



Daly, I., Tetley, A., Jared, S., How, M., & Roberts, N. (2017). Colour preference in *Odontodactylus scyllarus* (Linnaeus, 1758) (Stomatopoda). *Journal of Crustacean Biology*, 37(4), 374-379.
<https://doi.org/10.1093/jcbiol/rux038>

Publisher's PDF, also known as Version of record

License (if available):
CC BY

Link to published version (if available):
[10.1093/jcbiol/rux038](https://doi.org/10.1093/jcbiol/rux038)

[Link to publication record in Explore Bristol Research](#)
PDF-document

This is the final published version of the article (version of record). It first appeared online via Oxford University Press at <https://academic.oup.com/jcb/article-lookup/doi/10.1093/jcbiol/rux038>. Please refer to any applicable terms of use of the publisher.

University of Bristol - Explore Bristol Research

General rights

This document is made available in accordance with publisher policies. Please cite only the published version using the reference above. Full terms of use are available:
<http://www.bristol.ac.uk/pure/about/ebr-terms>



Colour preference in *Odontodactylus scyllarus* (Linnaeus, 1758) (Stomatopoda)

Ilse M. Daly, Anna E. Tetley, Sheryl L. Jared, Martin J. How and Nicholas W. Roberts

School of Biological Sciences, University of Bristol, Tyndall Avenue, Bristol, BS8 1TQ, UK

Correspondence: I.M. Daly; e-mail: ilse.daly@bristol.ac.uk

(Received 27 January 2017; accepted 5 April 2017)

ABSTRACT

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

INTRODUCTION

Stomatopod crustaceans are intriguing marine predators that pursue an active, rapid-fire lifestyle involving complex inter- and intra-species interactions. Stomatopods belong to an order of malacostracan crustaceans that evolved more than 400 million years ago (Schram, 1969). There are currently about 480 species of stomatopods (Ahyong *et al.*, 2017). They are found in all the oceans of the world except for the Arctic, occurring at depths from the shallow inter-tidal region to 300 m (Caldwell & Dingle, 1975). Their common name, the mantis shrimps, arises from the superficial similarity in some species between their dactyls, an enlarged pair of primary maxillipeds that form ballistic raptorial appendages (Fig. 1A), and the forelegs of the praying mantis. As active predators, they use their raptorial appendages to stun or kill prey, as well as for ritualised combat over territory or mating rights (Dingle & Caldwell, 1969; Caldwell & Dingle, 1975). Functionally speaking, there are two types of stomatopods, the ‘smashers’ and the ‘speakers’ based on the morphology of their raptorial appendages (Caldwell & Dingle, 1975).

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; Chiou *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. Since the visual pigment determines the sensitivity profile and thus the peak sensitivity (λ_{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 &

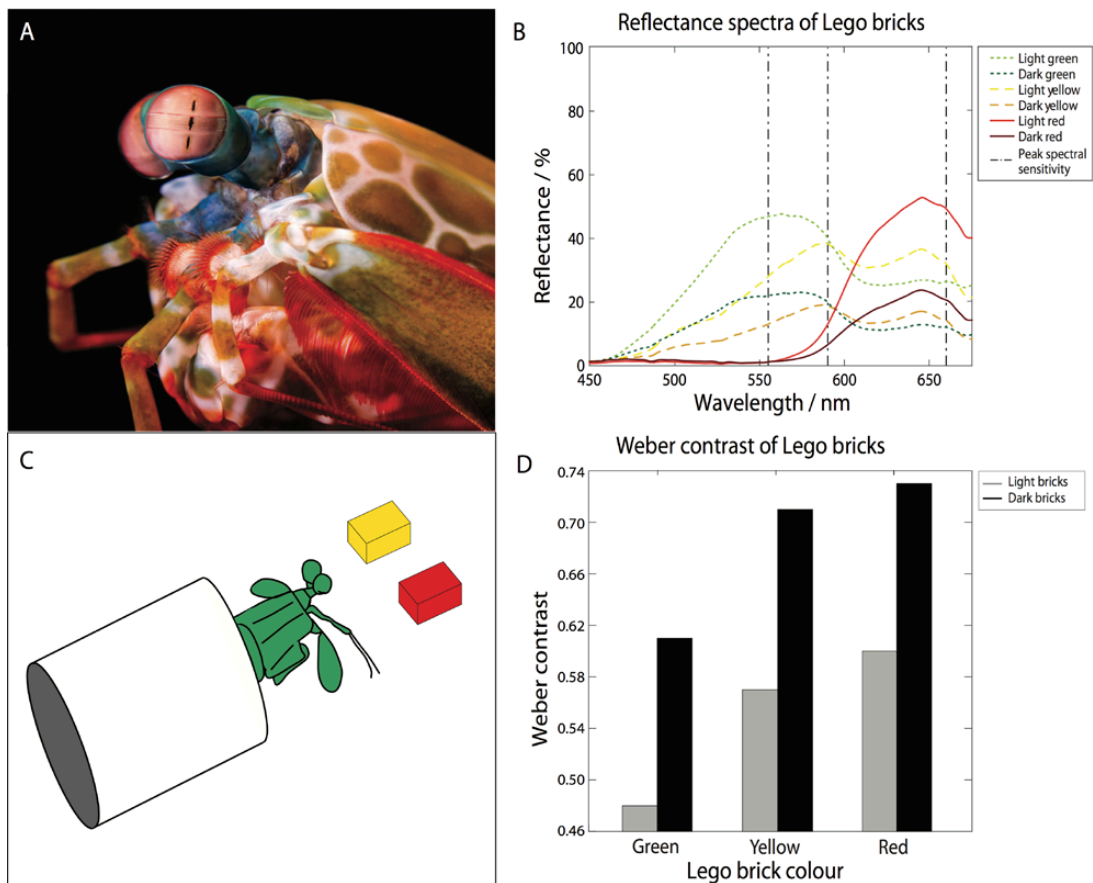


Figure 1. **A**, *Odontodactylus scyllarus*, the mantis shrimp species used in this study. Image courtesy of Mike Bok. **B**, The reflectance spectra of the light and dark versions of the red, green, and yellow bricks. The reflectance of all bricks in the UV (300–400 nm) was < 4.5%. **C**, A schematic of the experimental design. Each stomatopod was presented with a choice between two bricks in its home aquarium. **D**, The Weber contrast values between the absolute irradiance under the lighting conditions of the experiment of all wavelengths and reflectance levels of Lego bricks and the marine sand of the aquarium floor. This figure is available in colour at *Journal of Crustacean Biology* online.

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 multi-spectral 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 ($< 40^\circ \text{ s}^{-1}$) 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 smasher 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 *O. scyllarus* visual system (green = 553 nm versus λ_{Gmax} = 555 nm; yellow = 589 nm versus λ_{Ymax} = 590 nm; red = 645 nm versus λ_{Rmax} = 660 nm; Fig 1B) (Cronin *et al.*, 1994a, 1994b; 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 blue was not chosen as *O. scyllarus* has previously been shown to be unable to reliably distinguish blue from grey (Marshall *et al.*, 1996). Light/dark versions of each colour were created by wrapping the brick in neutral density (ND) filter (0.15 (298); Lee Filters, Andover, UK). The light version of the green and red bricks had a single layer of ND filter whilst the yellow had two layers since its reflectance was greater than the others. Similarly, the dark version of the red and green bricks had two layers of ND filter while the yellow had three.

Statistical analysis

Data were analysed in R (R Core Team, 2014) using a generalized linear mixed effects model (GLMM) to account for individual differences and repeated trials (library lme4). The response variable was the 'yes' or 'no' choice of a colour in a particular trial.

Table 1. The 12 brick pair combinations presented to each stomatopod. R, = red; G, = green; Y, = yellow; D, = dark; L, = light. The side of the tank on which each brick type was presented was randomised.

| | | |
|-----------------------------------|-----------------------------------|-----------------------------------|
| R _L vs. G _L | Y _L vs. R _L | Y _L vs. G _L |
| R _L vs. G _D | Y _L vs. R _D | Y _L vs. G _D |
| R _D vs. G _L | Y _D vs. R _L | Y _D vs. G _L |
| R _D vs. G _D | Y _D vs. R _D | Y _D vs. G _D |

Fixed factors included in the experimental design were the colour type of the objects, the object reflectance, sex, and the interaction terms of colour:sex and reflectance:sex. The individual identity of each stomatopod nested within the tank size group was included as a random factor.

Visual contrast

In order to determine the visual contrast between the Lego bricks and the aquarium sand against which the bricks were viewed, six absolute irradiance spectra were taken of 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 (I_b) 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

$$C = \frac{I - I_b}{I_b}$$

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 wavelength was a significant factor in brick choice (GLMM, $N = 10$, $\chi^2 = 29.213$, $p < 0.001$). *Odontodactylus scyllarus* showed a significant positive preference for yellow bricks over both green (overall percentage of yellow choices made: $N_{\text{yellow}} = 45.8\%$; overall percentage of green choices made: $N_{\text{green}} = 35\%$, $N = 10$, $z = 2.455$, $p = 0.014$) and red ($N_{\text{yellow}} = 45.8\%$; overall percentage of red choices made: $N_{\text{red}} = 19.2\%$, $N = 10$, $z = 5.123$, $p < 0.001$), and significantly preferred green over red ($N_{\text{green}} = 35\%$, $N_{\text{red}} = 19.2\%$, $N = 10$, $z = 2.927$, $p = 0.003$; Fig 2A). *Odontodactylus scyllarus* also showed a significant positive preference for darker bricks over lighter bricks (overall percentage of dark choices made: $N_{\text{dark}} = 60\%$, overall percentage of light choices made: $N_{\text{light}} = 40\%$, GLMM $\chi^2 = 9.190$, $p = 0.024$; Fig 2B). The choice of brick colour or intensity was nevertheless independent of the sex of the stomatopods (colour:sex, GLMM, $N = 10$, $\chi^2 = 0.183$, $p = 0.9126$; reflectance:sex, GLMM, $N = 10$, $\chi^2 = 0.856$, $p = 0.836$; colour:reflectance, GLMM, $N = 10$, $\chi^2 = 0.93$, $p = 0.630$).

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 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

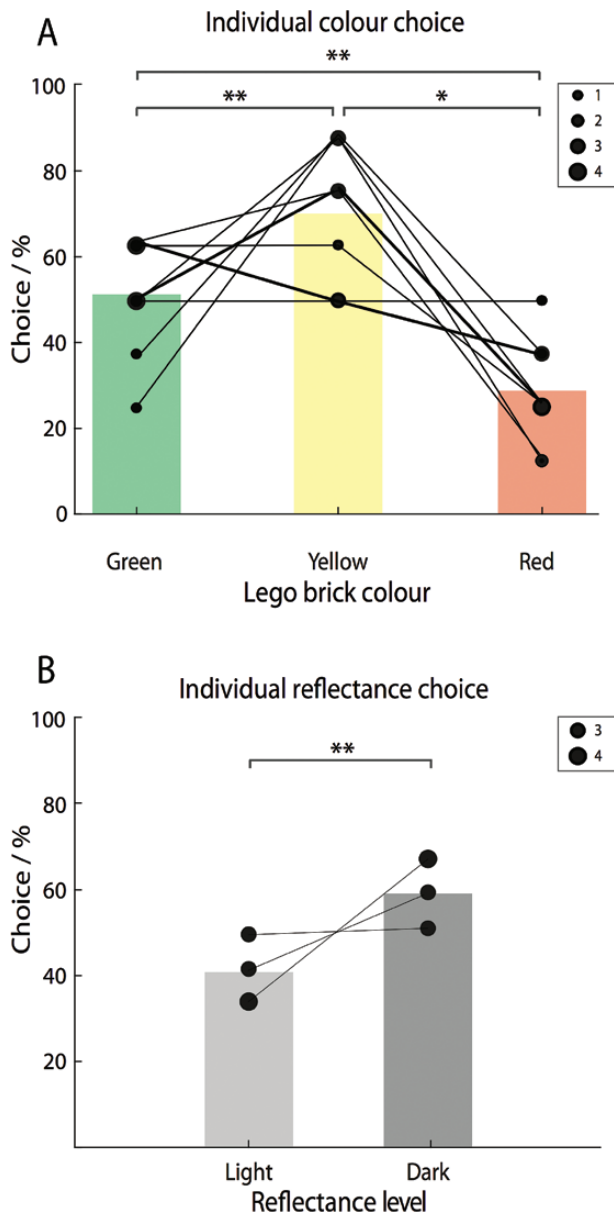


Figure 2. **A**, The percentage of colour choices made by each individual ($N = 10$). The size of the marker dot indicates the number of stomatopods at each choice level as indicated by the key. The thick black line indicates two individuals making the same choice. The coloured bars represent the average 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 sparid

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 naive 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 (Chiou 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 naive 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 *Pieris 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 distinctive 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

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 midband 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.

ACKNOWLEDGEMENTS

The study was funded by the Air Force Office of Scientific Research (grant no. FA8655-12-2112) and the Biotechnology and Biological Sciences Research Council (grant no. BB/J014400/1). We thank Michelle Cole and Holly Campbell for their help with the care of the stomatopods. Thanks also to Mike Bok for his wonderful photographs. We also thank the two anonymous reviewers for their constructive comments and suggestions.

BIBLIOGRAPHY

- Ahyong, S.T., Caldwell, R.L. & Erdmann, M.V. 2017. Collecting and processing stomatopods. *Journal of Crustacean Biology*, **37**: 109–114.
- Arikawa, K. 2003. Spectral organization of the eye of a butterfly, *Papilio*. *Journal of Comparative Physiology A*, **189**: 791–800.
- Briscoe, A.D. & Chittka, L. 2001. The evolution of colour vision in insects. *Annual Review of Entomology*, **46**: 471–510.
- Bruce, M.J., Herberstein, M.E. & Elgar, M.A. 2001. Signalling conflict between prey and predator attraction. *Journal of Evolutionary Biology*, **14**: 786–794.
- Caldwell, R.L. & Dingle, H. 1975. Ecology and evolution of agonistic behavior in stomatopods. *Naturwissenschaften*, **62**: 214–222.
- Caldwell, R.L. & Dingle, H. 1976. Stomatopods. *Scientific American*, **234**: 80–89.
- Cheroske, A.G., Cronin, T.W., Durham, M.F. & Caldwell, R.L. 2009. Adaptive signaling behavior in stomatopods under varying light conditions. *Marine and Freshwater Behaviour and Physiology*, **42**: 219–232.
- Chiao, C.C., Cronin, T.W. & Marshall, N.J. 2000. Eye design and color signaling in a stomatopod crustacean *Gonodactylus smithii*. *Brain, Behavior and Evolution*, **56**: 107–22.
- Chiou, T.-H., Kleinlogel, S., Cronin, T.W., Caldwell, R.L., Loeffler, B., Siddiqi, A., Goldizen, A. & Marshall, N.J. 2008. Circular polarization vision in a stomatopod crustacean. *Current Biology*, **18**: 429–34.
- Chiou, T.H., Marshall, N.J., Caldwell, R.L. & Cronin, T.W. 2011. Changes in light-reflecting properties of signalling appendages alter mate choice behaviour in a stomatopod crustacean *Haptosquilla trispinosa*. *Marine and Freshwater Behaviour and Physiology*, **44**: 1–11.
- Chittka, L., Ings, T.C. & Raine, N.E. 2004. Chance and adaptation in the evolution of island bumblebee behaviour. *Population Ecology*, **46**: 243–251.
- Collins, S.A. 1999. Is female preference for male repertoires due to sensory bias? *Proceedings of the Royal Society B: Biological Sciences*, **266**: 2309–2314.
- Cronin, T.W., Marshall, N.J. & Caldwell, R.L. 1994a. The intrahamdomal filters in the retinas of mantis shrimps. *Vision Research*, **34**: 279–291.
- Cronin, T.W., Marshall, N.J. & Caldwell, R.L. 1994b. The retinas of mantis shrimps from low-light environments (Crustacea; Stomatopoda; Gonodactylidae). *Journal of Comparative Physiology A*, **174**: 607–619.
- Daly, I.M., How, M.J., Partridge, J.C., Temple, S.E., Marshall, N.J., Cronin, T.W. & Roberts, N.W. 2016. Dynamic polarization vision in mantis shrimps. *Nature Communications*, **7**: 1–9.
- Daly, I.M., How, M.J., Partridge, J.C. & Roberts, N.W. 2017. The independence of eye movements in a stomatopod crustacean is task dependent. *Journal of Experimental Biology*, **220**: 1360–1368.
- Dawkins, M.S. & Guilford, T. 1996. Sensory bias and the adaptiveness of female choice. *American Naturalist*, **148**: 937–942.
- Dingle, H. & Caldwell, R.L. 1969. The aggressive and territorial behaviour of the mantis shrimp *Gonodactylus bredini* Manning (Crustacea: Stomatopoda). *Behaviour*, **33**: 115–136.
- El-Sayed, A.F.M. & El-Ghobashy, A.E. 2011. Effects of tank colour and feed colour on growth and feed utilization of thinlip mullet (*Liza ramada*) larvae. *Aquaculture Research*, **42**: 1163–1169.
- Gagnon, Y.L., Templin, R.M., How, M.J. & Marshall, N.J. 2015. Circularly polarized light as a communication signal in mantis shrimps. *Current Biology*, **25**: 3074–3078.
- Hazlett, B.A. 1979. The meral spot of *Gonodactylus oerstedii* Hansen as a visual stimulus (Stomatopoda, Gonodactylidae). *Crustaceana*, **36**: 196–198.
- How, M.J., Porter, M.L., Radford, A.N., Feller, K.D., Temple, S.E., Caldwell, R.L., Marshall, N.J., Cronin, T.W. & Roberts, N.W. 2014. Out of the blue: the evolution of horizontally polarized signals in *Haptosquilla* (Crustacea, Stomatopoda, Protosquillidae). *Journal of Experimental Biology*, **217**: 3425–31.
- Jones, J. 1994. Architecture and composition of the muscles that drive stomatopod eye movements. *Journal of Experimental Biology*, **188**: 317–31.
- Jordan, T.M., Wilby, D., Chiou, T.-H., Feller, K.D., Caldwell, R.L., Cronin, T.W. & Roberts, N.W. 2016. A shape-anisotropic reflective polarizer in a stomatopod crustacean. *Scientific Reports*, **6**: 21744.
- Kawamura, G., Kasedou, T., Tamiya, T. & Watanabe, A. 2010. Colour preference of five marine fishes: bias for natural and yellow-dyed krill in laboratory tanks, sea cages and an earthen pond. *Marine and Freshwater Behaviour and Physiology*, **43**: 169–182.
- Kawamura, G., Bagarinao, T., Yong, A.S.K., Jeganathan, I.M.X. & Lim, L.S. 2016. Colour preference and colour vision of the larvae of the giant freshwater prawn *Macrobrachium rosenbergii*. *Journal of Experimental Marine Biology and Ecology*, **474**: 67–72.
- Land, M.F., Marshall, J.N., Brownless, D. & Cronin, T.W. 1990. The eye-movements of the mantis shrimp *Odontodactylus scyllarus* (Crustacea: Stomatopoda). *Journal of Comparative Physiology A*, **167**: 155–166.
- Linnaeus, C. 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. **Vol. 1**, Edn. 10. Reformata. Laurentii Salvii, Holmiae [= Stockholm].
- Man, J.G. de 1879. On some species of the genus *Palaemon* Fabr. with descriptions of two new forms. *Notes from the Leyden Museum*, **41**: 165–184.
- Marshall, N.J. 1988. A unique colour and polarization vision system in mantis shrimps. *Nature*, **333**: 557–560.
- Marshall, J. & Arikawa, K. 2014. Unconventional colour vision. *Current Biology*, **24**: R1150–R1154.
- Marshall, N.J., Land, M.F., King, C.A. & Cronin, T.W. 1991a. The compound eyes of mantis shrimps (Crustacea, Hoplocarida, Stomatopoda). I. Compound eye structure: The detection of polarized light. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **334**: 33–56.
- Marshall, N.J., Land, M.F., King, C.A. & Cronin, T.W. 1991b. The compound eyes of mantis shrimps (Crustacea, Hoplocarida, Stomatopoda). II. Colour pigments in the eyes of stomatopod crustaceans: Polychromatic vision by serial and lateral filtering. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **334**: 57–84.
- Marshall, N.J., Jones, J.P. & Cronin, T.W. 1996. Behavioural evidence for colour vision in stomatopod crustaceans. *Journal of Comparative Physiology A*, **179**: 473–481.
- Marshall, N.J., Cronin, T.W. & Kleinlogel, S. 2007. Stomatopod eye structure and function: A review. *Arthropod Structure and Development*, **36**: 420–48.
- Marshall, N.J., Land, M.F. & Cronin, T.W. 2014. Shrimps that pay attention: saccadic eye movements in stomatopod crustaceans. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **369**: 20130042.
- R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

- Raine, N.E. & Chittka, L. 2007. The adaptive significance of sensory bias in a foraging context: Floral colour preferences in the bumblebee *Bombus terrestris*. *PLoS One*, **2**: 1–8.
- Roberts, N.W., Chiou, T.-H., Marshall, N.J. & Cronin, T.W. 2009. A biological quarter-wave retarder with excellent achromaticity in the visible wavelength region. *Nature Photonics*, **3**: 641–644.
- Schiff, H. & Manning, R.B. 1984. Description of a unique crustacean eye. *Journal of Crustacean Biology*, **4**: 604–614.
- Schram, F.R. 1969. Some Middle Pennsylvanian Hoplocarida (Crustacea) and their phylogenetic significance. *Fieldiana, Geology*, **12**: 235–289.
- Toen, H.H., How, M.J., Chiou, T.-H. & Marshall, N.J. 2014. A different form of color vision in mantis shrimp. *Science*, **343**: 411–413.