INTRODUCTION

Stomatopods engage in a highly dynamic lifestyle that includes ritual combat, territoriality, and active predation of live prey. Adaptations to this lifestyle include powerful raptorial appendages and an extraordinarily complex visual system, which includes 12-channel colour vision and the ability to discriminate the polarization of light. The neural processing underlying their colour vision has yet to be determined, though there is some evidence that the stomatopod colour vision system is based on wavelength recognition rather than spectral discrimination. We show that *Odontodactylus scyllarus* has an innate preference for objects that reflect wavelengths between 575 nm and 600 nm (corresponding to the human ‘yellow’). Comparatively, they show a reduced preference for objects that reflect both at shorter wavelengths, between 525 nm and 575 nm (human ‘green’) and at longer wavelengths, between 600 nm and 650 nm (human ‘red’). Within the wavelength preference, decisions are affected by the contrast of the object, with choice directed towards the version of the object that exhibited a greater Weber contrast against the background, despite reflecting in the same wavelength interval. As for other animals, the innate preference for objects reflecting particular wavelengths may act to increase the fitness of naive animals.

**Key Words:** decision-making, mantis shrimps, neural processing, vision

Perhaps the most enigmatic feature of stomatopods is their visual system. Each of their apposition compound eyes is divided into three distinct regions, a dorsal and ventral hemisphere separated about the equator by a two, three, or six ommatidial row depending on the species) midband. Species-specific intra-retinal adaptations to the photoreceptors particular to each of the regions can confer both linear and circular polarization vision as well as up to 12-channel colour vision (Marshall, 1988; Marshall et al., 1991a, 1991b; Marshall et al., 2007; Chion et al., 2008; Roberts et al., 2009; Thoen et al., 2014). Stomatopods have the largest diversity of visual pigments yet discovered, with colour vision in those species with a six-row midband mediated by the first four rows (Marshall et al., 1991b, 1996). Three different pigment types are found in each of the four rows, with each row distinct from the others. The visual pigment determines the sensitivity profile and thus the peak sensitivity ($\lambda_{\text{max}}$) of a photoreceptor, this gives rise to a colour visual system with twelve narrow colour channels spanning the 300–720 nm portion of the spectrum (Marshall et al., 1991b).

The colour vision of stomatopods has been shown to contribute to both inter- and intra-specific visual interactions (Caldwell &...
Dingle, 1975; Hazlett, 1979; Chiao et al., 2000; Chiou et al., 2011; How et al., 2014). There are nevertheless indications that their system of colour vision is far from conventional. By confining the receptors governing colour perception to four ommatidial rows, stomatopod colour vision is approximately reduced to a 10° strip of space about the equator of the eye (Land et al., 1990; Marshall et al., 2014). As a consequence, only a narrow portion of a multispectral pattern may be viewed concurrently by the animal, with the appearance of the coloured pattern depending on the orientation of an eye. To counter the extremely reduced field of view of the midband, stomatopods have developed unusually mobile eyes, being able to rotate each eye independently from the other through at least 90° in all three degrees of rotational freedom: pitch, yaw, and roll (Land et al., 1990; Jones, 1994; Daly et al., 2016, Daly et al., 2017). The eyes frequently perform scanning movements, in which the eye is slowly (< 40° s⁻¹) scanned across the visual scene in a direction perpendicular to the midband (Land et al., 1990).

Despite the large number of narrow band and spectrally distinct visual pigments, stomatopods have surprisingly poor wavelength discrimination, worse than most butterflies, birds, bees, and mammals (Marshall & Arikawa, 2014; Thoen et al., 2014). It has therefore been proposed that instead of the stomatopod visual system having an opponent basis and multi-dimensional colour space, such as in the human trichromatic visual system, colours may instead be identified as a series of excitation patterns (Marshall & Arikawa, 2014; Thoen et al., 2014). Consequently, they may have a ‘look-up’ table of learned and/or innate responses associated with certain colours or spectral combinations. It is possible, therefore, that visual patterns containing specific wavelengths, or combination of wavelengths, induce particular behaviours in stomatopods in a similar way to some butterflies (Arikawa, 2003; Marshall & Arikawa, 2014).

We examined this hypothesis further by investigating whether stomatopods have an innate colour preference. Our study animal, Odontodactylus scyllarus (Linnaeus, 1758), is one of the smashers stomatopod species that inhabits the colour-rich environment of shallow tropical coral reefs (Fig. 1A). We investigated whether, during foraging behaviour, O. scyllarus exhibits a colour preference for different objects that reflected different wavebands between 525 nm to 600 nm, 575 nm to 600 nm and 600 nm to 650 nm, which correspond to objects humans perceive as green, yellow, and red, respectively. We also tested for a preference for the absolute reflectance level by presenting both a light and a dark version of each object.

**METHODS**

The study involved ten adult O. scyllarus (three females, seven males; carapace lengths between 90 and 150 mm), purchased from the marine trade (Tropical Marine Centre, Bristol, UK). All experiments were performed in the home aquaria of the stomatopods under the fluorescent room lighting conditions (S1) in which the animals are housed. Due to space restrictions, seven of the O. scyllarus specimens were housed in 45 l aquaria and the other two in 90 l aquaria. Stomatopods were fed a variety of prawns, clams, and mysids in the morning of the day prior to the experimental procedure. Each animal was tested twice a day, twice weekly, at the same times, for a period of three weeks.
In each trial, individual stomatopods were presented with a choice between two differently coloured plastic bricks (The Lego Group, Billund, Denmark). Brick pairs were presented as follows. Initially, the front portion of the tank was partitioned off from the stomatopod using a piece of white corrugated plastic, while two bricks were placed equidistant from the stomatopod’s home burrow on the pale aquarium sand covering the base of the tank (Fig. 1C). In order to prompt an interest in the bricks, each hollow in the base was filled with raw shrimp and sealed such that the odour could escape, but the stomatopods could not access the food. Each brick had been left in a sample of water from the stomatopod’s home aquarium for at least 5 min before presentation. The front of the tank was also covered with white corrugated plastic in order to minimise distraction. A GoPro camera (Hero4 Silver; San Mateo, CA, USA) was mounted on the top front of the tank, facing the layout of the bricks and the stomatopod in its home burrow. These videos were used to record the brick choice by each stomatopod. Each individual was given 5 min in which to make a choice between the two bricks. A choice was considered to have been made once the stomatopod had left its home burrow to clasp one of the bricks with its maxillipeds. The first brick grasped by the stomatopod was recorded as its choice, regardless of whether it then clasped the second brick. If no brick was clasped within the 5 min window, the stomatopod was recorded as not having made a choice.

Three different brick colours (green, yellow, and red) were tested at two different levels of reflectance (light and dark), resulting in a total of twelve brick pair combinations (Table 1). Although we refer here to these bricks as ‘green’, ‘yellow’, and ‘red’, such colour names are specific to human visual perception. Both the order and side of the tank that the blocks were placed was fully randomized. Brick reflectance was measured using a spectrophotometer (USB2000, OceanOptics, Dunedin, FL, USA) coupled to a 200 μm core diameter optic fibre under the same illumination conditions as the experiment. Brick colour was chosen so that its peak reflectance wavelength coincided closely with separate spectral sensitivity channels previously recorded in the Odontodactylus visual system (green = 553 nm versus λmax = 555 nm; yellow = 589 nm versus λmax = 590 nm; red = 645 nm versus λmax = 660 nm; Fig. 1B) (Cronin et al., 1999a, 1999b; Marshall et al., 2007). The reflectance in the UV portion (300–400 nm) of the spectrum for all bricks was < 4.1%. A shorter wavelength stimulus corresponding to wavelengths in the UV portion (300–400 nm) of the spectrum for all bricks in at two different levels of reflectance (light and dark), resulting in six absolute irradiance spectra were taken for each colour and reflectance level (light and dark) of Lego brick as well as of the aquarium sand using a QE6500 photospectrometer (Ocean Optics, Largo, FL, USA) under illumination from the fluorescent room lighting as per the conditions of the experiment. From the absolute irradiance measurements of the bricks (I) and the sand (Ib) in the 450–675 nm region of the spectrum (S1), the Weber contrast (C) between the Lego bricks and the aquarium sand was calculated using

\[ C = \frac{I - Ib}{Ib} \]

C is wavelength dependent, but on average across the 450–675 nm region of the spectrum, the dark brick had a higher absolute Weber contrast than the light brick (Fig. 1D). C for each brick was calculated across the spectral interval 450–675 nm and not for individual photoreceptors as the relative spectral sensitivities of each spectral class have not been established.

### RESULTS

All ten stomatopods made choices in 100% of trials. The reflected wavelengths was a significant factor in brick choice (GLMM, N = 10, χ² = 29.215, p < 0.001). Odontodactylus scyllarus showed a significant positive preference for yellow bricks over both green (overall percentage of yellow choices made: Ngreen = 45.8%; overall percentage of green choices made: Ngreen = 35%, N = 10, z = 2.455, p = 0.014) and red (Nred = 45.8%; overall percentage of red choices made: Nred = 19.2%, N = 10, z = 5.123, p < 0.001), and significantly preferred green over red (Ngreen = 35%, Nred = 19.2%, N = 10, z = 2.927, p = 0.003; Fig. 2A). Odontodactylus scyllarus also showed a significant positive preference for darker bricks over lighter bricks (overall percentage of dark choices made: Ndark = 60%, overall percentage of light choices made: Nlight = 40%, GLMM χ² = 9.190, p = 0.024; Fig. 2B). The choice of brick colour or intensity was nevertheless independent of the sex of the stomatopods (colour:sex, GLMM, N = 10, χ² = 0.193, p = 0.9126; reflectance:sex GLMM, N = 10, χ² = 0.836, p = 0.836; colour:reflectance GLMM, N = 10, χ² = 0.93, p = 0.630).

### DISCUSSION

We have shown that O. scyllarus displays a positive preference for yellow colours and a negative preference for red colours. To the best of our knowledge, given the long-term conditions under which these experimental animals are kept, this preference for yellow is an innate response. Although stomatopods can have as many as twelve distinct spectral sensitivities, it is considered highly unlikely that they have a dodecahedral comparative colour space. Rather, it has been speculated that stomatopod colour vision is based on wavelength recognition rather than spectral discrimination (Marshall et al., 2007; Marshall & Arikawa, 2014; Thoen et al., 2014). Within the framework of this ‘look-up table’ hypothesis, the innate preference that O. scyllarus has for yellow over both red and green may be due to the excitation of particular photoreceptor combinations that are behaviourally relevant to specific behavioural tasks. Further experiments are required to fully test
fishes have also been shown to have an innate preference for krill that have been dyed yellow over krill that have been dyed blue, black, green, or red (Kawamura et al., 2010). Whilst colour vision can provide an animal with multiple ecological advantages, a sensory bias in the form of innate colour preference may act to further enhance the fitness of a naïve animal during visual tasks such as predator avoidance (Bruce et al., 2001), mate choice (Dawkins & Guilford, 1996; Collins, 1999), foraging (Raine & Chittka, 2007) or inter- and intra-species signalling (How et al., 2014).

Most stomatopod species have bright and distinctive colouration patterns on their bodies, including a circular region on the inner side of their raptorial appendages known as the meral spot. During threat or mating displays, the raptorial appendages are drawn apart from one another, clearly showing both the brightly coloured base of the dactyls and the meral spots (Caldwell & Dingle, 1976; Schiff & Manning, 1984; Cheroske et al., 2009). Other vividly coloured body regions, such as those found on the primary maxillipeds in several species, also play a role in signalling (Chiao et al., 2000; Chiou et al., 2011; How et al., 2014). An innate preference for certain colours may influence the behaviour of a stomatopod in both inter- and intra-species signalling and recognition. As an avenue of further investigation, the question of the relevance of yellow in this context should be addressed. Additionally, stomatopods have polarization vision, with many brightly coloured patterns on their bodies also incorporating polarizing reflecting regions (Chiao et al., 2011; How et al., 2014; Gagnon et al., 2015; Jordan et al., 2016). There is evidence that some species of stomatopods have an innate avoidance response to circularly polarized signals (Gagnon et al., 2015) and modifications to the blue linearly polarizing maxillipeds used by other species causes a significant change in mating behaviour (Chiou et al., 2011). The possible interaction between innate colour and polarization preferences also remains to be fully investigated.

As well as informing the behaviour of a naïve animal, innate colour preferences displayed through wavelength recognition rather than spectral discrimination may provide an animal with a faster response time due to a potential reduction in neuronal processing (Marshall & Arikawa, 2014). A reduction in neuronal computational complexity would be of particular advantage to animals, like stomatopods, with a large number of spectral classes. For instance, the butterfly Paro rapae (Linnaeus, 1758), which has six distinct classes of spectral receptors, shows specific ecological responses to certain wavelength categories, an escape response when presented with a UV/violet cue and a feeding response (proboscis extension) to blue and an egg laying response to green wavelengths (Arikawa, 2003; Marshall & Arikawa, 2014). Evolutionarily, this is a simple solution: each time a new behavioural task arises, an animal simply adds an additional spectral class. This is perhaps an explanation for the apparently excessive number of distinct spectral classes of the stomatopod eye.

 Whilst the spectral sensitivity of O. scyllarus is known (Cronin et al., 1994a, 1994b; Marshall et al., 2007), the relative sensitivities of each spectral class have not been established. In order to control for possible confounds in colour choice due to apparent differences in the level of absolute reflectance, both a light and a dark version of each coloured brick was presented. For all three colours, the dark version was preferred over the light version. It is likely that this is due to the dark brick having a higher Weber contrast with the background (Fig. 1D) and therefore presented the stomatopod with a more salient cue than the lighter version. A similar result was found for juvenile thin-lipped mullet, Liza ramada (Risso, 1827). Groups of larvae fed on dark-coloured food viewed against a lighter background had higher performance and a greater survival rate than those fed on light-coloured food on a dark background (El-Sayed & El-Ghobashy, 2011). The level of reflectance did not have an influence on the colour choice of

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**Figure 2.** A. The percentage of colour choices made by each individual (N = 10). The size of the marker dot indicates the number of stomatopods at each choice level as indicated by the key. The thick black line indicates two individuals making the same choice. The coloured bars represent the average percentage of choices made for each colour brick across all individuals and trials. Due to the pairwise experimental design, across the three colour combinations (yellow/green, yellow/red, green/red), the sum of choice percentage is 150% for each colour. B. The percentage of reflectance level choices made by each individual (N = 10). The bars represent the average percentage of choices of light and dark bricks across all individuals and trials. The size of the marker dot indicates the number of stomatopods at each choice level, as indicated by the key. For both panels, stars represent levels of statistical significance: *P < 0.05; **P < 0.01; ***P < 0.001.

the parameters and the validity of the ‘look-up table’ model of stomatopod colour vision.

Many other animals also show an innate colour preference. For instance, Bumble bees (Bombus terrestris (Linnaeus, 1758)) prefer (human) ‘blue’, as do hatchery-reared larvae of the giant freshwater prawn (Macrobrachium rosenbergii (De Man, 1879)) (Briscoe & Chittka, 2001; Chittka et al., 2004; Raine & Chittka, 2007, Kawamura et al., 2016). Several species of spariid...
O. scyllarus. Whilst O. scyllarus preferred the dark version of the yellow brick to the light, both versions of the yellow bricks were preferable to the red bricks. This is true despite both light and dark red bricks having a higher Weber contrast than either version of the yellow bricks (Fig. 1D). This indicates that, for stomatopods during foraging, colour may be a more influential dimension of visual information than the absolute reflectance level.

We have demonstrated that O. scyllarus displays an innate colour preference when involved in a task involving foraging for food. Although our findings may not answer the fundamental questions of why stomatopods have such a numerous array of spectral classes within their mandib and how such information is processed, they allow us further insight into this unique visual system.

SUPPLEMENTARY MATERIAL
Supplementary material is available at Journal of Crustacean Biology online.

S1 Figure. The absolute irradiance spectra of the Lego bricks, aquarium sand (blue), and fluorescent room lighting (black dashed line) measured from the experimental position of the bricks in the aquarium shelving.

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BIBLIOGRAPHY


