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Rock pool fish use a combination of colour change and substrate choice to improve camouflage

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Camouflage can be achieved by both morphological (e.g. colour, brightness and pattern change) and behavioural (e.g. substrate preference) means. Much of the research on behavioural background matching has been conducted on species with fixed coloration and body patterns, while less is known about the role background choice plays in species capable of rapid (within minutes or seconds) colour change. One candidate species is the rock goby, *Gobius paganellus*, a common rock pool fish capable of rapid changes in colour and brightness when placed on different backgrounds. However, their ability to match different backgrounds is not unbounded, with some colours and brightness being easier to match than others, thus raising the possibility that gobies may use behavioural background matching to make up for their limited ability to match certain backgrounds. We used digital image analysis and a model of predator vision to investigate the ability of rock gobies to match chromatic (beige and greenish-grey) and achromatic (varying brightness) backgrounds. We then conducted choice experiments to determine whether gobies exhibited a behavioural preference for the backgrounds they were best at matching. Gobies rapidly changed their colour and brightness when placed on the different backgrounds. However, the level of camouflage differed between backgrounds: fish were better at matching beige than greenish-grey, and darker than lighter backgrounds. When given the choice, gobies displayed a behavioural preference for the backgrounds they were best at matching. Our findings therefore show that rock gobies, and probably other animals, use a combination of morphological and behavioural means to achieve camouflage and in doing so mitigate limitations in either approach alone.

Camouflage through cryptic coloration is one of the most widespread antipredator strategies in nature (Cott, 1940; Ruxton, Sherratt, & Speed, 2004; Stevens & Merilaita, 2009; Thayer, 1909). The term crypsis is used to describe coloration that primarily prevents detection, and encompasses several different forms of camouflage including countershading, background matching and disruptive coloration (Stevens & Merilaita, 2009). Probably the most common form of crypsis is background matching (Merilaita & Stevens, 2011), which occurs when an animal's appearance matches the overall colour (hue and saturation), brightness and pattern of one or several background types (Stevens & Merilaita, 2009).

The overall appearance of many species, for example numerous members of the Lepidoptera, has evolved to match the appearance of specific backgrounds, such as tree bark (e.g. Endler, 1984; Kettlewell, 1955). Other species may have evolved coloration and body patterns that are a compromise between the attributes of multiple backgrounds rather than specializing to match a single specific background (Houston, Stevens, & Cuthill, 2007; Merilaita, Lyytinen, & Mappes, 2001; Merilaita, Tuomi, & Jormalainen, 1999). For crypsis to be effective, many animals of fixed appearance exhibit behavioural background matching: they actively choose backgrounds that match their own species, morph or individual level appearance (e.g. Kang, Moon, Lee, & Jablonski, 2013, 2012; Kettlewell & Conn, 1977; Lovell, Ruxton, Langridge, & Spencer, 2013; Marshall, Philpot, & Stevens, 2016; Stevens, Troscianko, Wilson-Aggarwal, & Spottiswoode, 2017; reviewed by Stevens & Ruxton, 2018). However, although a fixed camouflage pattern increases survival against predators (Troscianko, Wilson-Aggarwal, Stevens, & Spottiswoode, 2016) it can carry a number of costs (Ruxton et al., 2004). For instance, a fixed appearance restricts an animal to remaining on a specific background and may prevent prey from taking advantage of potential opportunities, such as foraging on a nonmatching substrate

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(Ruxton et al., 2004), and being limited in their ability to cope with spatial or temporal uncertainty in the environment (Caro, Sherratt, & Stevens, 2016).

One way that animals may overcome the constraints that arise due to camouflage being tied to a specific background type(s) is to actively alter their appearance in response to changes in their visual background (Duarte, Flores, & Stevens, 2017; Stuart-Fox & Moussalli, 2009). Colour change (here used to encompass changes in pattern and brightness as well as colour) has been documented in many animal linages, including reptiles (e.g. Stuart-Fox, Moussalli, & Whiting, 2008), fish and amphibians (e.g. Sköld, Aspengren, & Wallin, 2013), crustaceans (e.g. Stevens, Lown, & Wood, 2014; Stevens, Rong, & Todd, 2013) and cephalopods (e.g. Hanlon & Messenger, 1988). While cephalopods provide the most extensively studied examples of rapid (seconds) colour change it is also common among teleost fishes (Sköld et al., 2013), with several species known to change colour and brightness in response to changes in the prevailing light conditions of their environment (e.g. Clarke & Schluter, 2011; Kelley, Phillips, Cummins, & Shand, 2012). Other species change colour and brightness to match that of different substrates (Kelman, Tiptus, & Osorio, 2006; Lanzing, 1977; Ramachandran et al., 1996; Sumner, 1935). The speed of colour change does, however, vary considerably between species. Among flatfish for instance, species such as English sole, *Parophrys vetulus*, northern rock sole, *Lepidopsetta polyxystra*, and Pacific halibut, *Hippoglossus stenolepis*, take several hours to days to fully change colour (Ryer, Lemke, Boersma, & Levas, 2008), while eyed flounder, *Bothus ocellatus*, take 2–8 s to match their background (Ramachandran et al., 1996).

While the ability to change colour and brightness for camouflage is likely to provide a clear survival advantage (Duarte et al., 2017; Fairchild & Howell, 2004; Sumner, 1935), the ability of animals to match different backgrounds is not unbounded, with some backgrounds being easier to match than others (e.g. Stevens, Lown, & Denton, 2014). Furthermore, colour change is also widely thought to involve some degree of energetic cost and constraints, probably limiting its use (Rodgers, Gladman, Corless, & Morrell, 2013; Polo-Cavia & Gomez-Mestre, 2017; reviewed by Duarte et al., 2017). Potentially as a result of these and other issues, a number of colour-changing species also exhibit some degree of behavioural background matching (e.g. Duarte et al., 2017; Garcia & Sih, 2003; Polo-Cavia & Gomez-Mestre, 2017; Ryer et al., 2008; Stevens & Ruxton, 2018; Tyrie, Hanlon, Siemann, & Uyarra, 2015). The peacock flounder, *Bothus lunatus*, for example, prefers substrates that it is able to match while avoiding those it cannot (Tyrie et al., 2015). However, the relative importance of both colour and brightness change and substrate choice for camouflage is still little known, and rarely quantified in the context of predator vision.

Stevens, Lown, & Denton (2014) found that although rock gobies, *Gobius paganellus*, are capable of rapid (occurring within 1 min) changes in colour (hue and saturation) and brightness, the level of achievable background matching depends heavily on the colour and brightness of their background. However, the coloured backgrounds used by Stevens, Lown, & Denton (2014) did not resemble those found within natural habitats. Smithers, Wilson, and Stevens (2017) went on to show that these fish also change their body pattern when placed on backgrounds with different-sized features. When the fish were tested on backgrounds resembling backgrounds with different-sized features found in natural substrates, the level of camouflage achievable differed greatly between backgrounds (Smithers et al., 2017). This raises questions regarding whether fish such as the rock goby also exhibit behavioural background matching, to make up for their limited ability to match certain backgrounds.

This study aimed to test whether intertidal species such as the rock goby use background choice, in combination with colour and brightness change, to achieve camouflage. Being an intertidal species, rock gobies are exposed to both marine and terrestrial predators and a wide range of backgrounds and physical disturbance such as tides and waves that can push individuals around the habitat. We first investigated the ability of rock gobies to match (1) two different hues (beige and greenish-grey) inspired by natural substrates found within rock pools in experiment 1, and (2) four achromatic backgrounds that differed in brightness (black, dark grey, light grey and white) in experiment 2. In the rock pool environment where the work was undertaken, there exists a range of features (including rocks) that vary from bright white through to black. We then tested whether the fish displayed a behavioural preference for either (1) beige or greenish-grey in experiment 3, and (2) black or white in experiment 4. We predicted that the fish would be better at matching one hue (in experiment 1) or brightness (in experiment 2) than the others tested, and that fish would display a behavioural preference for the hue (in experiment 3) or brightness (in experiment 4) that they were best at matching. If, however, there was no difference in the level of background-matching camouflage between the backgrounds tested then we predicted the fish would show no behavioural background preference. Digital image analysis and a model of predator vision were used to quantify changes in hue, saturation, luminance (perceived brightness) and overall camouflage as per previously outlined methods.

METHODS

The study was carried out in situ on Gyllyngvase beach, Falmouth, Cornwall, U.K. (50.1441°N, 5.0684°W) where rock gobies were collected using a dip net from the local rock pools.

Ethical Note

All work was conducted under approval from the University of Exeter Biosciences ethics committee (application 2015/739). Gyllyngvase beach is public land and no further licences or permits were needed. The experimental set-up was designed to minimize stress to the animals and all individuals were returned unharmed to their original rock pool area immediately after being tested. Rock gobies are not an endangered or protected species.

Generating the Experimental Backgrounds

All backgrounds were generated in the graphics program inkscape v0.48 (https://inkscape.org/en/release/0.48) and printed on either HP LaserJet Tough paper (Hewlett Packard, Palo Alto, CA, U.S.A.; experiment 1) or Xerox Premium NeverTear waterproof paper (Xerox, Norwalk, CT, U.S.A.; all other experiments) with a Hewlett Packard LaserJet 500 colour M551 PCL6 printer.

Beige and green-grey chromatic backgrounds

Our approach to generating the printed chromatic backgrounds was similar to that used by Kang, Kim, and Jang (2016). To make our printed colours somewhat representative of those within the rock pools we took photos (from above) of two common substrate types that we subjectively classified as being either beige (four photos of wet sand) or greenish-grey (nine photos of rock which was often covered in a greenish biofilm; see Appendix Fig. A1 for examples). A Spectralon grey reflectance standard (Labsphere, Congleton, U.K.), which reflects 40% of all wavelengths between 300 and 750 nm was included in each photo (see section below on image analysis for