Animal Behaviour 229 (2025) 123347

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Plastic or natural? The impact of marine debris on the shell preference of a terrestrial hermit crab

Peter A. Cotton *, Maisie Benham, Ashley O. Hardoin, Hannah M. Lazenby, Robert Puschendorf, Mark Briffa

School of Biological and Marine Sciences, University of Plymouth, Plymouth, U.K.

ARTICLE INFO

Article history:
Received 7 January 2025
Initial acceptance 14 April 2025
Final acceptance 14 July 2025
Available online 10 October 2025
MS. number: 25-00020R

Keywords:
Coenobita compressus
HIREC
human-induced rapid environmental change
plastic pollution
shell selection

Plastic pollution is one of the main human-induced rapid environmental changes threatening marine organisms. Terrestrial hermit crabs, which inhabit coastal areas where litter accumulates, are increasingly documented using plastic debris as shells, and a recent study hypothesized that this shift may be an adaptive response. They suggested that 'plastic shells' may reduce transport costs, provide camouflage in a polluted environment, and may even be favoured by sexual selection. Our study is the first to quantify plastic shell use in a population, to examine shell preference and to test the hypothesis that plastic shells optimize the ratio of weight to volume. We investigated the prevalence of plastic shell use by *Coenobita compressus* at Playa Nancite, Costa Rica. We conducted field surveys to assess shell use among hermit crabs, evaluated the environmental availability of natural and plastic shells, and performed a choice trial experiment to determine their shell preference. Of the 714 crabs collected, all were found in natural shells, despite the shoreline survey revealing a far greater abundance of available artificial shells, primarily plastic. Choice trials showed a strong preference for natural shells, with crabs only occasionally entering, and never retaining, plastic shells. Despite the widespread availability of plastic debris at Playa Nancite, hermit crabs strongly prefer natural shells, suggesting limited current impacts on this population's shell selection behaviour and evolution. However, the pervasive presence of plastic on beaches necessitates urgent measures to mitigate its environmental impact. Furthermore, research across different species and locations is essential to understand the broader implications of marine debris on hermit crabs.

Global production of plastic now exceeds 438 million tonnes per annum and is expected to more than double by 2050 (Geyer, 2020). Plastic debris is known to be present in all marine habitats, from surface waters to the most remote points in the oceans (Barnes et al., 2009; Pham et al., 2014), constituting one of the major threats to marine biodiversity due to its abundance, durability and persistence in the environment (Gall & Thompson, 2015). Human-induced rapid environmental change often puts organisms into evolutionarily novel conditions, exerting strong selective pressures that can cause species declines or drive rapid evolutionary responses as organisms adapt to their new environment (Sih, 2013; Sih et al., 2011). Plastic debris can affect diverse marine species through various routes, including entanglement and internal damage via ingestion of large plastic items, and toxicity via exposure to microplastic fragments and exudates.

Hermit crabs are a model system for investigating the behavioural effects of pollution (Briffa et al., 2024), and several studies have shown how plastic can affect their behaviour. Primarily, they can be attracted to exudates from decomposing plastic (Greenshields et al., 2021), and exposure to microplastic particles can alter their risk-aversiveness (Nanninga et al., 2020), contest behaviour (Cunningham et al., 2021) and assessment of natural shells (McDaid et al., 2023). Terrestrial hermit crabs inhabit coastal areas, typically along the strandline of beaches, which are hotspots of litter accumulation (Corcoran et al., 2009). In addition, they may be especially vulnerable through two distinct routes linked to their obligate use of empty gastropod shells as 'portable burrows'. First, Lavers et al. (2020) estimated that over half a million strawberry hermit crabs, *Coenobita perlatus*, could die annually following entrapment in plastic debris in the Cocos (Keeling) Islands. Crabs crawl into discarded containers, typically empty plastic bottles,

* Corresponding author.
E-mail address: p.cotton@plymouth.ac.uk (P. A. Cotton).

https://doi.org/10.1016/j.anbehav.2025.123347

and, once trapped, they dehydrate and die within 5–9 days (Lavers et al., 2020). As gastropod shells are a severely limiting resource for hermit crabs, the smell of decomposition attracts conspecifics in search of a new home (Valdes & Laidre, 2019). A chance accident, in which an individual crab becomes trapped in a bottle, becomes a chain reaction, then becomes a lethal lure, increasing in potency with every new arrival. Lavers et al. (2020) recorded over 500 hermit crabs inside one bottle, and with the high concentrations of marine debris, this has the potential to seriously impact hermit crab populations. Second, terrestrial hermit crabs may choose to occupy certain types of plastic debris that approximate the size and shape of natural gastropod shells. Unlike marine hermit crabs, terrestrial hermit crabs extensively remodel their shells to create extra space by eliminating much of the shell's interior (including the entire columella) and by thinning the walls (Laidre, 2012). While they differ from gastropod shells in many respects, terrestrial hermit crabs can still insert their abdomen into items such as bottle tops and, if the item is sufficiently large, retract into it when threatened. The first published record of hermit crabs using an artificial plastic shell appears to be Barreiros and Luiz (2009), and since then, the phenomenon has been documented only infrequently within the scientific literature (de Carvalho-Souza et al., 2018; Laidre, 2014; Sasazuka et al., 2019; Sharma, 2018). However, a recent paper analysing images posted on digital online platforms such as iNaturalist reported that 10 out of 16 terrestrial hermit crab species use debris instead of natural shells (Jagiello et al., 2024). Of the 386 images of crabs using artificial shells, 84.5% were in plastic, in particular, white and black plastic container caps. This study, therefore, raises the possibility that this novel behaviour, resulting from exposure to plastic debris, may be underappreciated.

Thus, there is evidence that some individuals are using artificial objects in place of natural gastropod shells, but at present, there is little information on the frequency of this phenomenon, its causes, or its potential consequences for hermit crabs. For example, Jagiello et al. (2024) provide no information on the proportion of individuals of any species using artificial shells; we can, however, infer from the 83 cases of artificial shell use found in 28 994 images on iNaturalist that the incidence is low (0.29%, 95% CI: 0.23%–0.36%). Even then, this frequency may be inflated, as people are more likely to post unusual behaviour online (Ladle et al., 2019). Nevertheless, the reporting of artificial shell use has increased rapidly over the past decade, leading Jagiello et al. (2024) to suggest that the rise may reflect either greater availability of inhabitable plastic objects over natural shells, a preference for plastic over natural shells, or a combination of the two. Therefore, Jagiello et al. (2024) concluded that this form of pollution has the potential to impact natural selection and sexual selection in terrestrial hermit crabs and thus influence their evolution.

All 16 species of terrestrial hermit crab in the genus *Coenobita* require shells to provide physical protection and prevent desiccation. The Ecuadorian (Pacific) hermit crab, *Coenobita compressus*, is a common detritivore (Thacker, 1996) found on strandlines from Mexico to Peru (Ball, 1972) and is the only terrestrial hermit crab species found on the Pacific coast of Costa Rica. It is one of the smallest *Coenobita* species, and throughout its range, they typically inhabit the shells of small *Nerita*, Vasula (*Thais*) *and Turbo* species (Abrams, 1978; Ball, 1972; Osorno et al., 2005). In Mexico, *C. compressus* prefers shells of *Nerita scabricosta,* which are lighter and have a higher internal volume to weight ratio than the second most preferred shell species, *Vasula speciosa* (Osorno et al., 1998, 2005). Between 70% and 85% of all individuals were found using shells of these two gastropod species, with *Cerithium* species making up most of the remainder (Guillén & Osorno, 1993).

In this study, we investigated the impact of plastic pollution on the shell selection behaviour of *C. compressus*. Marine hermit crabs are adapted to live in unmodified gastropod shells (Laidre & Trinh, 2014). In contrast, terrestrial hermit crabs are specialized to live in gastropod shells that have been internally remodelled by conspecifics, a greatly limiting resource, reused and passed down across generations (Laidre, 2014). However, recently, Jagiello et al. (2024) reported that *C. compressus* will also use plastic detritus as artificial shells. Furthermore, they suggested that because of the prevalence of plastic debris, terrestrial hermit crabs may actually be showing a behavioural shift in shell preference towards items such as plastic bottle caps. To test this, we chose a study site, Playa Nancite, documented to be in an area where beach macroplastic pollution is particularly abundant (Botterell et al., 2024). We conducted field surveys to determine (1) the availability of inhabitable items of plastic debris (henceforth 'plastic shells') compared with empty natural gastropod shells and (2) the frequencies of occupation of plastic and natural shells. Additionally, as hermit crabs may choose homes with a greater internal volume per unit of mass (Jagiello et al., 2024), we calculated these measures for both natural and plastic shells and (3) tested for an interaction between object type and mass on internal volume. Finally, we (4) conducted a choice experiment, based on established protocols for shell choice in hermit crabs (e.g. Elwood & Neil, 1992; Hills & Webster, 2022), to determine whether these hermit crabs prefer to occupy natural or plastic shells. Although our data are limited to a single population, this study is the first to conduct some of the field surveys and experiments suggested by Jagiello et al. (2024) as urgent priorities to help understand the prevalence and fitness consequences of plastic shell use in hermit crab biology.

METHODS

Fieldwork was conducted in July 2024 at Playa Nancite, Área de Conservación Guanacaste, Costa Rica (10.8051, −85.6997, Fig. 1). To assess the prevalence of artificial shell use by *C. compressus*, we systematically collected all hermit crabs encountered along the strandline in an area of approximately 1000 m^2. All 714 crabs collected were photographed with an Olympus TG-6 (OM Digital Solutions, Tokyo, Japan). This allowed later measurement of the shell length, characterization of the shell (natural or artificial), and identification of the species of gastropod shell or type of artificial material used. Natural shells were mainly identified using Cortés (2017) and the World Register of Marine Species (WoRMS Editorial Board, 2024).

Following the recommendation by Jagiello et al. (2024), we used field sampling to identify the environmental availability of empty natural shells and artificial shells. Twenty shoreline surveys, each measuring 10 × 5 m (total = 1000 m^2), at the top of the beach (Fig. 1), were searched systematically for all empty natural and artificial shells within a suitable size range (5–50 mm). All shells were placed individually on an 18% grey card with a ruler for scale and photographed in RAW format. Shells (natural and artificial) were photographed from multiple angles to determine shell length and maximum aperture diameter (Fig. 2).

Finally, we conducted a simultaneous choice trial, based on established protocols for shell choice in hermit crabs (e.g. Elwood & Neil, 1992; Hills & Webster, 2022), and modified for terrestrial hermit crabs following Steibl and Laforsch (2020). We provided naked hermit crabs with a binary choice between natural and plastic shells. A total of 93 hermit crabs were removed from their shells; we then measured their cephalothoracic shield length (CSL) using dial callipers to the nearest 0.1 mm and their body mass to

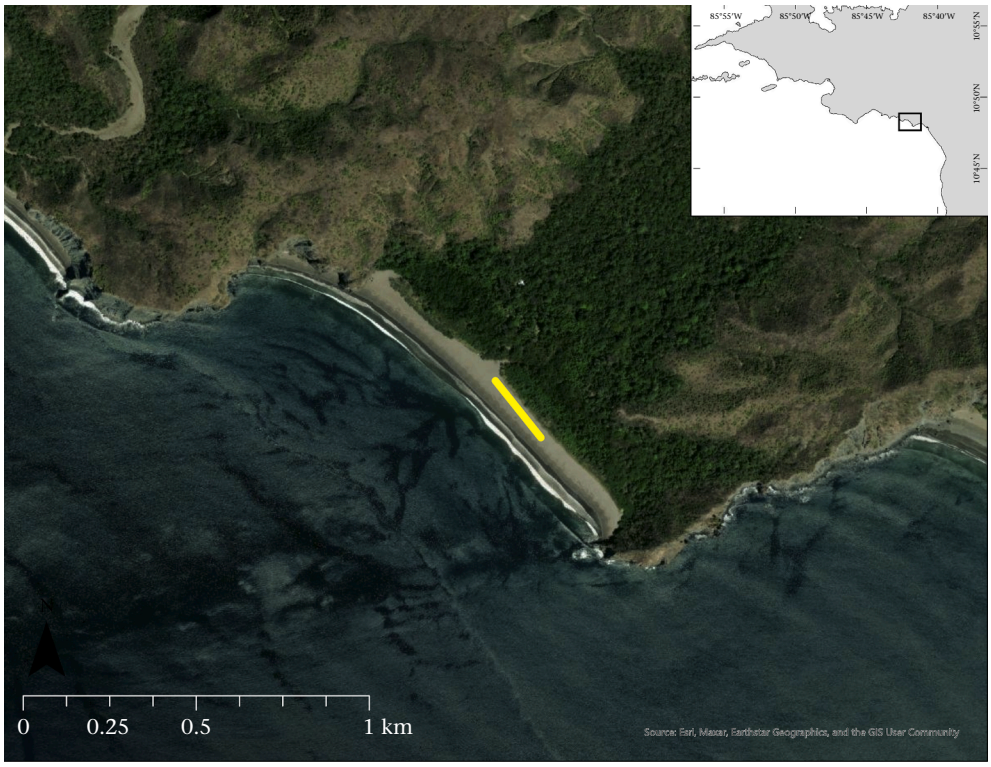

Figure 1. The study site at Playa Nancite, Costa Rica. The yellow bar indicates the location of the shoreline surveys, and the inset shows the northwest coast of Costa Rica, and the location of Nancite in Guanacaste Province. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

the nearest 0.01 g (Smart Weigh GEM20 scale). Crabs were then placed individually into a translucent plastic container (17 × 11 × 6 cm) with approximately 1 cm depth of damp sand in the bottom. The experiments were conducted in a field laboratory out of direct sunlight and at ambient air temperature (28 °C). Each container held two objects: a natural gastropod shell previously used by a hermit crab and an artificial shell made of plastic collected from the strandline at Nancite. While an alternative design would have been to select new natural gastropod shells of an appropriate size, the total number we could remove from their shells was constrained by welfare considerations and our research permit. Nevertheless, our design is justified in this case, as we were testing the hypothesis proposed by Jagiello et al. (2024) that terrestrial hermit crabs have evolved a behavioural shift in shell choice and that they now prefer plastic shells over their natural gastropod shells (that is, they would abandon their original natural shell upon encountering a habitable plastic object of similar size). The plastic shells were the types of objects that hermit crabs have been reported to occupy (mainly bottle and pen tops). Because we were constrained by the availability of plastic shells, they were selected

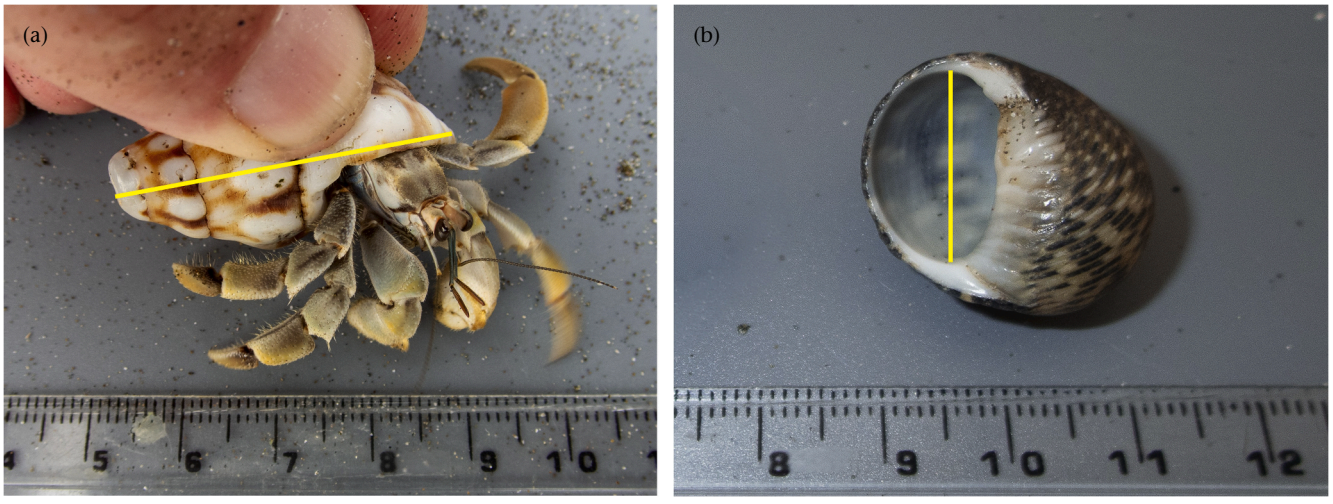

Figure 2. Example photographs illustrating the determination of (a) maximum shell length and (b) maximum aperture diameter.

primarily to ensure a close size match to the gastropod shell and to the crab (on average, natural shells had an aperture width 13% smaller than the plastic shell with which they were paired). Selection was haphazard with respect to the type and colour of the plastic shell. Each observer watched one crab at a time, recording the initial shell contacted (natural or plastic), the first shell entered (natural or plastic), and the final shell choice (natural or plastic), defined as the shell occupied at the end of the 20 min observation period. In almost all cases, shell choice was very rapid (under 1 min); in only one trial did we reach the maximum duration of 20 min without the crab selecting a shell. In addition to aperture diameter, we recorded the mass (to 0.01 g) and internal volume (to 0.1 ml) of both the natural and plastic shells. Volume was measured by filling the shell with water using 1 ml BD Microfine syringes graduated in 0.05 ml increments.

We used chi-square goodness-of-fit tests to compare rates of shell investigation, entry, and final choice between natural and plastic shells, with the null hypothesis of no preference (that is, equal rates of occupation of shells of each type). To determine whether the relationship between internal volume and mass differed for natural and plastic shells, we used a linear model where internal volume was modelled on object type, object mass and their interaction. Data were $\log_{10}(x+1)$ transformed to ensure normality of residuals. F-values were calculated using type III sums of squares via the car (Fox & Weisberg, 2019) package in R version 4.2.0 (R Core Team, 2022). Differences in crab weight were assessed using the Wilcoxon rank sum test. The power of the nonsignificant Wilcoxon rank sums test was assessed using the wmwpow package (Mollan et al., 2020).

Ethical Note

All crabs in the field survey were collected and photographed in situ, minimizing the potential stress of handling. The 93 crabs involved in the shell choice experiment were removed from their shells by gripping the crab's anterior body parts and then gently wiggling it free. In contrast to marine hermit crabs, terrestrial hermit crabs do not fit tightly into their shell and can be removed in this manner very easily (Laidre, 2012). Once removed from their shell, the crabs were immediately weighed, measured, photographed and then used once in the shell choice trial. We did not record the sex of the hermit crabs, and to minimize the number removed from their shells, we used all crabs irrespective of sex. All animals were returned to the area of the beach from which they were collected within a maximum of 4 h. This study was conducted at the Nancite Research Station under a Sistema Nacional de Áreas de Conservación research permit (R-SINAC-ACG-PI-034-2024) and approved by the Animal Welfare and Ethical Review Body, School of Biological and Marine Sciences, University of Plymouth (Project ID 5519).

RESULTS

Field Survey

In the field survey, we collected 714 hermit crabs, all of which were *C. compressus* in natural shells ($\chi^2_1 = 714$, $P < 0.0001$). Shells used by *Coenobita* are often in short supply and are passed from one crab to another over periods of years (Laidre, 2014). Many of the occupied shells at Nancite were worn or mechanically damaged (30.1%), often to the point that we could not reliably identify the gastropod species. For the 629 shells that we could identify, *Nerita scabricosta* (32.8%) was the most commonly used shell, followed by *Mexacanthina angelica* (19.2%), *Acanthais brevidentata* (14.6%) and *Supplanaxis planicostatus* (12.1%), with 12 additional species making up the remaining 21.3%.

The shoreline survey yielded 66 unoccupied artificial shells and only one unoccupied natural one ($\chi^2_1 = 63.06$, $P < 0.0001$). The mean aperture for the artificial shells was 25.82 mm, the mean length was 36.14 mm, and the mean weight was 3.165 g. The only natural shell was that of a nut; it weighed 3.110 g and measured 22 mm long with a 16 mm aperture. Laidre and Vermeij (2013) report similar palm nut shells being used by *C. compressus* in the Osa Peninsula, Costa Rica. Most artificial shells were plastic (98.5%), primarily high-density polyethylene (74.24%); only one was made of metal. Most of the artificial plastic shells were bottle caps and lids (61.54%) or small plastic bottles under 50 ml (24.25%). The most common colours were white (53.03%), transparent (10.61%), black (9.09%) and yellow (7.58%).

For crabs found in natural shells, crab CSL length and body mass correlated strongly with natural shell mass ($R^2 = 0.63$, $df = 92$, $P < 0.001$ and $R^2 = 0.79$, $df = 92$, $P < 0.001$, respectively; Fig. 3a). On average, crabs weighed about the same as their natural shells (mean = 102.6%), but the range was large (28.9%–311.7%). There was a significant interaction between shell material (plastic or natural) and mass on internal volume, where internal volume increased more markedly per unit mass increase for plastic shells compared with natural shells ($F_{2,181} = 9.5$, $P < 0.0002$; Fig. 3b). Thus, while natural shells were on average heavier (mean = 4.53 g ± SE = 0.43 g) than plastic shells (mean = 2.34 g ± SE = 0.21 g), their average internal volume was lower (natural shells mean = 3.62 ml ± SE = 0.27 ml; plastic shells mean = 6.87 ml ± SE = 0.67 ml). Seven natural shells exceeded the mass range of plastic shells. Visual inspection of Fig. 4a indicates a possible nonlinear relationship between shell mass and volume across the full range of natural shell masses, such that this low number of large shells may have had a high degree of leverage on the calculated linear relationship between mass and volume for natural shells. By excluding these natural shells from the analysis, the interaction between mass and shell material was no longer significant ($F_{2,174} = 1.2$, $P < 0.05$; Fig. 4b), leaving the main effects of mass ($F_{1,174} = 32.9$, $P < 0.0001$) and material ($F_{1,174} = 32.4$, $P < 0.0001$). Across most of the mass range, plastic shells provide a greater internal volume per unit mass, but the relation between mass and internal volume is similar for both natural and plastic shells.

Shell Choice Experiment

Crabs were more likely to investigate natural shells than plastic shells ($\chi^2_1 = 39.13$, $P < 0.0001$, Fig. 5); 16 individuals initially investigated plastic shells, while 76 investigated only natural shells, with one individual investigating neither. Similarly, the shell entered was more likely to be a natural shell rather than a plastic one ($\chi^2_1 = 73.09$, $P < 0.0001$, Fig. 5), with 87 out of 92 crabs first entering a natural shell. Those crabs that entered a plastic shell would almost immediately investigate the natural shell and swap (Video 1). In all but one case, this exchange occurred rapidly following a very brief period of investigation of the natural shell. In contrast, crabs that first entered a natural shell showed no investigation behaviour towards the plastic shell. A total of 92 crabs ended the trial (max = 20 min) in a natural shell ($\chi^2_1 = 92.00$, $P < 0.0001$, Fig. 5), with the one individual that did not investigate or enter a shell remaining naked. Interestingly, crabs that initially investigated plastic shells were significantly heavier than those that went first to natural shells ($W = 414$, $P < 0.05$; Fig. 6). Crabs that entered plastic shells first were also heavier than those entering natural shells, but this difference was not significant ($W = 168$, $P > 0.05$), probably because as few individuals entered plastic shells, leading to low statistical power (empirical power = 0.682).

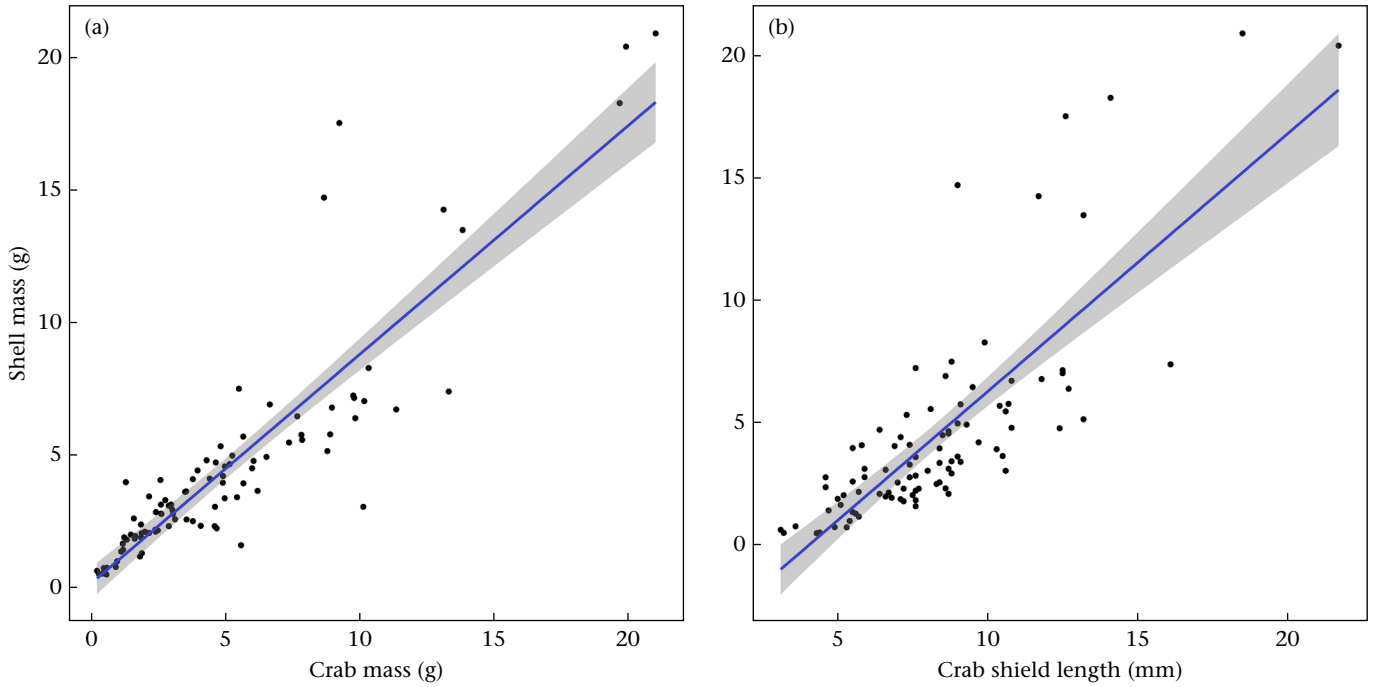

Figure 3. The relationship between (a) crab mass, (b) crab shield length and the mass of the natural shell the crab inhabited. Shaded areas indicate the standard errors of the regression lines.

DISCUSSION

Jagiello et al. (2024) documented terrestrial hermit crabs around the world using plastic shells instead of natural ones and suggested that this phenomenon may represent an evolutionary shift in their shell preference, such that upon encountering a plastic item, hermit crabs would abandon an occupied natural shell in favour of it. In contrast to their findings, during our survey, we did not encounter any hermit crabs using marine debris as shells. Given the frequency of use reported by Jagiello et al. (2024), our sample of over 700 hermit crabs collected using standardized methods should have been sufficient to detect approximately two individuals in plastic shells. As suggested by Jagiello et al. (2024), we did find that artificial shells were predominantly plastic and that they far exceeded the availability of natural alternatives. Their occupancy, however, did not match this availability; no crabs

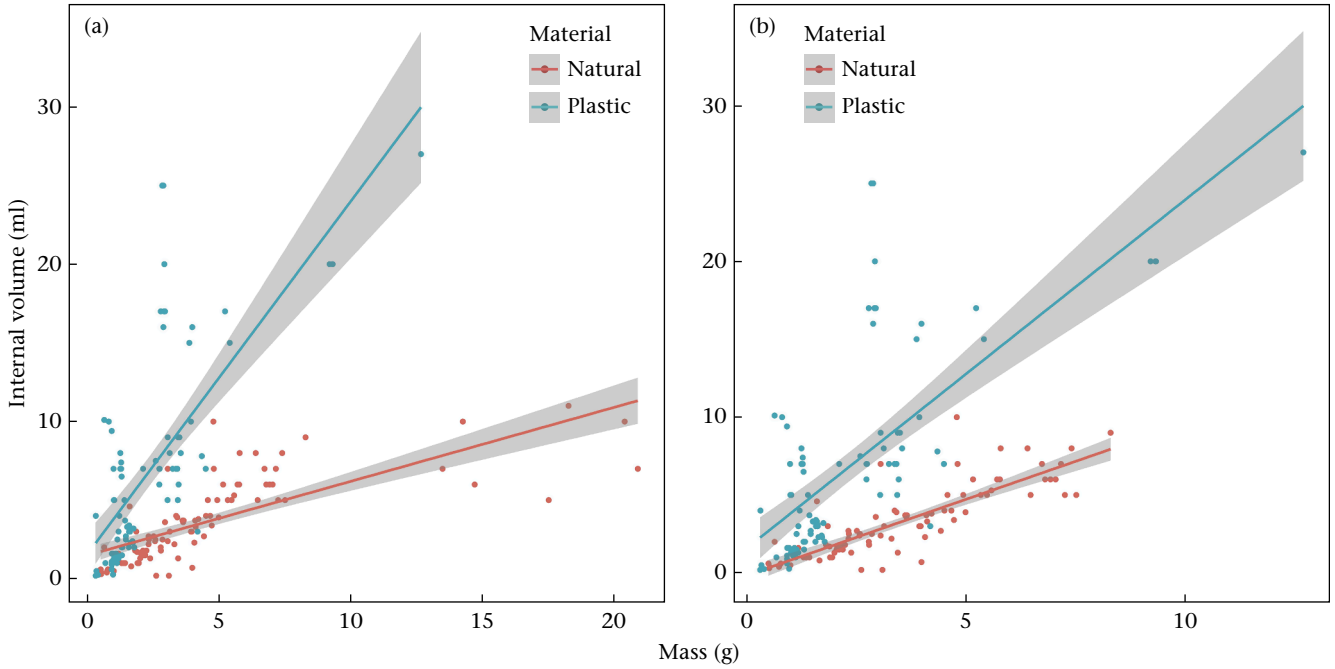

Figure 4. The relationship between object mass and internal volume for natural and plastic shells (a) including the full mass range of natural shells and (b) excluding natural shells that exceeded the mass of the largest plastic shells. Shaded areas indicate the standard error of the regression lines. Untransformed data are plotted for clarity.

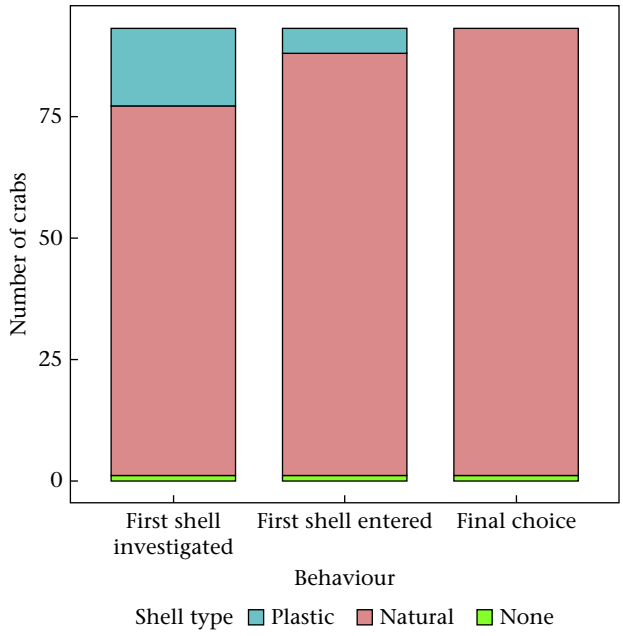

Figure 5. The number of hermit crabs investigating, making an initial entry into and a final choice of plastic and natural shells.

occupied the plastic items, despite their high abundance, while many crabs had damaged natural shells, consistent with the observation that shells are passed down across generations (Laidre, 2014).

Nevertheless, Jagiello et al. (2024) found artificial shell use in their global survey of social media reports. Our experimental data suggest such instances are rare and may be exaggerated due to observer bias, as unusual events are more likely to be reported online (Ladle et al., 2019). Our experiment showed that while hermit crabs occasionally inspect and enter plastic shells, such events are probably rare and are only likely to occur when natural alternatives are scarce. The novelty of a hermit crab using a red bottle top, for instance, increases its likelihood of being reported.

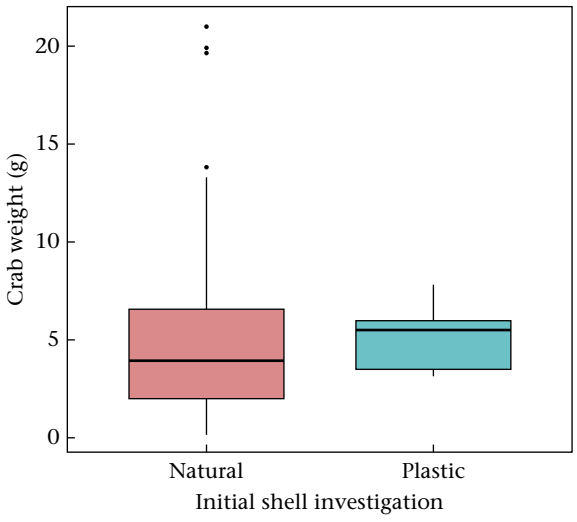

Figure 6. The average weight (g) of hermit crabs in relation to whether they initially investigated natural or plastic shells. The box spans from the first quartile (Q1) to the third quartile (Q3), and the bar represents the median. The whiskers extend to 1.5 times the interquartile range and the points indicate outliers.

Despite abundant artificial shells, hermit crabs showed a strong preference for natural ones, even when the latter were damaged. Even the low number of individuals who initially inspected plastic shells failed to enter them in the vast majority of cases, and none of those that did so remained in the plastic shell, ultimately choosing the natural shell in every case. Individuals that inspected plastic shells were larger, on average, than those that did not. The reason for this variation is unclear at present, but it may represent an ontogenic shift in inquisitiveness or the ability to discriminate suitable shells from other objects. Nevertheless, our results show a clear pattern of preference for natural shells over plastic ones. This result initially seems surprising for two reasons: first, terrestrial hermit crabs are known to trade off the internal volume of shells for their mass (Osorno et al., 1998, 2005). The strong relationship between crab size and shell size is consistent with these findings and shows that *Coenobita* is sensitive to shell mass. However, despite these observations and the ready availability of light-weight plastic alternatives, all crabs were found in relatively heavier natural shells. If crabs prioritized obtaining shells of low mass (or the ratio of shell weight to volume) above other criteria, then they should choose plastic. The fact that they prefer the heavier natural shells agrees with Osorno et al. (2005) but contradicts the hypothesis of minimizing energy expenditure proposed by Jagiello et al. (2024). Our results raise two questions: First, given that our analysis confirms that plastic shells are more beneficial in this sense, why do they favour their natural counterparts? Second, during ontogeny, hermit crabs must undergo a series of shell exchanges, sequentially swapping their current shell for a larger one to accommodate growth. If the abundance of natural shells is very low, how do they obtain the new shells they require?

We propose that examining the natural history of hermit crabs can provide answers to these questions. The result that some hermit crabs (albeit only around 5%) will enter plastic shells is interesting because it potentially shows the ability of some individuals to recognize the utility of novel objects, which is compatible with the idea of decapod sentience (Briffa, 2022; Elwood, 2022). An alternative explanation, however, is that the inspection of plastic shells before natural ones reflects errors in assessment or simply a stochastic process in terms of which item was visually detected first. The latter explanation seems more likely because around 18% of individuals initially inspected a plastic shell, but only 5% of crabs subsequently entered it, and of those individuals, all soon exchanged it for a natural one. This clear selection of natural shells directly contradicts Jagiello et al. (2024)'s suggestion that plastic shells could be preferred and is consistent with the interpretation that terrestrial hermit crabs may enter plastic shells as a last resort in the case of a shortage of natural alternatives, rather than as an adaptive strategy to minimize shell weight or as a means of adaptive camouflage on a shore polluted with plastic debris. The abundance of unoccupied gastropod shells may be low for many populations, but there are alternative mechanisms for acquiring new ones. Shells are frequently exchanged between individuals through aggression (Elwood & Neil, 1992) or nonaggressive vacancy chains (e.g. Edquist & Rotjan, 2012; Laidre, 2021). These processes lead to the persistence of natural shells in the population, allowing for adequate shells to be obtained even when the rate of arrival of new unoccupied shells through snail mortality and subsequent transport is low. For large hermit crabs, shell availability may be even more limiting (e.g. Barnes & Grave, 2002; Hsu & Soong, 2017; Laidre, 2014; Morrison & Spiller, 2006; Rotjan et al., 2010), and these individuals may be more likely to resort to using plastic shells. These phenomena may explain our result that individual hermit crabs that initially investigated plastic shells were

significantly heavier than those that went immediately to the natural shell.

Jagiello et al. (2024) suggested that artificial shell use could influence hermit crab evolution. For such an event to happen, there must be heritable variation in the tendency to select artificial shells and a fitness advantage to doing so. For a labile trait such as behaviour, heritability largely depends on repeatability (Dohm, 2002). Most studies of hermit crab personality focus on startle responses (e.g. Briffa et al., 2008), but there is evidence for repeatable individual differences in shell investigation behaviour as well (Mowles et al., 2012). In this study, we found that a minority of individuals did investigate plastic shells, but at present, the repeatability of this behaviour is unknown. As noted above, these individuals quickly abandoned plastic items for a natural shell when an empty one was present, indicative of chance encounters with plastic shells. This conclusion suggests that, under situations of abundant empty shells, investigating and temporarily occupying an artificial shell could be maladaptive due to the time and energy allocated to assessing a suboptimal shelter. However, while hermit crabs can still acquire suitable shells through alternative mechanisms, aggression is a costly activity (Briffa & Sneddon, 2007) and waiting for a new shell in a vacancy chain is time-consuming (Laidre, 2012, 2019). Thus, under conditions of low natural shell supply, occupying artificial shells could be adaptive if the costs of the mismatch between artificial shell architecture and hermit crab morphology are outweighed by the benefits of carrying a relatively lighter shell, avoidance of agonistic behaviour and of time allocated to waiting in vacancy chains, and any direct reproductive benefits (e.g. enhanced attractiveness) deriving from a plastic shell. Thus, although occupation of artificial shells is very infrequent in our study population, we do not rule out the possibility that evolutionary change in response to them could theoretically occur. To address this question, we first need longitudinal data to determine whether this behaviour is merely a chance event or a repeatable (and thus potentially heritable) trait, alongside studies of the energetics of carrying and protection afforded by plastic shells.

Many of the hypotheses proposed by Jagiello et al. (2024) remain to be tested; however, evolutionary change towards favouring plastic shells over natural ones seems unlikely within our study population. Further research is required on other *Coenobita* species and in more locations. Plastic debris is extremely prevalent on many beaches, including Playa Nancite, and is likely to have an impact on hermit crabs. Either through a shift in their shell choice towards anthropogenic litter (Jagiello et al., 2024), exposure to exudates or microplastic fragments of larger items (Briffa et al., 2024) or the more immediate and direct impact of entrapment in plastic debris (Lavers et al., 2020).

Author Contributions

Peter A. Cotton: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Maisie Benham:** Writing – original draft, Investigation. **Ashley O. Hardoin:** Writing – original draft, Investigation. **Hannah M. Lazenby:** Writing – original draft, Investigation. **Robert Puschendorf:** Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Mark Briffa:** Writing – original draft, Methodology, Formal analysis, Conceptualization.

Data Availability

Raw data are available at: https://data.mendeley.com/public-files/datasets/zprj4h8hwv/files/a7fa6ca2-f897-4072-9605-e9c158fa4963/file_downloaded.

Declaration of Interest

The authors have no competing interests to declare.

Acknowledgments

We thank Anna Jung, Jakob Goulding, Joseph Jayasekera and Phoebe Blizzard for help with the data collection. Our stay at the Nancite research station was made both possible and far more enjoyable by Pablo Aguilar and Wilbert Villachica. The fieldwork in Costa Rica for this work was made possible by support from the School of Biological and Marine Sciences, University of Plymouth.

Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2025.123347.

References

Abrams, P. (1978). Shell selection and utilization in a terrestrial hermit crab, *Coenobita compressus* (H. Milne Edwards). *Oecologia, 349*(2), 239–253. https://doi.org/10.1007/BF00345169

Ball, E. E. (1972). Observations on the biology of the hermit crab, *Coenobita compressus* H. Milne Edwards (Decapoda; Anomura) on the west coast of the Americas. *Revista de Biologia Tropical, 20*(2), 265–273.

Barnes, D. K., Galgani, F., Thompson, R. C., & Barlaz, M. (2009). Accumulation and fragmentation of plastic debris in global environments. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1526), 1985–1998. https://doi.org/10.1098/rstb.2008.0205

Barnes, D. K. A., & Grave, S. D. (2002). Temporospatial constraints in resources available to and used by hermit crabs: Tests of models. *Functional Ecology, 16*(6), 714–726. https://doi.org/10.1046/j.1365-2435.2002.00677.x

Barreiros, J. P., & Luiz, O. J., Jr. (2009). Use of plastic debris as shelter by an unidentified species of hermit crab from the Maldives. *Marine Biodiversity Records, 2*, e33. https://doi.org/10.1017/S1755267208000377

Botterell, Z. L., Ribeiro, F., Alarcón-Ruales, D., Alfaro-Córdova, E., Alfaro-Shigueto, J., Allan, N., Becerra, N., Braunholtz, L., Cardenas-Diaz, S., de Veer, D., Escobar-Sanchez, G., Gabela-Flores, M. V., Godley, B. J., Grønneberg, I., Howard, J. A., Honorato-Zimmer, D., Jones, J. S., Lewis, C., Mangel, J. C., … Galloway, T. S. (2024). Plastic pollution transcends marine protected area boundaries in the eastern tropical and south-eastern pacific. *Marine Pollution Bulletin, 201*, Article 116271. https://doi.org/10.1016/j.marpolbul.2024.116271

Briffa, M. (2022). When should we ascribe sentience to animals? A commentary on "Hermit crabs, shells and sentience" (Elwood 2022). *Animal Cognition, 25*(6), 1375–1380. https://doi.org/10.1007/s10071-022-01633-5

Briffa, M., Arnott, G., & Hardege, J. D. (2024). Hermit crabs as model species for investigating the behavioural responses to pollution. *Science of the Total Environment, 906*, Article 167360. https://doi.org/10.1016/j.scitotenv.2023.167360

Briffa, M., Rundle, S. D., & Fryer, A. (2008). Comparing the strength of behavioural plasticity and consistency across situations: Animal personalities in the hermit crab *Pagurus bernhardus*. *Proceedings of the Royal Society B: Biological Sciences, 275*(1640), 1305–1311. https://doi.org/10.1098/rspb.2008.0025

Briffa, M., & Sneddon, L. U. (2007). Physiological constraints on contest behaviour. *Functional Ecology, 21*(4), 627–637. https://doi.org/10.1111/j.1365-2435.2006.01188.x

Corcoran, P. L., Biesinger, M. C., & Grifi, M. (2009). Plastics and beaches: A degrading relationship. *Marine Pollution Bulletin, 58*(1), 80–84. https://doi.org/10.1016/j.marpolbul.2008.08.022

Cortés, J. (2017). Marine biodiversity baseline for Área de Conservación Guanacaste, Costa Rica: Published records. *ZooKeys, 652*, 129–179.

Cunningham, E. M., Mundye, A., Kregting, L., Dick, J. T. A., Crump, A., Riddell, G., & Arnott, G. (2021). Animal contests and microplastics: Evidence of disrupted behaviour in hermit crabs *Pagurus bernhardus*. *Royal Society Open Science, 8*(10), Article 211089. https://doi.org/10.1098/rsos.21108

de Carvalho-Souza, G. F., Llope, M., Tinôco, M. S., Medeiros, D. V., Maia-Nogueira, R., & Sampaio, C. L. (2018). Marine litter disrupts ecological processes in reef systems. *Marine Pollution Bulletin, 133*, 464–471. https://doi.org/10.1016/j.marpolbul.2018.05.049

Dohm, M. R. (2002). Repeatability estimates do not always set an upper limit to heritability. *Functional Ecology*, 273–280. https://doi.org/10.1046/j.1365-2435.2002.00621.x

Edquist, S. K., & Rotjan, R. D. (2012). Testing vacancy chain predictions in *Pagurus longicarpus* hermit crabs: Does ecological gain and behavioral motivation match environmental context? *Journal of Experimental Marine Biology and Ecology, 430*, 78–86. https://doi.org/10.1016/j.jembe.2012.06.018

Elwood, R. W. (2022). Hermit crabs, shells, and sentience. *Animal Cognition, 25*(5), 1241–1257. https://doi.org/10.1007/s10071-022-01607-7

Elwood, R. W., & Neil, S. J. (1992). *Assessments and decisions. A Study of Information Gathering by Hermit Crabs*. New York: Chapman & Hall.
Fox, J., & Weisberg, S. (2019). *An {R} Companion to Applied Regression* (3rd ed.). Thousand Oaks, California: Sage.
Gall, S. C., & Thompson, R. C. (2015). The impact of debris on marine life. *Marine Pollution Bulletin, 92*(1–2), 170–179. https://doi.org/10.1016/j.marpolbul.2014.12.041
Geyer, R. (2020). Production, use, and fate of synthetic polymers. In T. M. Letcher (Ed.), *Plastic waste and recycling* (pp. 13–32). Academic Press. https://doi.org/10.1016/B978-0-12-817880-5.00002-5.
Greenshields, J., Schirrmacher, P., & Hardege, J. D. (2021). Plastic additive oleamide elicits hyperactivity in hermit crabs. *Marine Pollution Bulletin, 169*, Article 112533. https://doi.org/10.1016/j.marpolbul.2021.112533
Guillén, F. C., & Osorno, J. L. (1993). Elección de concha en *Coenobita compressus* (Decapoda: Coenobitidae). *Revista de Biologia Tropical, 41*(1), 65–72.
Hills, A., & Webster, M. M. (2022). Sampling biases and reproducibility: Experimental design decisions affect behavioural responses in hermit crabs. *Animal Behaviour, 194*, 101–110. https://doi.org/10.1016/j.anbehav.2022.09.017
Hsu, C., & Soong, K. (2017). Mechanisms causing size differences of the land hermit crab *Coenobita rugosus* among eco-islands in southern Taiwan. *PLoS One, 12*(4), Article e0174319. https://doi.org/10.1371/journal.pone.0174319
Jagiello, Z., Dylewski, Ł., & Szulkin, M. (2024). The plastic homes of hermit crabs in the Anthropocene. *Science of the Total Environment, 913*, Article 168959. https://doi.org/10.1016/j.scitotenv.2023.168959
Ladle, R. J., Jepson, P., Correia, R. A., Malhado, A. C., & Gould, R. (2019). A culturomics approach to quantifying the salience of species on the global internet. *People and Nature, 1*(4), 524–532. https://doi.org/10.1002/pan3.10053
Laidre, M. E. (2012). Homes for hermits: Temporal, spatial and structural dynamics as transportable homes are incorporated into a population. *Journal of Zoology, 288*(1), 33–40. https://doi.org/10.1111/j.1469-7998.2012.00921.x
Laidre, M. E. (2014). The social lives of hermits. *Natural History, 122*(5), 24–29.
Laidre, M. E. (2019). Architectural modification of shells by terrestrial hermit crabs alters social dynamics in later generations. *Ecology, 100*(9), 1–10. https://doi.org/10.1002/ecy.2767
Laidre, M. E. (2021). The architecture of cooperation among non-kin: Coalitions to move up in nature's housing market. *Frontiers in Ecology and Evolution, 9*, Article 766342. https://doi.org/10.3389/fevo.2021.766342
Laidre, M. E., & Trinh, R. (2014). Unlike terrestrial hermit crabs, marine hermit crabs do not prefer shells previously used by conspecifics. *Crustaceana, 87*(7), 856–865. https://doi.org/10.1163/15685403-00003320
Laidre, M. E., & Vermeij, G. J. (2013). A biodiverse housing market in hermit crabs: Proposal for a new biodiversity index. *UNED Research Journal/Cuadernos de Investigación UNED, 4*(2), 175–179. https://doi.org/10.22458/urj.v4i2.5
Lavers, J. L., Sharp, P. B., Stuckenbrock, S., & Bond, A. L. (2020). Entrapment in plastic debris endangers hermit crabs. *Journal of Hazardous Materials, 387*, Article 121703. https://doi.org/10.1016/j.jhazmat.2019.121703
McDaid, A., Cunningham, E. M., Crump, A., Hardiman, G., & Arnott, G. (2023). Does microplastic exposure and sex influence shell selection and motivation in the common European hermit crab, *Pagurus bernhardus*? *Science of the Total Environment, 855*, Article 158576. https://doi.org/10.1016/j.scitotenv.2022.158576
Mollan, K. R., Trumble, I. M., Reifeis, S. A., Ferrer, O., Bay, C. P., Baldoni, P. L., & Hudgens, M. G. (2020). Precise and accurate power of the rank-sum test for a continuous outcome. *Journal of Biopharmaceutical Statistics, 30*(4), 639–648. https://doi.org/10.1080/10543406.2020.1730866
Morrison, L. W., & Spiller, D. A. (2006). Land hermit crab (*Coenobita clypeatus*) densities and patterns of gastropod shell use on small Bahamian islands. *Journal of Biogeography, 33*(2), 314–322. https://doi.org/10.1111/j.1365-2699.2005.01399.x
Mowles, S. L., Cotton, P. A., & Briffa, M. (2012). Consistent crustaceans: The identification of stable behavioural syndromes in hermit crabs. *Behavioral Ecology and Sociobiology, 66*(7), 1087–1094. https://doi.org/10.1007/s00265-012-1359-7
Nanninga, G. B., Horswill, C., Lane, S. M., Manica, A., & Briffa, M. (2020). Microplastic exposure increases predictability of predator avoidance strategies in hermit crabs. *Journal of Hazardous Materials Letters, 1*, Article 100005. https://doi.org/10.1016/j.hazl.2020.100005
Osorno, J. L., Contreras-Garduno, J., & Macías-Garcia, C. (2005). Long-term costs of using heavy shells in terrestrial hermit crabs (*Coenobita compressus*) and the limits of shell preference: An experimental study. *Journal of Zoology, 266*(4), 377–383. https://doi.org/10.1017/S0952836905007028
Osorno, J. L., Fernández-Casillas, L., & Rodríguez-Juárez, C. (1998). Are hermit crabs looking for light and large shells?: Evidence from natural and field induced shell exchanges. *Journal of Experimental Marine Biology and Ecology, 222*(1–2), 163–173. https://doi.org/10.1016/S0022-0981(97)00155-X
Pham, C. K., Ramirez-Llodra, E., Alt, C. H., Amaro, T., Bergmann, M., Canals, M., Company, J. B., Davies, J., Duineveld, G., Galgani, F., & Howell, K. L. (2014). Marine litter distribution and density in European seas, from the shelves to deep basins. *PLoS One, 9*(4), Article e95839. https://doi.org/10.1371/journal.pone.0095839
R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing [Computer software]. https://www.R-project.org/.
Rotjan, R., Chabot, J., & Lewis, S. M. (2010). Social context of shell acquisition in *Coenobita clypeatus* hermit crabs. *Behavioral Ecology, 21*(3), 639–646. https://doi.org/10.1093/beheco/arq027
Sasazuka, M., Hamasaki, K., & Dan, S. (2019). Shell utilization and shell-shedding behaviour by the land hermit crab *Coenobita spinosus*. *Ethology Ecology & Evolution, 31*(6), 544–556. https://doi.org/10.1080/03949370.2019.1630013
Sharma, K. (2018). Hazardous hermit crab homes. *Frontiers in Ecology and the Environment, 16*(5). https://doi.org/10.1002/fee.1815, 287–287.
Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: A conceptual overview. *Animal Behaviour, 85*(5), 1077–1088. https://doi.org/10.1016/j.anbehav.2013.02.017
Sih, A., Ferrari, M. C. O., & Harris, D. J. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications, 4*(2), 367–387. https://doi.org/10.1111/j.1752-4571.2010.00166.x
Steibl, S., & Laforsch, C. (2020). Shell resource partitioning as a mechanism of coexistence in two co-occurring terrestrial hermit crab species. *BMC Ecology, 20*(1), 1–9. https://doi.org/10.1186/s12898-019-0268-2
Thacker, R. W. (1996). Food choices of land hermit crabs (*Coenobita compressus* H. Milne Edwards) depend on past experience. *Journal of Experimental Marine Biology and Ecology, 199*(2), 179–191. https://doi.org/10.1016/0022-0981(95)00192-1
Valdes, L., & Laidre, M. E. (2019). Scent of death: Evolution from sea to land of an extreme collective attraction to conspecific death. *Ecology and Evolution, 9*(4), 2171–2179. https://doi.org/10.1002/ece3.4912
WoRMS Editorial Board. (2024). *World register of marine species*. https://www.marinespecies.org.