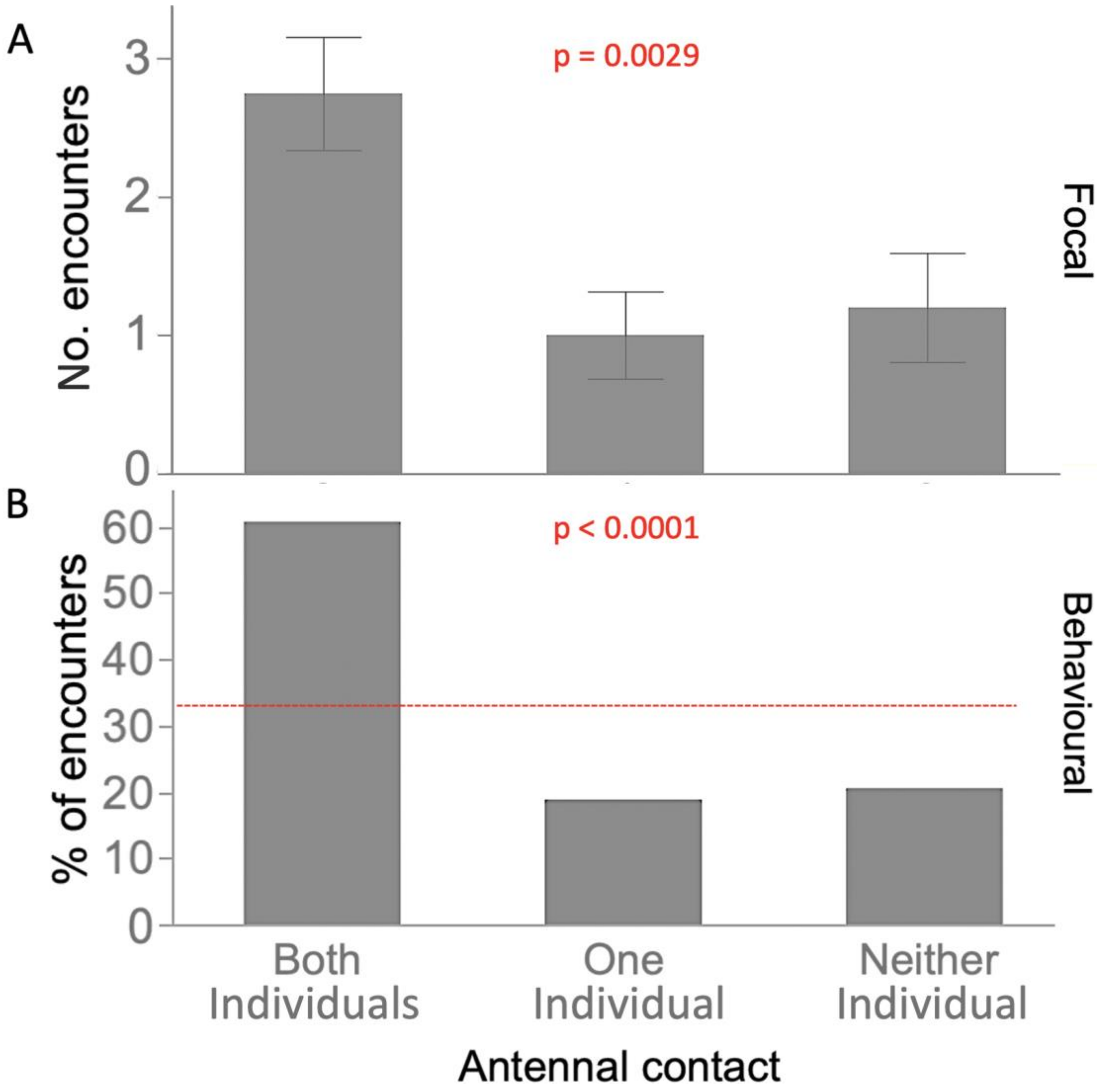

Figure 2. Natural encounters involving antennal contact by both individuals, one individual, or neither individual. (A) Number of encounters (Mean ± SE) for each category during focal sampling. P-value for One-way ANOVA. (B) Percent of encounters for each category during behavioural sampling. P-value indicates Chi-square.

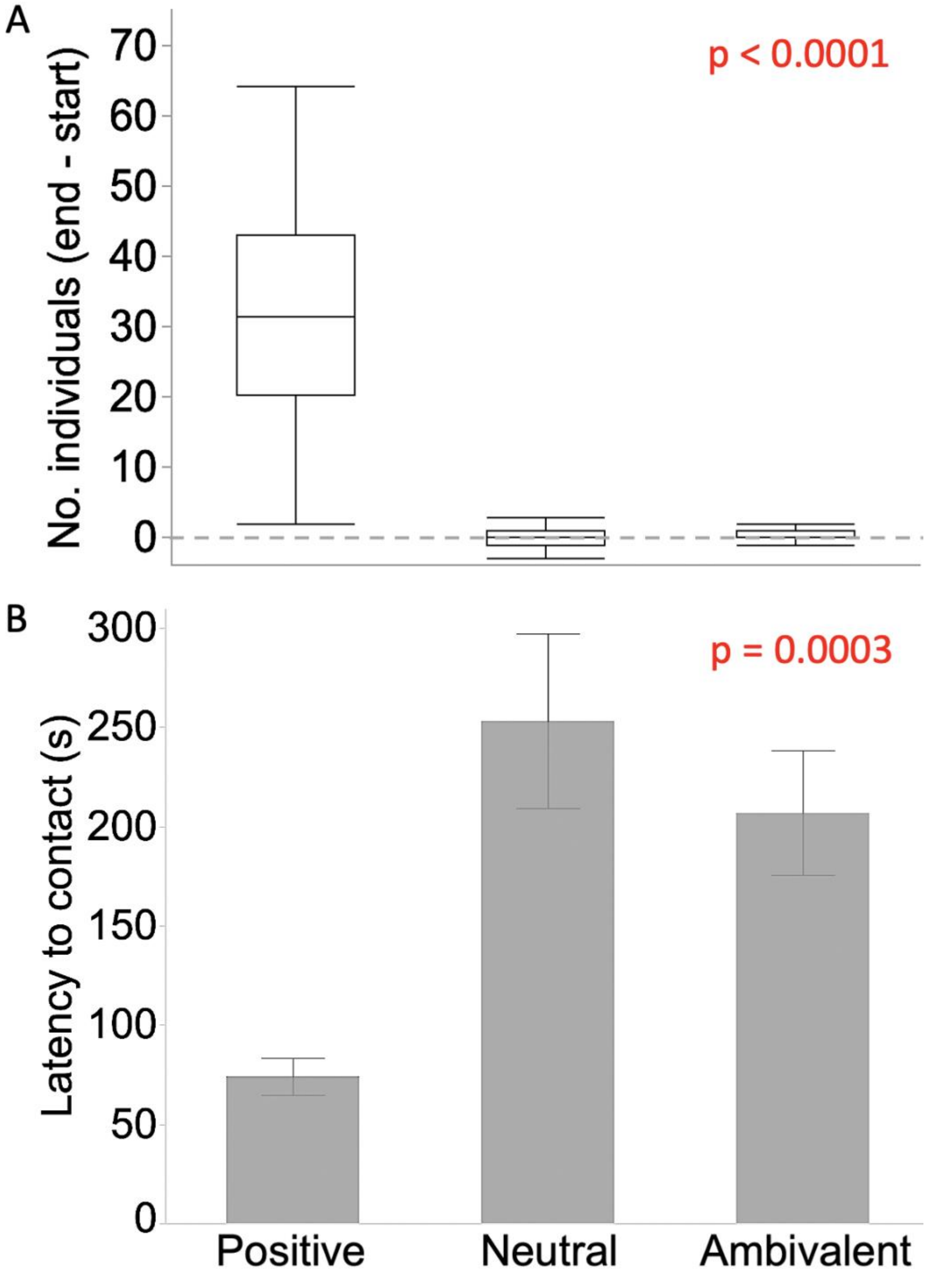

Figure 3. Overall attraction of individuals in the wild to chemical stimuli in dishes: (A) Change in the number of individuals within 30 cm of the dish from directly prior to the the start of the trial (t = 0) to the end of the trial (t = 10 min). Box plots display: interquartile range (box), median (horizontal line within box), and 1.5*IQR (whiskers). P-value indicates Kruskal-Wallis test. (B) Latency to contact stimuli (s) (Mean ± SE). P-value indicates One-way ANOVA.

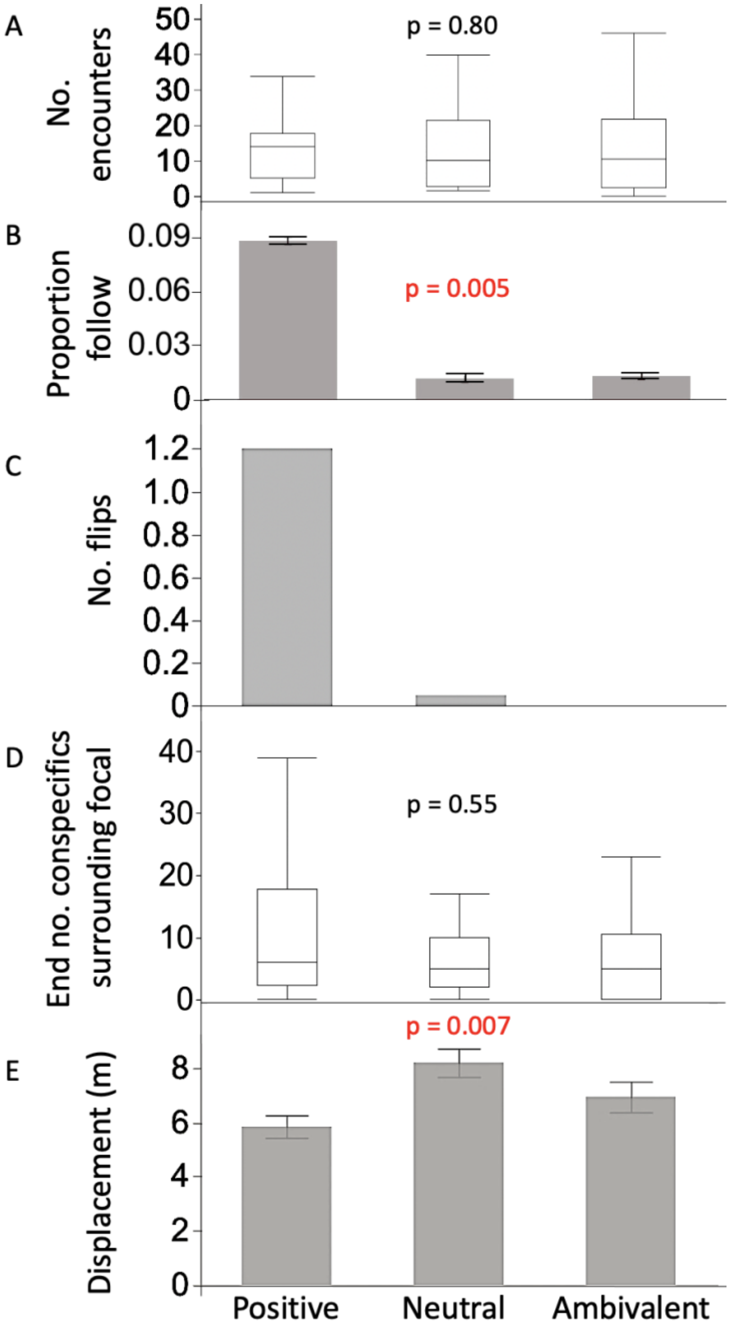

Figure 4. Measures of costs to bearers and benefits to receivers for experimentally-seeded social information of three different types (positive, neutral, and ambivalent). (A) Number of conspecific encounters experienced by the focal individuals. (B) Proportion of follows per encounter; (C) Number of times focal individuals were flipped by conspecifics; (D) Number of conspecifics that surrounded focal individuals at the end of the 5-min experiments. (E) Displacement achieved by focal individuals. (A& D) Box plots display: interquartile range (box), median (horizontal line within box), and 1.5*IQR (whiskers). P-value indicates Kruskal-Wallis test. (B & E) Bar plots display: Mean ± SE. P-value indicates One-way ANOVA. (C) Bar plot shows average no. of flips per trial, see results for analysis comparing no. flips using GLM with a Poisson distribution.

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Appendix

Tables

Table S1. Operational definitions of behaviours for video coding

Term	Description
Body length	Widest visible length between any two points on the focal crab's body, including shell.
Encounters	When the focal crab starts more than three body lengths away from, and then comes within a single body length of a visibly moving conspecific. If the focal crab and conspecific subsequently move to beyond three body lengths from one another and then back to within one body length, this is counted as a separate encounter. Body lengths and distances between individuals were always measured on a 2D plane.
Follow	When a conspecific follows the focal crab for three or more seconds after the initial encounter (this includes conspecifics piggybacking on focal crabs and holding on as the focal crab moves forward). As with encounters, the focal crab and conspecific must move to beyond three body lengths from one another and then back to within one body length, for bouts of following to be counted separately.
Flip	When a focal crab is manoeuvred onto its back or side by a conspecific, such that a dorsal or lateral portion of the focal crab's shell is contacting the ground. If the focal crab regains an upright position with all appendages on the ground (i.e., not withdrawn) and is again forced onto its side or back by a conspecific, this is counted as a separate flip.