Evolutionary Ecology
https://doi.org/10.1007/s10682-024-10308-1

RESEARCH

# Behaviourally mediated camouflage in the furrowed crab (*Xantho Hydrophilus*)

**Emilia Dyer[1] · Martin Stevens[1]**

Received: 16 April 2024 / Accepted: 24 July 2024


## Abstract
Camouflage is a classic adaptation used to conceal an individual and avoid detection or recognition by both predator and prey. Research on camouflage spans both artificial systems and real animals, often focussing on the types of camouflage that exist and how they work. It has long been known that many animals also use behaviour to facilitate camouflage, but many questions remain, and most studies are limited to certain taxa such as moths and birds. Here we use behavioural choice experiments, testing the responses of furrowed crabs (*Xantho hydrophilus*) to backgrounds differing in brightness, substrate grain size, and complexity to determine if individuals use behavioural choice to facilitate camouflage. Crabs preferentially chose backgrounds that were more similar in brightness to their own appearance but showed no preference for substrate size. In addition, crabs showed some tentative, but not statistically significant, preferences for complex, high contrast environments, providing some support for recent theories on the importance of environmental complexity in facilitating improved camouflage. We also found that furrowed crabs exhibit reduced intraspecific variation in carapace colour with age, which most likely reflects ontogenetic changes in coloration that are common in crabs or may be due to greater predation on less well-camouflaged individuals. There was also some evidence that the propensity to choose backgrounds increased with age. Thus, individuals can improve their camouflage through substrate choice, and this may improve with age. These findings provide insights into the camouflage behaviour and ecology of crabs and other animals, with implications for the tuning and efficacy of camouflage strategies.

**Keywords** Camouflage · Background matching · Masquerade camouflage · Background complexity

✉ Emilia Dyer
ed463@exeter.ac.uk

Martin Stevens
martin.stevens@exeter.ac.uk

1 Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Cornwall TR10 9FE, UK

Published online: 09 August 2024

## Introduction

Camouflage is an essential mechanism for avoiding detection and recognition by both predator and prey species across the animal kingdom. An organism's ability to achieve concealment in an environment will determine their ability to survive and links with many aspects of their life history (Cott 1940; Stevens and Merilaita 2009; Cuthill 2019). Currently, there are a number of recognised methods of camouflage that work in different ways, from transparency to matching the background, and a great deal of work has tested these ideas in both artificial and natural systems (see reviews by Stevens and Merilaita 2009; Ruxton et al. 2019; Cuthill 2019). The evolution of camouflage is a classic example of natural selection and was a founding premise in Wallace's theory of protection as he observed the camouflage coloration of, for example, arctic mammals (Wallace 1889), and a great deal of other early work of Thayer (1909), Cott (1940), and others.

Much work on camouflage has focussed on the various strategies that exist, and aspects related to phenotype-environment matching, though Wallace also noted that behaviour is key. That is, animals will often choose environments that facilitate their own camouflage (Wallace 1867). Since these initial observations, researchers have sought to understand the mechanisms by which the evolution of animal coloration and behaviour occurs, with early work focussing on background choice in moths (e.g., Kettlewell 1955a; Sargent 1966), which continue to be a key study species and have been widely shown to select both backgrounds and resting postures that enhance camouflage (Kang et al. 2014, 2015). Since then, work has often explored questions of camouflage and substrate choice in birds and a few other taxa (e.g., Lovell et al. 2013; Stevens et al. 2017), and the key role that behaviour has in mediating successful camouflage across many species is increasingly recognised (Stevens and Ruxton 2019; Tan et al. 2024). The importance of behaviour is particularly relevant for individuals constrained by the bounds of their coloration that are unable to change appearance. In spite of a growing body of work, important gaps in knowledge remain regarding how animals choose backgrounds for camouflage, what features they choose, and how this relates to aspects of appearance such as intraspecific variation in colour patterns (Stevens and Ruxton 2019).

As almost all environments are heterogenous, non-colour changing species must rely on their habitat or substrate choices for camouflage to be effective. Early work on behavioural choice in camouflage focussed on moths, whereby work by Kettlewell (1955b) and Sargent (1966) found that lighter moths chose lighter backgrounds and darker moths chose darker backgrounds, using a camouflage technique referred to as background matching. These experiments were limited by the simplicity of the backgrounds but work since then with more natural backgrounds has obtained similar results in moths (Kang et al. 2013; Kang et al. 2014; Kang et al. 2015), and in various species across other taxa (Boardman et al. 1974; Kang et al. 2016; Stevens et al. 2017; Twort and Stevens 2023; reviewed by Stevens and Ruxton 2019). For example, ground nesting birds improve their egg camouflage by matching the appearance of their eggs to that of the substrate (Lovell et al. 2013; Stevens et al. 2017). Research in moths shows that individuals can also adjust their position and orientation to improve camouflage, if their initial position is not cryptic enough (Kang et al. 2013). In crustaceans, crabs have been shown to choose backgrounds of matching brightness (Jensen and Egnotovich 2015; Stevens et al. 2013; Uy et al. 2017; Price et al. 2019; Twort and Stevens 2023), and prawns will select seaweed that matches individual colour variants (Green et al. 2019). Other aquatic species, such as cuttlefish (Buresh et al. 2011; Hanlon et al. 2009) and freshwater fish (Kelley and Merilaita 2015; Kelley et al. 2017) have been shown to choose matching backgrounds to avoid detection.

Many animals that utilise camouflage vary in coloration from one individual to the next, either in the form of discrete polymorphisms or continuous variation. Such variability may arise under frequency-dependent selection stemming from predator search image formation and hunting strategies (Clarke 1962; Allen 1988; Bond and Kamil 2002; Karpestam et al. 2014; Troscianko et al. 2021). However, in many instances, intraspecific variation will arise either due to divergence in populations among habitats of different appearance (e.g. Rosenblum et al. 2010), or phenotypic plasticity with individuals changing colour to match the prevailing substrates that they live on (e.g. Green et al. 2019). Changes may also occur owing to ontogenetic processes and changes in life history with age (Booth 1990), such as in crabs (e.g. Nokelainen et al. 2019), or even with the use of different camouflage strategies among habitats (e.g. Price et al. 2019). Intraspecific variation is common in a number of brachyuran crabs (Todd et al. 2009). For example, juvenile Atlantic rock crabs (*Cancer irroratus*) exhibit a wide range of colours including white, brown and yellow, but individuals larger than 10 mm are mostly brown or very dark (Palma and Steneck 2001). Nonetheless, for all the above cases, the question arises as to whether animal groups that exhibit intraspecific variation show behavioural preferences for matching substrates, and the nature of such choices. In birds and crabs in particular, there is growing evidence that individuals can make substrate choices to improve their camouflage even in species that show continuous variation in appearance (Lovell et al. 2013; Stevens et al. 2017; Twort and Stevens 2023).

While in general we would expect animals to select backgrounds that are closer in appearance to their own colour or brightness, there may be other important considerations. For example, it is appreciated that there is a role of background complexity on an individual's camouflage success (Merilaita 2003), with camouflage being facilitated in backgrounds of higher complexity (Dimitrova and Merilaita 2010; Xiao and Cuthill 2016). This idea has been confirmed in various studies, such as those using birds, which have found detection times of targets to be longer on backgrounds of complex shapes and high contrast (Dimitrova and Merilaita 2012). As such, we may expect that animals show preferences for backgrounds that are of higher complexity. This has rarely been tested although experiments with fish have found some evidence of preferences for complex environments (Kjernsmo and Merilaita 2012).

Furrowed crabs (*Xantho hydrophilus*) are an intertidal crab species distributed around the coasts of the UK and Mediterranean (Fish and Fish 1996). They exhibit a range of colours and brightness, with lighter individuals sometimes possessing patterns that appear to vary with age. Although little research on furrowed crabs exists, it is likely their coloration and variability facilitates concealment, particularly in the furrowed crab's early life history stages, when predation threat is greatest. To our knowledge, the existence of colour change to match the background has not been properly tested in this species, and we did not observe any changes in colour or brightness during this experiment (personal observation). Likewise, our basic, provisional tests of colour change in the laboratory did not yield evidence of change (unpublished data) over a period of a few weeks, at least compared to other species such as shore crabs (e.g. Carter et al. 2020). This is perhaps not surprising since furrowed crabs have a noticeably thicker carapace than many other species. Certainly, any changes in colour that they can achieve, will be slow and, therefore, behaviour is likely to be essential for their camouflage. As a herbivorous marine decapod, living in the subtidal and littoral zone, they play an influential role in structing their benthic habitat and ecosystem, but can be heavily influenced by changes in predation (Boudreau and Worm 2012). Like many other camouflaging species, furrowed crabs are likely to use multiple, interacting camouflage mechanisms, and live on a variety of substrates that vary greatly in appearance. While there is no direct evidence, subjectively, small furrowed crabs resemble pebbles or stones (e.g., use masquerade) and will tuck their legs into a pebble form if disturbed, as well as likely using background matching. Thus, understanding whether furrowed crabs show behavioural preferences will enable a better understanding of how animals living in complex and variable environments, that themselves are diverse in appearance, achieve concealment.

Here, we use behavioural choice experiments of different habitat characteristics to establish if and how the furrowed crab uses behavioural choices to improve its camouflage. We utilise crabs of a range of colour morphs and sizes, and test these against habitat brightness, substrate grain size, and habitat complexity. We predict that each colour variant would select a substrate similar to their colour or brightness. Similarly, if furrowed crabs use masquerade camouflage, and crabs mimic pebbles in their environment, we expect crabs to show increased camouflage against a substrate with elements similar to their size. Such behaviour may also change with age, whereby as individuals increase in size, they may preferentially choose substrates with larger elements. Furthermore, we predict that crabs will preferentially camouflage in complex environments as opposed to more uniform ones, due to both concepts of background complexity improving camouflage and the heterogenous nature of the crabs' natural environment. Additionally, since we were able to sample crabs of a range of appearance, we expect the degree of variation in crab colour patterns to change with age as predation threat, and potentially the selection pressure on camouflage, changes.

## Materials and methods

### Crab collection

We sampled Furrowed crabs (*Xantho hydrophilus*) of varied sex and size from rockpools of the intertidal zone of Gyllyngvase beach, Falmouth, Cornwall, UK (50°08′33″N, 05°04′08″W). Crabs were collected from rockpools at low tide when the height was below 0.8 m (Tides4Fishing accessed 2020) between October and December 2020. To prevent overcrowding or anoxic conditions, crabs were collected in groups of four and kept in black, polyethene plastic 14.8 L buckets with 1 L of seawater in the bottom for a maximum of 45 min. At the top of the beach, with the choice chambers, individuals' carapace width was measured in millimetres, using Tacklife digital callipers (DC01), and they were weighed in grams, using Biliq waterproof, digital weighing scales, before being visually classified into colour types (brown, yellow brown, red brown grey, purple or white coloration), and assigned a light or dark shade type. Coloration and category assignment was further refined later using photos (see Colour standardisation below). Each crab was photographed on a whiteboard with their crab ID using an iPhone 6 S camera. Crabs were collected and treated in accordance with an ethics application approved by the University of Exeter Biosciences Ethics committee (eCORN003151).

## Choice chamber preparation

Two choice chambers were created using a 41.4×30.9×7.6 cm tray. The tray was split into three sections along the longest edge, using 30×10 cm pieces of 400 grit waterproof sandpaper, to create a central zone with variable habitats on either side (Fig. 1). Each side was then filled with equal weights of stones and 1 cm deep seawater straight from the sea to keep it at sea temperature, between 10-13°C. Heavy duty opaque black plastic, cut to 42.5×31.5 cm, was stretched over each habitat to create shelters on each side, whilst the central zone remained exposed. This design aimed to instigate a choice in the crabs by making the two habitats inviting, but keeping the central zone unpreferable, whilst keeping stress to a minimum by using the sandpaper for texture to help crabs grip. We haphazardly rotated the arena such that side of each habitat was changed among trials, and trays were always oriented to keep them flat and shaded to avoid a habitat being deemed preferable due to water, depth, or light conditions. There was a 5-minute interval between trials as contextual data was collected on each crab. Stones were washed, and water was changed after every second crab in each chamber to minimise any interference with crab behaviour from chemical cues left in the water.

## Experiment 1

Experiment 1 ($n=30$) tested whether crabs exhibited background matching behaviour based on the brightness of the substrate in relation to their own appearance. The two substrates were created using 1 kg each of dark and light stones, collected from Gyllyngvase beach and ranging from 1 to 45 mm in size (Fig. 1a), measured using Tacklife digital callipers. Although we did not use gravel of a specific and controlled size, we ensured that both substrates had a similar range of gravel sizes, by measuring them with callipers, such that gravel size itself would be unlikely to be a cue crabs could use for substrate choice. For this

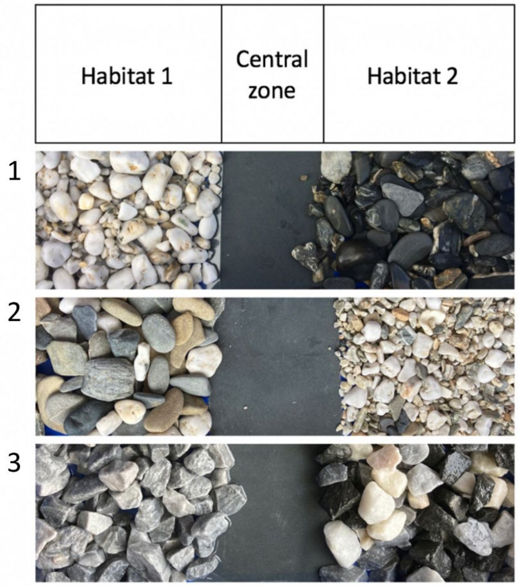


**Fig. 1** The choice chamber set-up for each of the three experiments; substrate (1) brightness, (2) size, and (3) complexity. Shelters were put over each end, keeping the central zone, made of sandpaper, exposed. Crabs acclimatised here under a cup before being released and observed as they chose between the two habitats, each made up of equal weights of stones

experiment, we collected crabs using a haphazard approach to ensure both light and dark crabs were sampled but other variables remained random.

### Experiment 2

Experiment 2 ($n=30$) was designed to explore the possible use of putative masquerade camouflage behaviour, or at least whether crabs selected gravel sizes closer to their own body size, in furrowed crabs by creating two environments with different sized stones. We tested if crabs preferentially chose habitats with stones that matched their carapace size. One substrate was made using 1 kg of small stones ranging 5–15 mm in size and the other with 1 kg of large stones ranging 25–35 mm (Fig. 1b). Both were measured using callipers. For this experiment, we adopted a targeted sampling approach to collect 15 crabs with carapace sizes within the range of the small stone substrate, and 15 crabs with carapace sizes matching the large stone substrate.

### Experiment 3

Experiment 3 ($n=30$) tested whether crabs would preferentially choose a more complex background for camouflage, regardless of substrate colour or size. For this, one substrate was made using 1.2 kg of only grey stones and the other, 1.2 kg of equal amounts of grey, black, and white stones, to retain a similar overall colour and brightness but to increase contrast complexity of the habitat (Fig. 1c). Stones were fish-safe from an approved retailer and ranged from 14 to 20 mm for both substrates. For this experiment, crabs were collected using a haphazard sampling method.

### Behavioural observations

After a 5-minute acclimatisation period under an opaque 600 ml cup, crabs were free to roam the choice chamber for 10 min. The time it took to make a choice was noted, along with the chosen background. We determined a choice to be made when the crab tucked its legs under itself and/or remained in the same place for more than 3 min. No choice was determined when the crab did not leave the central zone, even if they moved to the edge against the wall of the tray. Additionally, notes on carapace markings and behaviours, such as rigidness and curling up when touched, were taken throughout the experiment.

### Colour standardisation

Although objective quantification of colour was beyond the scope of the study here, our aim was simply to broadly categorise crabs based on general appearance. Nonetheless, to account for potential observer bias and to standardise colour assignment for crabs, two people, not affiliated with the experiment, were shown the ID photos taken of crabs and asked to assign each to one of the five colour groups: brown, yellow brown, red brown, grey, and purple. In addition, they marked each crab as either light or dark. This was checked against the original colour and shade assignment to prevent inconsistencies and improve repeatability. From this, each crab was assigned a colour category and either light or dark shade, to be used for the analysis. We acknowledge that it would have been desirable to undertake quantitative and objective analyses of crab coloration and direct matches to the background. However, the work here was undertaken during the COVID-19 pandemic and we were limited in various aspects and resources, making this not possible at the time. We note, however, that given the large differences in background appearance that analysis of substrate choice would be highly unlikely to differ with a quantitative analysis, though we would have been able to obtain more refined information on crab appearance and substrate matching.

### Size and weight analysis

Due to right skew in carapace size data, a Spearman's rank correlation was used to analyse the relationship between weight and crab carapace size, which showed a significant positive correlation between carapace size and weight (rS = 0.972, S = 3457, $n = 90$, $p < 0.001$). As the correlation was strong, we used carapace size alone in further analyses.

### Analysis/statistics

All data was analysed using statistical software R version 2024.04.01 (Build 748). Crab choices were analysed using fisher's exact tests for Experiments 1 and 2 to understand how crabs' features, brightness and size, affected their substrate choices. The small sample sizes of these experiments prevented us from using stronger tests. Experiment 3 was analysed using a binomial analysis to see whether crabs preferentially chose complex substrates, regardless of individual features. Here, a fisher's exact test could not be applied as there were not enough variables. An ANOVA was used to establish whether the carapace size of a crab, as a response variable, was dependent on the colour of the crab as the explanatory variable to assess the degree of variation across the size range, and therefore whether furrowed crabs exhibit ontogenetic colour change. A post-hoc Tukey analysis tested the direction of variation between crab colours and carapace sizes.

For the secondary analysis, exploring in more detail the behavioural choices crabs made, 'no choice' results were removed from the data set. To test the effects of crab size on the time to make a choice, data was plotted and analysed using a Spearman's rank correlation, due to skewed crab carapace size data in the data. A two-sample student's t-test was then used to establish whether or not the size/age of a crab influenced their ability to make a 'correct' choice.

## Results

### Experiment 1

To understand the distinct difference between crab shades and background shade preferences, we used a fisher's exact test. This analysis found that there was a significant, though weak, association between the two variables, suggesting that crabs will preferentially choose backgrounds of matching substrate shade (two tailed, odds ratio = 8.84, $p = 005$). Subsequent probability analysis showed that dark crabs chose matching dark backgrounds 90.9% of the time (binomial test: $p < 0.001$). Light crabs showed no detectable preference, with three crabs choosing light and three choosing dark ($p = 1$), but the sample size is too small to draw any firm conclusions (Fig. 2).

## Experiment 2

We conducted a fisher's exact test to determine if there was a significant association between crab carapace size and background susbstrate size. This test found no significant association between which shows that crabs carapace size does not have a significant effect on the chosen substrate size (two tailed, odds ratio = 1.550, $p = 0.711$) (Fig. 3).

## Experiment 3

In the third experiment, testing crabs' choices around habitat complexity, the only variable was habitat choice, so we used an exact binomial text which showed crabs had a tendency to choose a more complex than simple backgrounds, but not significantly so (Exact binomial test: proportion = 0.64, $n = 28$, $p = 0.185$) (Fig. 4).

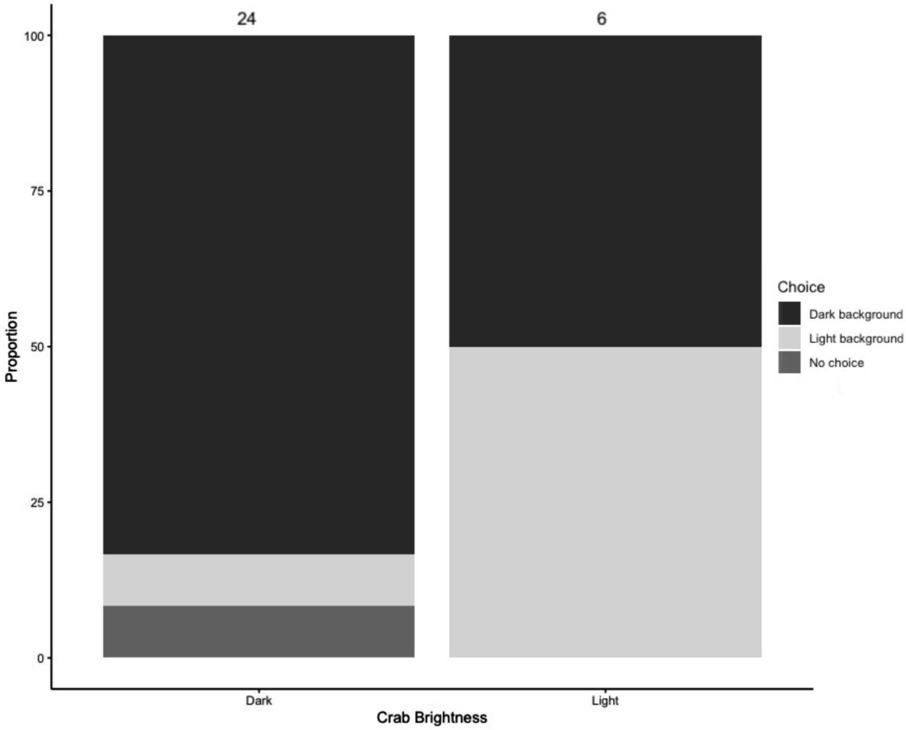


**Fig. 2** Behavioural choices for matching substrate, depending on carapace shade, facilitate crypsis. Distribution of choices made by furrowed crabs (Xantho hydrophilus) ($n = 30$) between light and dark backgrounds. Sample sizes shown above bars. When given a choice, there appears to be a preference for matching backgrounds

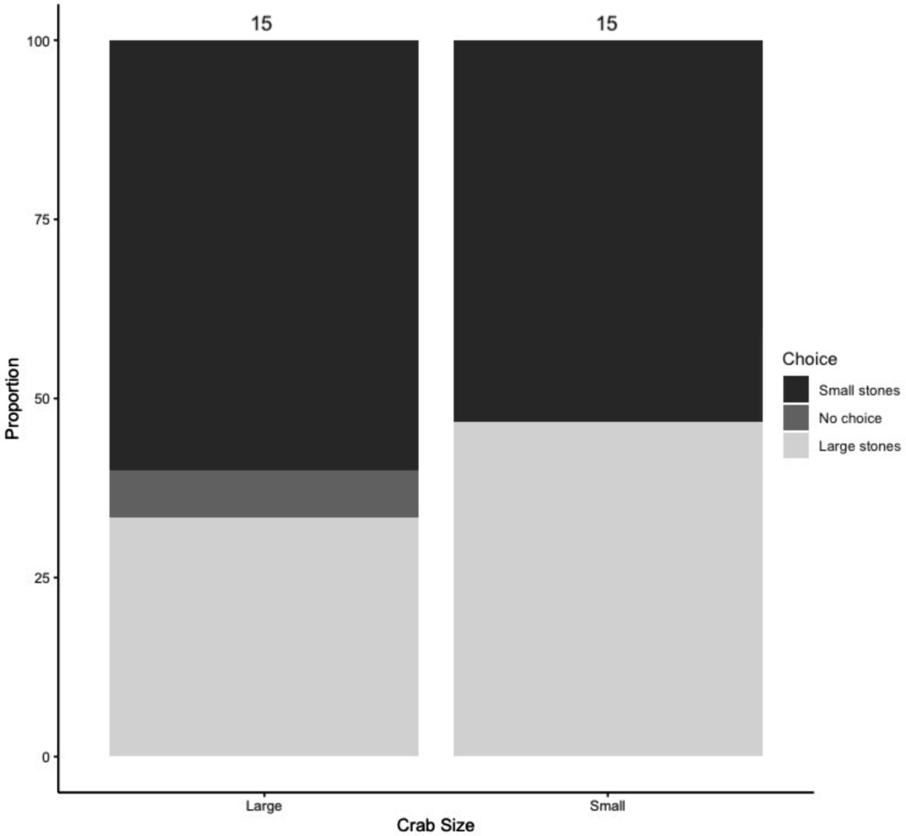


**Fig. 3** Substrate size appears not to facilitate crypsis. Distribution of background choices between the two categories of crab size, based on the substrate sizes. One habitat was comprised of small stones of 5–15 mm (light grey) and the other of large stones, 25–35 mm (black). Small and large crabs reflected these size brackets ($n=30$). Sample sizes are shown above bars. When given a choice crabs do not appear to make a preferential choice for substrate matching their body size

## Ontogenetic change in appearance

Carapace size data was log transformed due to non-normal, right skewed distribution of data. Log transformation created a normal distribution and a Levene test with a mean centre found equal variances among the log-transformed carapace size for each of the colour groups ($F_{5,84}$=1.47, $p=0.21$), so the assumptions of the model could be met. An ANOVA analysis found a significant relationship between log-transformed crab carapace size and crab carapace colour ($F_{5,84}$=9.87, $p<0.001$) (Fig. 5). Specifically, 34% of variation in colour could be accounted for by the effect of carapace size with red-brown crabs being the largest ($F_{2,84}$=4.250, $p<0.001$). A post-hoc Tukey analysis also found that red-brown crabs were larger than brown ($p=0.006$), grey ($p=0.008$), yellow brown ($p=0.001$), purple ($p=0.001$) and white ($p<0.001$) crabs. Additionally, the size of brown crabs was significantly different to the size of white crabs ($p<0.001$). All other pairs were non-significant. Small crabs exhibited a wider array of colour pattern variation than larger crabs.

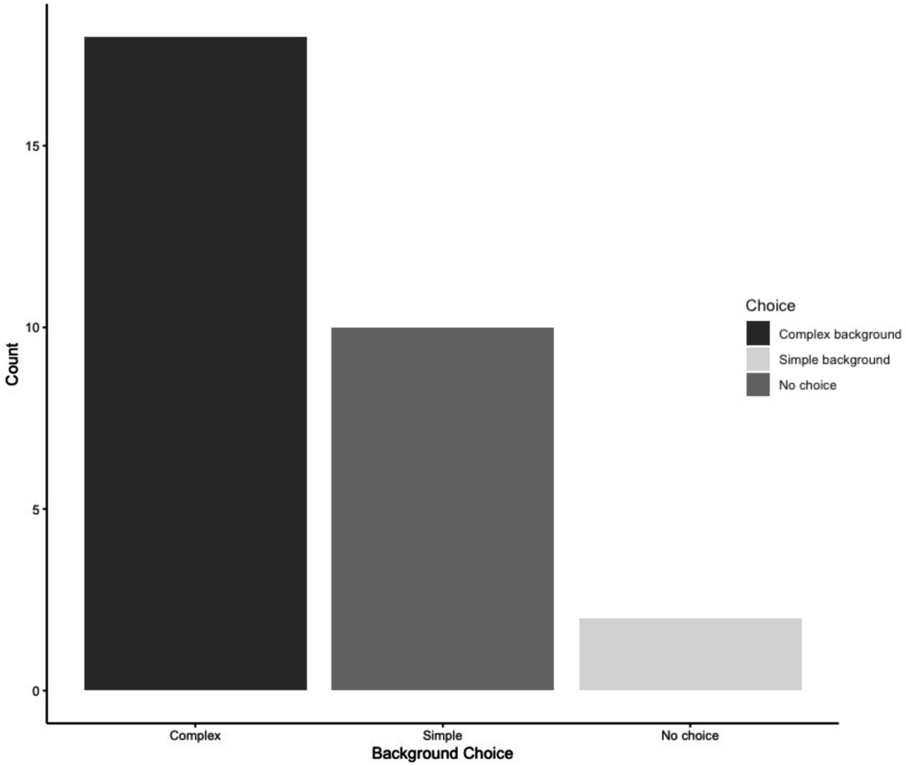


**Fig. 4** Substrate complexity facilitates crypsis. Distribution of background choices made by furrowed crabs (Xantho hydrophillus) for complex and simple backgrounds ($n=30$). Sample sizes are shown above. Complex backgrounds appear to be preferred

### Choice behaviour analysis

Due to a right skew in carapace size data, a Spearman's rank correlation was used to analyse the relationship between crab carapace size and their time to make a decision. Spearman's rank correlation showed no significant correlation between crab size and time to decision (rS = 0.003, S = 102,004, $n=85$, $p=0.9762$). This suggests that crab size, or age, does not have an effect on how long the crabs took to make a decision.

A two-sample student's t-test was used to analyse the difference between log transformed carapace size of crabs making correct and incorrect choices. The test found a significant difference between the carapace size of crabs making correct and incorrect choices ($t_{83}=2.791$, $p=0.007$): larger crabs made more correct choices in each experiment (Fig. 6.).

## Discussion

These results demonstrate that furrowed crabs (*Xantho hydrophillus*) use behaviour to facilitate camouflage according to environmental background characteristics. Crabs preferentially chose habitats that more closely match their own brightness and showed some preference

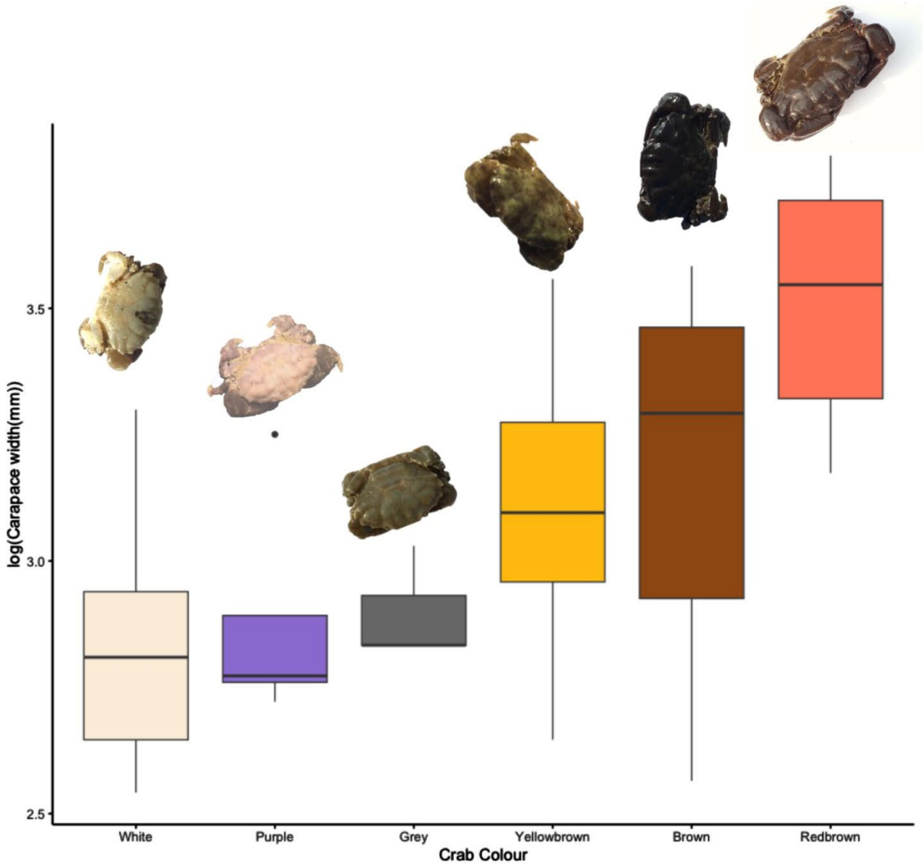


**Fig. 5** Crab colour morphs plotted against crab carapace size with a log transformation due to non-normal distribution ($n = 90$) to visualise the distribution of crab colours across the size range. Sample sizes are shown above boxes with a photo of a crab of corresponding colour. Boxes display medians and interquartile ranges, whiskers represent lowest and highest values, and black filled circles represent outliers. Smaller crabs display a greater variation in the range of colours whereas, larger crabs a predominantly brown or red brown

for more complex environments, though there are limitations in these conclusions due to the small sample sizes used. Although we did not test this directly with quantitative analyses of crab appearance, this behaviour should improve the camouflage of an individual. We found small crabs to exhibit a wide array of colour patterns, whereas large crabs were mostly red-brown or brown in colour, suggesting potential for ontogenetic colour change in the species. This is an important consideration in terms of camouflage behaviour and predation threat since colour pattern match is likely to be important for survival in this species in avoiding predation. Furthermore, we present evidence that furrowed crabs may show stronger and more appropriate choices as they age, potentially through experience or learning of certain cues in the environment. We found older, larger crabs to make more correct decisions. This suggests that older crabs exhibit more adaptive camouflage, though they were not quicker to make such choices. This could be due to reduced pressure on small crabs if they can hide

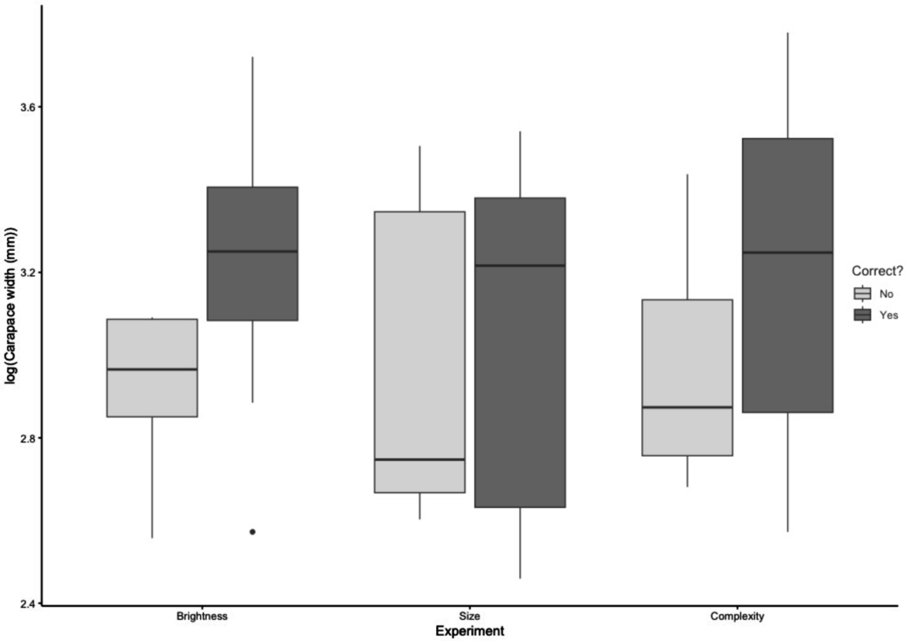


**Fig. 6** The distribution of correct and incorrect choices across the three experiments in relation to crab carapace size with a log transformation because of non-normal distribution ($n$=90). Boxes display medians and inter-quartile ranges, whiskers represent lowest and highest values, and black filled circles represent outliers. Sample sizes are shown above. Larger crabs in all three experiments make more correct choices

in the environment more easily. Alternatively, such differences could also arise if crabs that are less likely to make appropriate choices are removed from the population through predation with time.

We found that furrowed crabs chose backgrounds which better matched their own brightness (Fig. 2). This implies that their ability to camouflage in a natural environment, and thus their predation risk, is somewhat dependent on their environment and according behaviour. Dark crabs exhibited background matching behaviour more strongly than light crabs, which only chose light backgrounds 50% of the time, though we note that light crabs had a particularly small sample size. Background matching has been observed in other crustaceans such as the chameleon prawn (*Hippolyte varians*) (Green et al. 2019), yellow shore crab (*Hemigrapsus oregonensis*) (Jensen and Egnotovich 2015), and horned ghost crabs (*Ocypode ceratophthalma*), with individuals preferentially choosing backgrounds according to their own coloration (Stevens et al. 2013), though Uy et al. (2017) noted that intermediate colorations of the pallid ghost crab (*Ocypode pallidula*) showed little preference for either extreme. This is likely due to the fact that the environment of the pallid ghost crabs exhibits both of the extremes tested in the experiment.

While the fisher's exact test indicates that there is an association between crab colour and background choice, more research should be done with larger sample sizes to determine how strong this preference is and to what extent, environmental imprinting has an effect. In this experiment, furrowed crabs were collected from the rockpools of Gyllyngvase beach where the substrate is heterogenous in colour but, on the whole, is fairly dark. The contrasting light stones were collected from elsewhere on the same beach, in sandy areas, where crabs are not found as frequently, although lower on the shore the sandy patches can become quite light. Therefore, a preference for darker stones could have been largely due to the darker habitat better resembling crabs' natural habitat and could explain the weaker preference found in lighter crabs. Similarly, Twort and Stevens (2023) found common shore crabs (*Carcinus maenas*) to preferentially choose backgrounds which matched their own brightness, if the environment resembled a rockpool pattern. Our results align with these observations and suggest that, this species' overall camouflage strategy is potentially influenced by their predominant environment, driving a general preference for darker substrates, though an individual's specific coloration has some effect on their background matching behaviour to persist in the highly changeable littoral zone. The extent to which crabs learn or imprint on their environment, and to which choice is mediated by specific individual coloration is unknown, and lab-based experiments with more detailed colour classification to test this would help answer these issues. Indeed, previous experiments in newts have found imprinting to be a factor in background choice (Polo-Cavia and Gomex-Mestre 2017).

Crabs showed no preference for stones of corresponding size in Experiment 2 (Fig. 3), but the substrate of rockpools is heterogenous in size, and therefore it is perhaps unlikely that crabs have evolved under selection pressure to mimic the size of pebbles, not least since this will change with age and growth. Rather, it is more likely they broadly resemble pebbles of a spectrum of sizes and with their carapace colour, all of which can be found in rockpools, along with their behaviour. During crab collection and the trials, we noted that individuals would often remain very still, sinking down into the stones as they were approached, touched, or, in the trials, when they had settled on a choice. Therefore, rather than specifically matching the size of substrate around them, it seems possible that furrowed crabs resemble stones with carapace and behaviour as this has been shown to be a key aspect to success in masquerade camouflage (Stevens and Ruxton 2019; Suzuki and Sakurai 2015). However, research on cuttlefish (*Sepia officinalis*) found that whilst individuals will masquerade as something 3D, they will alter their camouflage mechanism if the 2D background has high contrast as this makes their camouflage easier (Buresch et al. 2011). This demonstrates how individuals will change their camouflage behaviour depending on the environment available but suggests that a complex environment is preferable.

High complexity environments offer a route to improved camouflage (Hughes et al. 2019; Merilaita 2003; Rowe et al. 2021; Stevens and Ruxton 2019; yet there is limited empirical research in natural systems. Our results here show some tentative (albeit non-significant) support for the concept (Fig. 4), though we suggest that more work be conducted with a larger sample size to determine the extent of this trend. In experiment 3, crabs showed a slight preference for a habitat with three contrasting colours, as opposed to one of the same overall brightness with uniform substrate. This suggests that furrowed crabs could have a potential ability to observe contrast and may recognise it as a benefit to camouflage. Empirical evidence is limited, so research on the extent to which other rockpool species can recognise contrast is an interesting area of potential future work. However, again, rockpools are a heterogenous environment and therefore often exhibit contrast so their preference for a natural habitat could be a potential reason for the behavioural choice observed. The preference for complexity has been studied behaviourally before in marine systems in the least killifish (*Heterandria formosa*), with the study finding preferences for complexity in backgrounds was only evident when individuals were faced with predation pressure, and only in females (Kjernsmo and Merilaita 2012). Nevertheless, our findings presented here, offer a further understanding of complexity-related camouflage behaviour which can be related to other common camouflage strategies found in rockpool environments, such as disruptive coloration (Price et al. 2019).

A strategy of high variation in camouflaged individual appearances has been shown to be most successful in heterogenous environments (Sherratt et al. 2006), such as rock pools. Our study found colour variation to be most evident among juvenile furrowed crabs (Fig. 5), whereas larger, older individuals tended to be brown or red brown. Juvenile crabs are known to be vulnerable to predation in their early life stages which could explain the high degree of variation here. Not mutually exclusively, the lower degree of variation in larger crabs could result from less effectively camouflaged individuals being preyed upon more heavily than darker, brown individuals, in early life history stages. Colour variation, or polymorphisms, can confuse the search image of predators and allow crabs some safety as they camouflage in their environment (Bond 2007; Karpestam et al. 2014), including in the sympatric and also highly variable shore crab (Troscianko et al. 2021). Crabs are desirable prey in their juvenile stages (Palma and Steneck 2001), which makes effective camouflage, particularly in early life stages, essential to survival. We present evidence here that colour variation may be a critical aspect of the juvenile furrowed crabs' camouflage strategy, but that this changes with age and size, potentially resulting from ontogenetic colour change. Evidence of ontogenetic colour change has previously been found in common shore crabs in response to changes in predation threat, behaviour, and habitat use (Todd et al. 2006; Palma and Steneck 2001; Nokelainen et al. 2019). Therefore, as furrowed crabs age and grow similar changes in selection pressure may arise. However, we acknowledge that our current work lacks quantitative assessment of crab appearance and camouflage, and future work should quantify levels of variation and match to the background objectively, or with regards to predator vision. We also recognise the potential that reduced variation in older crabs could be as a result of biased predation pressure in early life stages.

As crabs aged, they also chose the more advantageous habitat to camouflage in more frequently, making them more effective in their camouflage (Fig. 6.). We found larger crabs to make more 'correct' choices than smaller ones, which provides some evidence that crabs may learn improved camouflage tactics as they age (or that crabs with less refined behavioural choices are more heavily preyed upon). Such adaptive behaviour has been rarely experimentally tested before but there is some evidence to support the idea. Research in other species such as birds (Stevens et al. 2017) and cuttlefish (*Sepia pharaonis*) (Lee et al. 2012) has indicated evidence of learning in camouflage behaviour. It is also likely that ontogenetic colour change, or an increased fitness of darker coloration, plays a role in this behaviour too. More research on predation pressure and learning in furrowed crabs would be valuable to establish the linking mechanisms between ontogeny and background choice.

Our research provides insights into the behaviourally mediated camouflage of furrowed crabs (*Xantho hydrophilus*) and could be applied to a number of other under-studied, camouflaging species. Furrowed crabs appear to make finely tuned camouflage behavioural choices within their environment, likely to avoid detection, for both background brightness and complexity, favouring closely matching substrates and possibly also more complex backgrounds, though future work with larger sample size would provide further insights into these behavioural dynamics. There was little preference for matching substrate size, though there is potential for masquerade behaviour, independent of size and preferences may occur between more extreme backgrounds, such as fine sand and larger pebbles. We also provide evidence that camouflage strategies change with age in that there is evidence of ontogenetic colour change in the species, tentatively linked to a change in predation threat with size and age. There is some evidence that crabs learn and improve camouflage behaviour with age, but future work with a greater focus on habitat imprinting in crabs would decipher the extent to which our results are due to the crabs choosing habitats that they recognised, as opposed to a camouflage driven preference for high contrast and complexity. The potential for such fine-tuned behaviour to be exhibited in a number of other rockpool species is an interesting line of potential subsequent work and would create a better understanding of the ecological environment and how adaptive coloration is tuned in complex real-world habitats.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s10682-024-10308-1.

**Author contributions** E.D and M.S developed experimental design. E.D carried out the experiments and conducted analysis under guidance of M.S. E.D wrote the main manuscript text and produced all figures. M.S reviewed the manuscript.

**Funding** Not applicable.

**Data availability** Data is provided within the manuscript or supplementary information files.

**Code availability** Not applicable.

## Declarations

**Ethical approval** Ethics approved by the University of Exeter Biosciences Ethics committee (eCORN003151).

**Consent to participate** Not applicable.

**Consent for publication** Not applicable.

**Competing interests** The authors declare no competing interests.



## References

Allen JA (1988) Frequency-dependent selection by predators. Philosophical Trans Royal Soc Lond B Biol Sci 319(1196):485–503

Boardman M, Askew RR, Cook LM (1974) Experiments on resting site selection by nocturnal moths. J Zool 172:343–355

Bond AB (2007) The evolution of color polymorphism: crypticity, searching images, and apostatic selection. Annual Review of Ecology, Evolution, and Systematics 38

Bond AB, Kamil AC (2002) Visual predators select for crypticity and polymorphism in virtual prey. Nature 415(6872):609–613

Booth CL (1990) Evolutionary significance of ontogenetic colour change in animals. Biol J Linn Soc 40(2):125–163

Boudreau SA, Worm B (2012) Ecological role of large benthic decapods in marine ecosystems: a review. Mar Ecol Prog Ser 469:195–213

Buresch KC, Mäthger LM, Allen JJ et al (2011) The use of background matching vs. masquerade for camouflage in Cuttlefish Sepia officinalis. Vision Res 51(23–24):2362–2368

Carter EE, Tregenza T, Stevens M (2020) Ship noise inhibits colour change, camouflage and anti-predator responses in shore crabs. Curr Biol 30(5):211–212

Clarke BC (1962) Balanced polymorphism and the diversity of sympatric species. In Taxonomy and geography

Cott HB (1940) Adaptive coloration in animals

Cuthill IC (2019) Camouflage. Abstr J Zool 308(2):75–92. https://doi.org/10.1111/jzo.2019.308.issue-210.1111/jzo.12682

Dimitrova M, Merilaita S (2010) Prey concealment: visual background complexity and prey contrast distribution. Behav Ecol 21(1):176–181

Dimitrova M, Merilaita S (2012) Prey pattern regularity and background complexity affect detectability of background-matching prey. Behav Ecol 23(2):384–390

Fish JD, Fish S (1996) A Student's Guide to the Seashore, 2nd Edition, Cambridge, New York, Cambridge University Press, viewed 20 October 2020, <>//archive.org/details/studentsguideto00fish/page/404/mode/2up?q=xantho+

Green SD, Duarte RC, Kellett E et al (2019) Colour change and behavioural choice facilitate chameleon prawn camouflage against different seaweed backgrounds. Commun Biology 2(1):1–10

Hanlon RT, Messenger JB (1988) Adaptive coloration in young cuttlefish (Sepia officinalis L.): the morphology and development of body patterns and their relation to behaviour. Philosophical Transactions of the Royal Society, Series B 320: 437–487.

Hanlon RT, Chiao CC, Mäthger LM, Barbosa A, Buresch KC and Chubb C (2009 Cephalopod dynamic camouflage: bridging the continuum between background matching and disruptive coloration. Philosophical Transactions of the Royal Society B: Biological Sciences, 364(1516): 429–437.

Hughes A, Liggins E, Stevens M (2019) Imperfect camouflage: how to hide in a variable world? Proc Royal Soc B 286(1902):20190646

Jensen GC, Egnotovich MS (2015) A whiter shade of male: Colour background matching as a function of size and sex in the yellow shore crab Hemigrapsus oregonensis (Dana, 1851). Curr Zool 61(4):729–738

Kang CK, Moon JY, Lee SI, Jablonski PG (2013) Moths on tree trunks seek out more cryptic positions when their current crypticity is low. Anim Behav 86:587–594

Kang C, Moon JY, Lee SI, Jablonski PG (2014) Moths use multimodal sensory information to adopt adaptive resting orientations. Biol J Linn Soc 111:900–904

Kang C, Stevens M, Moon JY, Lee SI, Jablonski PG (2015) Camouflage through behavior in moths: the role of background matching and disruptive coloration. Behav Ecol Sociobiol 26:45–54

Kang CK, Kim YE, Jang Y (2016) Colour and pattern change against visually heterogeneous backgrounds in the tree frog Hyla japonica. Sci Rep 6:22601

Karpestam E, Merilaita S, Forsman A (2014) Natural levels of colour polymorphism reduce performance of visual predators searching for camouflaged prey. Biol J Linn Soc 112(3):546–555

Kelley JL, Merilaita S (2015) Testing the role of background matching and self-shadow concealment in explaining countershading coloration in wild-caught rainbowfish. Biol J Linn Soc 114(4):915–928

Kelley JL, Taylor I, Hart NS, Partridge JC (2017) Aquatic prey use countershading camouflage to match the visual background. Behav Ecol 28(5):1314–1322

Kettlewell HBD (1955a) Recognition of appropriate backgrounds by the pale and black phases of Lepidoptera. Nature 175:943–944

Kettlewell HBD (1955b) Selection experiments on industrial melanism in the Lepidoptera Heredity. 9(3):323–342. https://doi.org/10.1038/hdy.1955.36

Kjernsmo K, Merilaita S (2012) Background choice as an anti-predator strategy: the roles of background matching and visual complexity in the habitat choice of the least killifish. Proc Royal Soc B 279(1745):4192–4198

Lee YH, Yan HY, Chiao CC (2012) Effects of early visual experience on the background preference in juvenile cuttlefish Sepia pharaonis. Biol Lett 8:740–743

Lovell PG, Ruxton GD, Langridge KV, Spencer KA (2013) Individual quail select egg-laying substrate providing optimal camouflage for their egg phenotype. Curr Biol 23:260–264

Merilaita S (2003) Visual background complexity facilitates the evolution of camouflage. Evolution 57:1248–1254

Nokelainen O, Maynes R, Mynott S et al (2019) Improved camouflage through ontogenetic colour change confers reduced detection risk in shore crabs. Funct Ecol 33(4):654–669

Palma AT, Steneck RS (2001) Does variable colouration in juvenile marine crabs reduce risk of visual predation? Ecology 82(10):2961–2967

Polo-Cavia N, Gomez-Mestre I (2017) Pigmentation plasticity enhances crypsis in larval newts: associated metabolic cost and background choice behaviour. Sci Rep 7:39739

Price N, Green S, Troscianko J et al (2019) Background matching and disruptive coloration as habitat-specific strategies for camouflage. Sci Rep 9(1):1–10

Rosenblum EB, Römpler H, Schöneberg T, Hoekstra HE (2010) Molecular and functional basis of phenotypic convergence in white lizards at White Sands. Proc Natl Acad Sci USA 107:2113–2117

Rowe ZW, Austin DJ, Chippington N, Flynn W, Starkey F, Wightman EJ, Scott-Samuel NE, Cuthill IC (2021) Background complexity can mitigate poor camouflage. Proc Royal Soc B 288(1963):20212029

Ruxton GD, Allen WL, Sherratt TN, Speed MP (2019) Avoiding attack: the evolutionary ecology of crypsis, aposematism, and mimicry. Oxford University Press

Sargent TD (1966) Background selections of geometrid and noctuid moths. Science 154(3757):1674–1675. https://doi.org/10.1126/science.154.3757.1674

Sherratt TN, Pollitt D, Wilkinson DM (2006) The evolution of crypsis in replicating populations of web-based prey. Oikos 116:449–460

Stevens M, Ruxton GD (2019) The key role of behaviour in animal camouflage. Biol Rev 94:116–134

Stevens S, Merilaita S (2009) Animal camouflage: current issues and new perspectives. Philos Trans R Soc B Sci 364(1516):423–427. https://doi.org/10.1098/rstb.2008.0217

Stevens M, Rong CP, Todd PA (2013) Colour change and camouflage in the horned ghost crab Ocypode Ceratophthalmus. Biol J Linn Soc 109(2):257–270

Stevens M, Troscianko J, Wilson-Aggarwal JK, Spottiswoode CN (2017) Improvement of individual camouflage through background choice in ground-nesting birds. Nat Ecol Evol 1(9):1325–1333

Suzuki TN, Sakurai R (2015) Bent posture improves the protective value of bird dropping masquerading by caterpillars. Anim Behav 105:79–84

Tan M, Zhang S, Stevens M, Li D, Tan EJ (2024) Antipredator defences in motion: animals reduce predation risks by concealing or misleading motion signals. Biological Reviews

Thayer GH (1909) Concealing-coloration in the animal kingdom: an exposition of the laws of disguise through color and pattern: being a summary of Abbott H. Thayer's discoveries. Macmillan, New York, NY

Tides for Fishing, Falmouth Tide Times, accessed (2020) https://tides4fishing.com/uk/england/falmouth#_tides

Todd PA, Briers RA, Ladle RJ, Middleton F (2006) Phenotype-environment matching in the shore crab (Carcinus maenas). Mar Biol 148:1357–1367

Todd PA, Qiu W, Chong KY (2009) Ontogenetic shifts in carapace patterning and/or colouration in intertidal and subtidal brachyuran crabs. Raffles Bull Zool 57(2):543–550

Troscianko J, Nokelainen O, Skelhorn J, Stevens M (2021) Variable crab camouflage patterns defeat search image formation. Commun Biology 4(1):1–9

Twort L, Stevens M (2023) Active background selection facilitates camouflage in shore crabs, Carcinus maenas. Anim Behav 203:1–9

Uy FMK, Ravichandran S, Patel KS et al (2017) Active background choice facilitates crypsis in a tropical crab. Biotropica 49(3):365–371

Wallace AR (1867) Mimicry and other protective resemblances among animals. Westminst Rev 1:1–43

Wallace AR (1889) Darwinism. An exposition of the theory of natural selection with some of its applications. Macmillan & Co, London, UK

Xiao F, Cuthill IC (2016) Background complexity and the detectability of camouflaged targets by birds and humans. Proceedings of the Royal Society B: Biological Sciences 283(1838): 20161527

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.