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**Doors to the homes:
signal potential of red colouration of claws in social hermit crabs**

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Abstract

Red colouration on a signaller's body may be an informative signal in many animals. For species that inhabit architecture (e.g., burrows, nests, or other structures), certain parts of the body are more exposed than others, potentially serving as superior platforms for signalling via colouration. Yet if animals differentially advertise red colouration on body parts that are more versus less exposed from their architecture remains to be tested. Here we systematically quantified red coloration in social hermit crabs (*Coenobita compressus*). These crabs inhabit architecturally remodelled shells and have claws that visibly block the shell entrance, like doors to their home. We hypothesised that red colouration of claws may be a signal of resource-holding potential (RHP). Consistent with this RHP signalling hypothesis, we found that within the same individuals' bodies, exposed claws showed significantly greater red colouration than unexposed carapaces. Furthermore, larger body size predicted greater red colouration of claws. Competing hypotheses (e.g., interspecific signalling, camouflage, and UV protection), while not explicitly tested, nevertheless appear unlikely based on natural history. Red claw coloration may therefore function as a signal to conspecifics, and experiments are now needed to test recipient responses. Broadly, relative to surrounding architecture, exposed body surfaces offer rich potential as signalling platforms for colouration.

Keywords: red colouration, claws, architecture, signal, RHP, *Coenobita compressus*

Introduction

Animal signals are acts or structures produced by signallers that convey information [1]. For signals to convey information about the signaller, the signal must correlate with an underlying trait of the signaller that elicits a response in the receiver, which on average, results in increased fitness of both the signaller and receiver [2, 3]. Often, substantial variation of traits exists within a population, but only signals have been specifically selected over evolutionary time to convey information about traits. Even when signals convey information imperfectly, they can still be useful, especially when combined with other information sources. Indeed, many multimodal signals (i.e., communication that incorporates signal components from two or more sensory modalities; [4]) work in such a way. While signals from many modalities can be informative, for species with vision, colour may be of great significance [5].

Red colouration, in particular, may be a potentially relevant signal in multiple contexts. For example, in fighting contexts, red has been found to be an indicator of signallers' resource-holding potential (RHP) (e.g., in red-shouldered widowbirds, *Euplectes axillaris*, red colouration of epaulets signals competitive ability [6, 7]). RHP is an individual's ability to win and maintain possession of a contested resource [8]. Measures of RHP can include size (e.g., [9]), weaponry, skill (e.g., [10]), strength and stamina [11], and anything else that may enable an animal to prevail in a contest [12]. Assessment of RHP by competitors can comprise pure self-assessment, cumulative assessment, or mutual assessment (for more details on assessment models see: [8, 13, 14]). Yet, regardless of the assessment type, signals of RHP, such as red colouration [6, 7], can evolve if the information conveyed can reduce the cost of fights for both signallers and receivers.

In addition to signals that convey RHP, examples of red colour signals also exist in sexual selection as indicators of mate attractiveness (e.g., in zebra finches red colouration of

beaks determines sexual attractiveness [15]). Other correlates of red colouration are immune function and antioxidant activity [16-18] as well as UV protection [19, 20]. One reason red colouration is thought to be a potentially useful signal across many taxa is that certain pigments which generate red colouration (e.g., carotenoids) cannot be synthesised *de novo* by animals [21] and must instead be obtained from food in the external environment [22-24]. Therefore, individuals with a differential ability to acquire these pigments (e.g., through more efficient discovery or a greater capacity to dominate at resource patches) will display more red. Effectively conveying this information may depend on the precise placement of red colouration on the signaller's body.

It is generally physically impossible for organisms to display all areas of their body at once. Thus, while some species exhibit full-body red colouration (e.g., male Northern cardinals), most animals with red colouration only have specific areas of their bodies on which red is more concentrated (e.g., the face of mandrills, the epaulets of red-winged blackbirds, and the dewlaps of Anolis lizards). Interestingly, organisms that inhabit architecture (e.g., burrows, nests, or other built structures) only have certain parts of their bodies that are regularly exposed [25, 26], typically at the architecture's entrance (e.g., mantis shrimp [27], phragmotic-headed ants [28], woodpeckers [29], and Pine martens [30]). Such partial exposure often occurs when owners are protecting their architectural structures from intruders, with the owner keeping the majority of its body inside the structure for protection [25]. Exposed body surfaces of owners, relative to their architecture, may make ideal platforms for signalling via colouration. Yet, whether animals differentially advertise red colouration on body parts that are more versus less exposed from their architecture remains to be tested.

The organisms with perhaps the most intimate connection to the architecture they inhabit are hermit crabs [31]. These animals' bodies are mostly covered by transportable gastropod shells [32], except for their anterior appendages, particularly claws, which represent a first line of defence of shells [33, 34]. Interestingly, for highly social, terrestrial hermit crabs (*Coenobita* spp.), the evolutionary transition to living on land [35] was accompanied by dramatic changes in both sociality [36-39] and claw morphology [40]. These social hermit crabs no longer produce threat displays with their claws [41]. Instead, their enlarged left claw now fits the shell entrance, essentially functioning as a 'door' or 'pseudo-operculum' [40-43], which is visible to conspecifics and blocks potential evictors [39]. Within one of these social hermit crab species (*Coenobita compressus*) the level of red colouration of claws varies greatly between individuals in the wild [44] (Fig. 1a). Yet no studies have systematically quantified colouration to test possible functional explanations. We hypothesised that red colouration on exposed body parts may be a potential signal, with the intensity of red providing information about RHP.

To test the hypothesis that red colouration serves as a signal of RHP, we systematically measured colour variation between different parts of the body for individuals spanning a range of sizes and both sexes. If the RHP signalling hypothesis is true, then exposed areas should differentially advertise red colouration compared to unexposed areas of the same individuals' bodies. Furthermore, if red colouration is a signal of RHP, then variation in red should correlate with body size, such that bigger individuals are redder in those exposed regions. Also, the sex that differentially benefits from attaining larger size (which is males in *C. compressus* [45, 46], see also Fig. S1) may be more likely to show a relationship between red colouration and body size. We therefore examined between-sex variation, assessing whether males showed a stronger relationship than females between red colouration and body size. We also evaluated variation

(based on residuals in exposed surface area, i.e., claw area, relative to body size), to determine if individuals with greater exposed surface area, relative to body size, were more red. If variation in red colouration is unrelated to RHP, then the above predictions should not follow. Note, red colouration could convey information as either a signal, which has been specifically selected to convey that information, or as a cue. Cues, like signals, also convey information and are likewise correlated with conditions of interest to receivers, though cues have not been specifically selected to convey information [1]. Here we use signal as a shorthand, and we consider in the discussion further criteria needed to tease apart signal and cue. We also consider the extent to which any alternative hypotheses, adaptive or non-adaptive, may explain the observed patterns in colouration.

Methods

Sample collection and study site

C. compressus specimens were collected in the wild from a long-term study population [47] along the beach-forest interface of Osa Peninsula, Costa Rica (8°23'40" N, 83°20'10" W). Individuals of all sizes across the population were collected. Collection was entirely blind with respect to colour and sex. The sole criteria for inclusion were that an individual must have all its appendages intact and not be moulting. Once the sample (N = 103 individuals) was collected, all individuals were then systematically measured. To test if body parts that are exposed out of the shell architecture could act as signalling platforms, a series of systematic morphological and colour measurements (see below) were taken on each individual. All measurements were made by the first author (CD) during February to March 2018. After measurements were completed, all collected individuals were then returned to the wild.

Morphological measurements

For each individual, we recorded sex (N = 47 females, N = 56 males; determined using the standard method as described in [48]), and made the following morphological measurements using electronic callipers to the nearest 0.01 mm: shield length (mm) [48], claw length (mm) [40], and claw width (mm) [40]. We also calculated exposed claw area (mm²) as claw length x claw width. In addition, we measured posterior carapace length to the nearest 0.01 mm and body weight to the nearest 0.01g. However, because shield length is regarded as the most reliable metric of overall body size [48], and also because shield length correlated strongly with both posterior carapace length and body weight (Table S1), all our analyses of body size focus on shield length.

Colour measurements

We measured spectral reflectances (from 250 to 800 nm) using a solarization-resistant reflectance probe (QR400-7-SR reflection probe, Ocean Optics Inc., Dunedin, FL) coupled with a pulsed xenon source (Ocean Optics) and a JAZ spectrometer (JAZ-COMBO, Ocean Optics; Fig. 1b). Reflectance measurements were taken on two body parts for each individual (Fig. 1c): (1) the enlarged left claw (i.e., the body part that is most exposed and visible at the shell opening) and (2) the carapace (i.e., the body part that is concealed within the shell and only becomes visible after an individual is removed from its shell). Both body parts represent hardened areas of the same overall exoskeleton as opposed to the soft fleshy tissue of the abdomen. Note, we did not make any colour comparisons with the smaller right claw or the walking legs since these body parts were too small to use spectrometer measures; and

furthermore, they are neither fully concealed nor fully exposed, so would not have provided informative comparisons. Only the enlarged left claw and the carapace, which were possible to measure, could provide a direct and informative test of the RHP signalling hypothesis.

Reflectance measurements were calibrated using a Spectralon plastic standard that reflects nearly 100% of the light at all wavelengths from 200 to 800 nm (WS-1-SL Diffuse Reflectance Standard, Ocean Optics), which allows the spectrometer to calculate processed spectrum values (i.e., reflectance corrected using the white reference; for example see Fig. 1d). To control for variation caused by the angles of illumination or measurement, a reflection probe holder (RPH-1) was used to ensure the end of the reflectance probe was always placed at the same distance from the measured surface and held at a consistent 45° angle to the surface. This arrangement, which uses an angle of collection that is not equal to the angle of incident light, measures diffuse reflectance (which is relatively angle-independent), and avoids detection of specularly reflected light [49].

For each body part, we quantified red colouration using the following formula [50] (Fig. 1d):

$$\frac{(\text{average red} - \text{average green})}{(\text{average red} + \text{average green})}$$

$$\frac{(\text{average red} - \text{average green})}{(\text{average red} + \text{average green})}$$

This formula calculates chromaticity (i.e., average red – average green) while controlling for brightness (i.e., average red + average green), and uses measurements in the 500-600 nm wavelength range to denote the green spectrum and measurements in the 600-700 nm wavelength range to denote the red spectrum.

Final sample

Of the original sample (N = 103 collected individuals), a subset was excluded from the analyses of colour for the following reasons: N = 1 individual had an abdominal abnormality, which was only detectable after it had been removed from its shell; N = 21 individuals were too small to accommodate the spectrometer to take colour measurements; N = 9 individuals were large enough to take colour measurements, but ultimately their spectrometer files could not be opened or were somehow corrupted. Hence, analyses of colour were performed on a final sample of N = 72 individuals (N = 28 females and N = 44 males).

Statistical analyses

To examine whether red colouration could function as a signal, we assessed the factors related to red colouration using a generalised linear mixed model (GLMM), with measures of red colouration being the response variable. We included a full factorial of body part (exposed or unexposed), sex (male or female) and body size (shield length) as fixed effects. We also included crab identity as a random effect in the model to account for multiple measurements per individual (i.e., one measurement on the exposed body part and one measurement on the unexposed body part of the same crab). All crabs in this study were collected in the same geographic vicinity, within an approximately 10-20 m stretch of beach, which crabs can readily traverse. Hence, geographic location was not considered as a variable in the model. Finally, to test if colouration was related to the size of the exposed claw area, relative to body size, we conducted a post-hoc linear regression of red colouration of claws against the residuals of exposed claw area relative to shield length. All analyses were performed in JMP® Pro 16.0.0.

Results

Consistent with the main prediction of the RHP signalling hypothesis, within-subject contrasts revealed a significant difference in red colouration between exposed vs unexposed body parts (i.e., claw vs carapace within the same individuals). In particular, claws showed significantly more intense red colouration than carapaces (GLMM: $F_{1,68} = 55.98$, $p < 0.0001$; Fig. 2), almost twice the intensity. Further aligning with the RHP signalling hypothesis, we found a marginally significant interaction between body part (exposed or unexposed) and body size (GLMM: $F_{1,68} = 4.07$, $p = 0.0477$). In particular, a positive relationship existed between body size and red colouration of claws ($r^2 = 0.09$, $p = 0.01$; Fig. 3), but not for carapaces ($r^2 = 0.00$; Fig. 3). There was no significant effect of sex on red colouration (GLMM: $F_{1,68} = 1.08$, $p = 0.30$).

Exposed claw area strongly correlated with body size (Fig. 4a; Table S1). However, red colouration of claws did not correlate with variation in exposed claw area relative to body size (linear regression: $F_{1,70} = 0.09$, $p = 0.76$; Fig. 4b). Thus, individuals with proportionately more exposed surface area did not show greater red colouration.

Discussion

Our systematic measurements of colouration and morphology among social hermit crabs revealed a stark difference in the level of red colouration between exposed and unexposed areas of the body, relative to architecture. In particular, exposed claws exhibited substantially more intense red colouration than unexposed carapaces, suggesting that red colouration could be a signal. Moreover, red colouration of claws increased with body size, suggesting that the level of red colouration in claws could be a signal of RHP. While the relationship between red

colouration of claws and body size is relatively weak, red colouration could still provide valuable information for receivers by supplementing other sources of information about RHP (e.g., visual motion [51], olfaction [52], tactile feedback [53] and size assessment [54]). Notably, one reason the relationship between colour and body size may have been weak is because measurement of colouration was impossible for the smallest individuals sampled (20.4 % of the original sample of $N = 103$ individuals; see Table S1, Fig. S2). Individuals of this small size, which were too small to accommodate the spectrometer, tend to exhibit little if any red colouration ([44]; ML & CD personal observation). Thus, the relationship we found between red colouration of claws and body size might have been stronger if it had been possible to include the smallest individuals. The prediction of the RHP signalling hypothesis regarding sex was not supported in the current study, suggesting that even if attaining a larger size is differentially important for one sex (Fig. S1), it may not be sufficient to favour differential colour between sexes, perhaps due to competition for resources other than mates (e.g., at food patches [51]). A relationship between the residuals of exposed claw area and red colouration of claws was not found. Such a relationship may have been impossible given the extremely tight correlation between exposed claw area and body size ($r^2 > 0.9$), which greatly restricted the range of residuals. Regardless, exposed areas could effectively advertise important information about RHP. Our results suggest that further tests of such possible signalling platforms on the body, in reference to architecture, are merited.

Further study of the pattern of red colouration we found will also be vital for testing potential alternative explanations that do not invoke intraspecific signalling. These alternative explanations (see Table 1), which cannot all be eliminated at present, include both adaptive and non-adaptive explanations. For example, one adaptive explanation is that red colouration of

claws is used for interspecific signalling to predators. However, predation on land is relaxed for terrestrial hermit crabs [55] and, furthermore, the architecturally remodelled shells used by our study species break at forces greater than their terrestrial predators are capable of producing [56]. Hence, explanations relating to interspecific signalling (e.g., aposematism [57, 58]), as well as camouflage against predators [50, 59-61], are unlikely. Another adaptive explanation for the greater red colouration of claws is that red colouration is used for UV protection of exposed areas [62]. However, the study species carries its claws ventrally [32, 44] in the shade of both its body and shell while locomoting [63], so the claws are the least exposed to the sun; and furthermore, individuals move to forested areas [47] and beneath leaves [64] during the day. Hence, explanations relating to UV protection are also unlikely. Interspecific signalling, camouflage, and UV protection, whilst unlikely explanations for the difference in red colouration between exposed claws and covered carapaces, can still be formally tested in the future. Also, non-adaptive explanations remain possible. For example, direct environmental impacts and relative exposure to external elements (e.g., weather, sand abrasion, salinity, or sunlight) could perhaps cause the different colouration of claws compared to carapaces, especially if such impacts accumulate over a crab's lifetime. Or, theoretically, differences in red colouration between claws and carapaces might arise as an incidental by-product of some other trait that is directly selected for besides colour (e.g., morphological structures, such as integument thickness [65]). More studies are needed to determine the plausibility of alternative adaptive and non-adaptive explanations and the extent to which they can better explain patterns of red colouration compared to the RHP signalling hypothesis that was the focus of the present study.

In addition to testing alternative hypotheses, more detailed tests of the RHP signalling hypothesis would also be informative. If this hypothesis is true, then multiple finer-grained

measures of RHP should correlate even more strongly with the level of red colouration in claws. For example, muscles both in the claw and the abdomen are undoubtedly critical for obtaining and retaining shells [39], thereby allowing individuals to successfully rise and maintain their positions in the housing market [66]. Future studies could therefore measure both claw pinching force and physical resistance to eviction, testing how well red colouration predicts individual's ability to evict others and withstand eviction. Furthermore, physiological studies could quantify the density of muscle fibres within both claws and abdomens, testing how well such internal musculature measures [67] correlate with red claw colouration. Ultimately, if further correlations exist between a variety of measures of RHP and red colouration, then this would bolster the RHP signalling hypothesis.

A key criterion for a signal, including a signal of RHP, is that recipients must be able to perceive and hence respond to the signal [1-3]. Interestingly, laboratory experiments in terrestrial hermit crabs have revealed that individuals can differentiate artificial red colouration from blue and green colouration [68]. However, the response to natural colour variation in claws has yet to be tested. Future experiments could exploit such natural variation by using postured or withdrawn models of dead crabs [41], thereby testing recipient responses in the wild, particularly when other factors (e.g., claw size and shell quality) are held constant. Experiments might also be able to manipulate claw colour itself, thereby directly testing whether recipients' attempts at evicting a target change in response to altered colour. If the level of red colouration of claws is indeed an effective signal, then recipients should make fewer attempts at evicting the signaller and give up earlier when the signaller's claw colouration is more red. Beyond signalling RHP, it is also possible that red claw coloration could simultaneously be used in sexual signalling [45, 46], in which case tests of female responses to males would be informative. Recent discoveries

in birds revealing that colour perception can be categorical, with discrete thresholds, rather than operating along a continuum [69] raises many further questions about the use and effectiveness of red colouration as a signal across taxa. In theory, multiple strategies could also be at play, with some individuals investing heavily in red colouration, whilst others invest little.

To fully elucidate the function of red colouration, it may also be critical to gain a deeper understanding of mechanism. Mechanistically, red colouration is often generated using pigments obtained from food [21], most notably carotenoids, such as astaxanthins in many crustaceans generally ([70]; see Table 2 in [71]), with astaxanthins also having been shown to impact colour in hermit crabs specifically (see Table 1 in [72]). Presently, it remains unknown which exact compounds in the diets of wild terrestrial hermit crabs contribute to their red colouration. Yet, interestingly, *C. compressus*, in particular, is a highly opportunistic omnivore, with one of the most diverse diets of any crustacean [73]. If specific dietary components required to achieve red colouration are hard to obtain in this species' environment, then variation in individuals' ability to find and gain access to such foods could provide a mechanistic basis for the RHP signalling hypothesis for red colouration. Determining what, if any, components of diet contribute to the accrual and retention of red colouration in this species will require experiments with controlled feeding regimens. Future experiments can also separately consider crabs' ages, which need not be equivalent to their body sizes, given that hermit crabs metabolically control their growth (e.g., [74, 75]), growing only when they acquire larger shells. By simultaneously monitoring individuals' colouration longitudinally, both within and across moults, it might be possible to reveal how individuals allocate colour differentially to certain body parts. Interestingly, six hermit crab species, when grown in the lab on the same feeding regimes, all exhibited different colouration, with differences that persisted across ontogeny [76]. Such feeding experiments

could be supplemented with nutritional analyses that isolate the exact chemical composition of a range of natural foods in the wild. Ultimately, understanding red colouration at the proximate level, including what compounds are involved, how limited those compounds are in nature, and how individuals incorporate these compounds, will further inform our understanding of potential functions of red colouration.

To summarise, here we tested the hypothesis that red colouration in claws serves as a signal of RHP. Several key predictions of this RHP signalling hypothesis have been supported by our systematic measurements of colour and morphology in social hermit crabs. A subset of competing hypotheses (Table 1) appear unlikely based on natural history. Future studies can further test the RHP signalling hypothesis, as well as other hypotheses, with behavioural experiments on the responses of recipients to colour variation being key. We suggest that studies of other animals, particularly those inhabiting architectural structures, consider exposed body parts, relative to architecture, as potential signalling platforms.

Declarations

Ethics approval and consent to participate

All measurements in this study were approved by the Costa Rican Ministerio de Ambiente y Energía (MINAE).

Consent for publication

Not applicable.

Availability of data and materials

All data available as Electronic Supplementary Material.

Conflict of Interest Statement

None declared.

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Authors' contributions

ML conceived the idea for the study; CD carried out the empirical measurements; both authors analysed the data and jointly wrote the manuscript.

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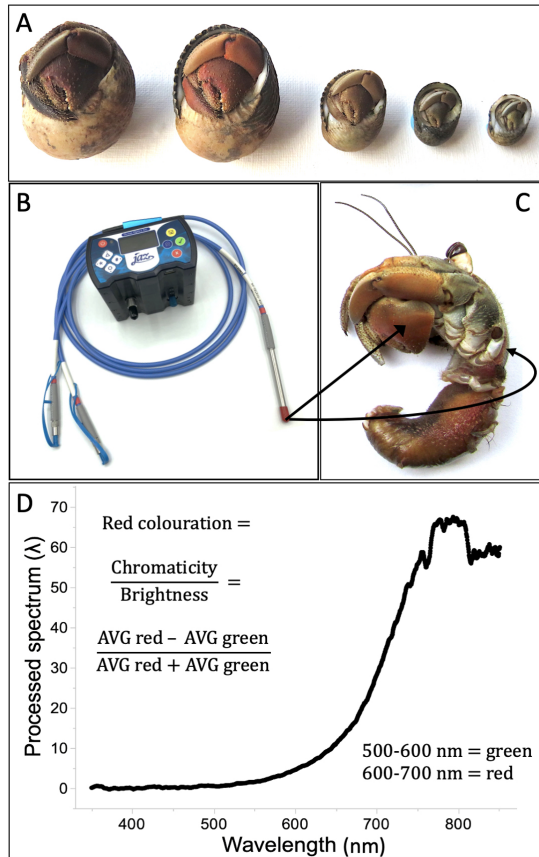


Figure 1. Measurements of body colour, in relation to shell architecture, within the social hermit crab (*Coenobita compressus*). (A) Photograph of colour variation across individuals (arrayed largest to smallest from left to right). Note, only part of each individual's body, particularly its enlarged left claw, is exposed out of the shell architecture, being visible as a 'door to the home'. (B) Reflectance was measured using a Jaz spectrometer. (C) Colour measurements focused on two areas of crabs' bodies: exposed claws (arrow on left) and unexposed carapaces (arrow on right). Individual pictured has been removed from its shell to show both areas. (D) Example of a reflectance curve for the claw of a male, including the formula used to calculate red colouration. (Photos for A and C: Mark Laidre, Photo for B: Elliott Steele).

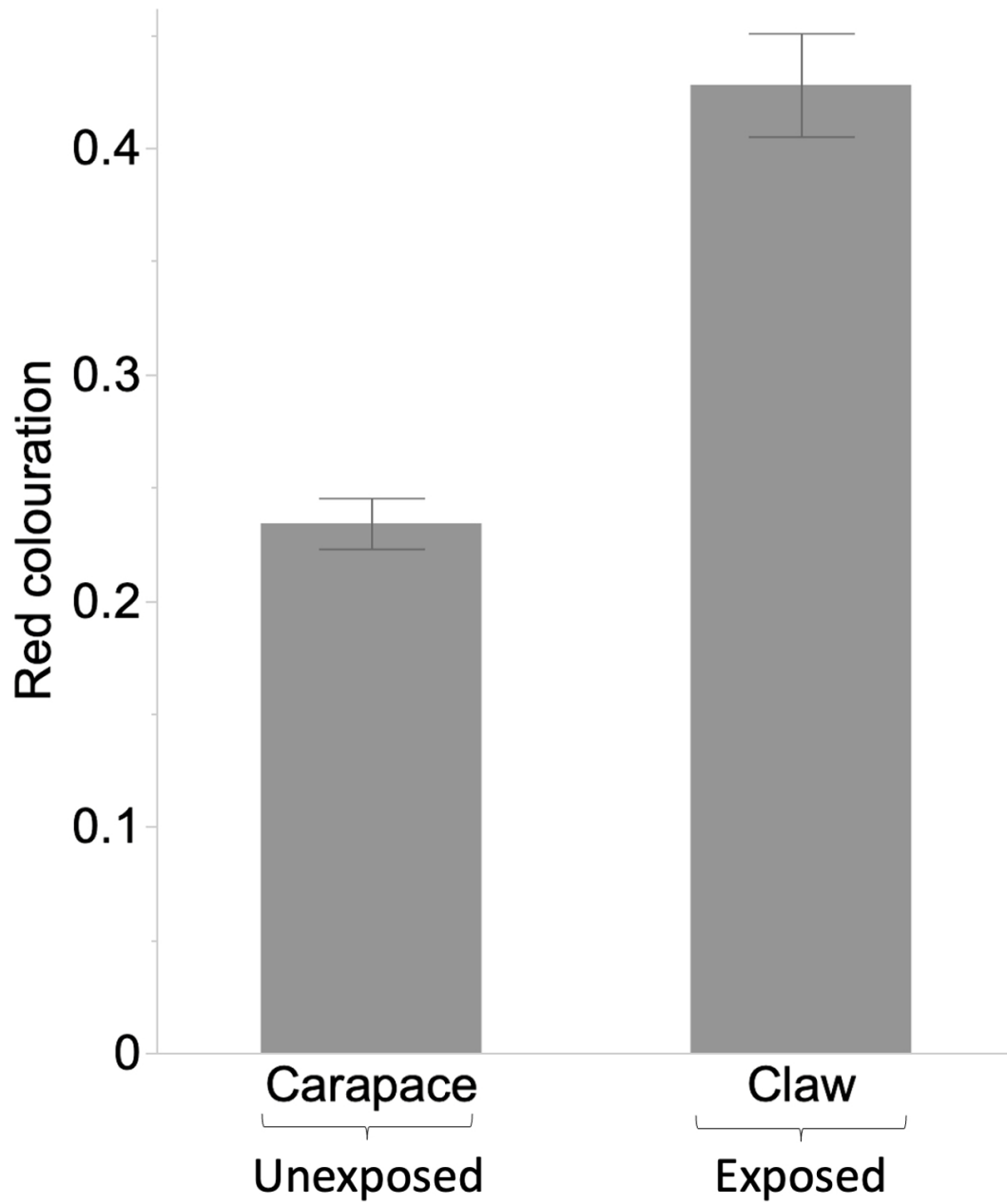


Figure 2. Red colouration (Mean \pm SE) of exposed claws versus unexposed carapaces for N = 72 individuals.

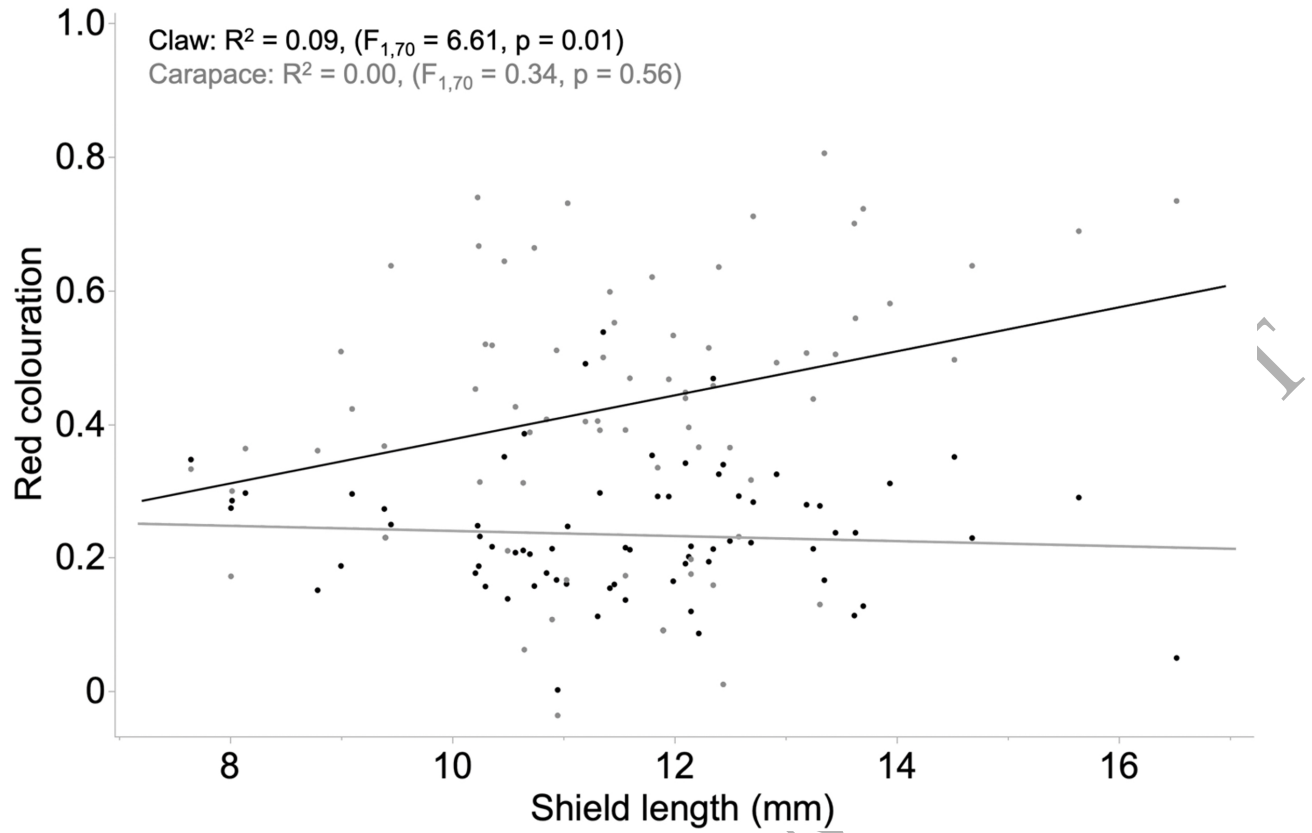


Figure 3. Interaction plot of red colouration of body parts against overall body size (shield length in mm) for $N = 72$ individuals. Exposed claws shown with black dots and black trendline, and unexposed carapaces shown with grey dots and grey trendline.

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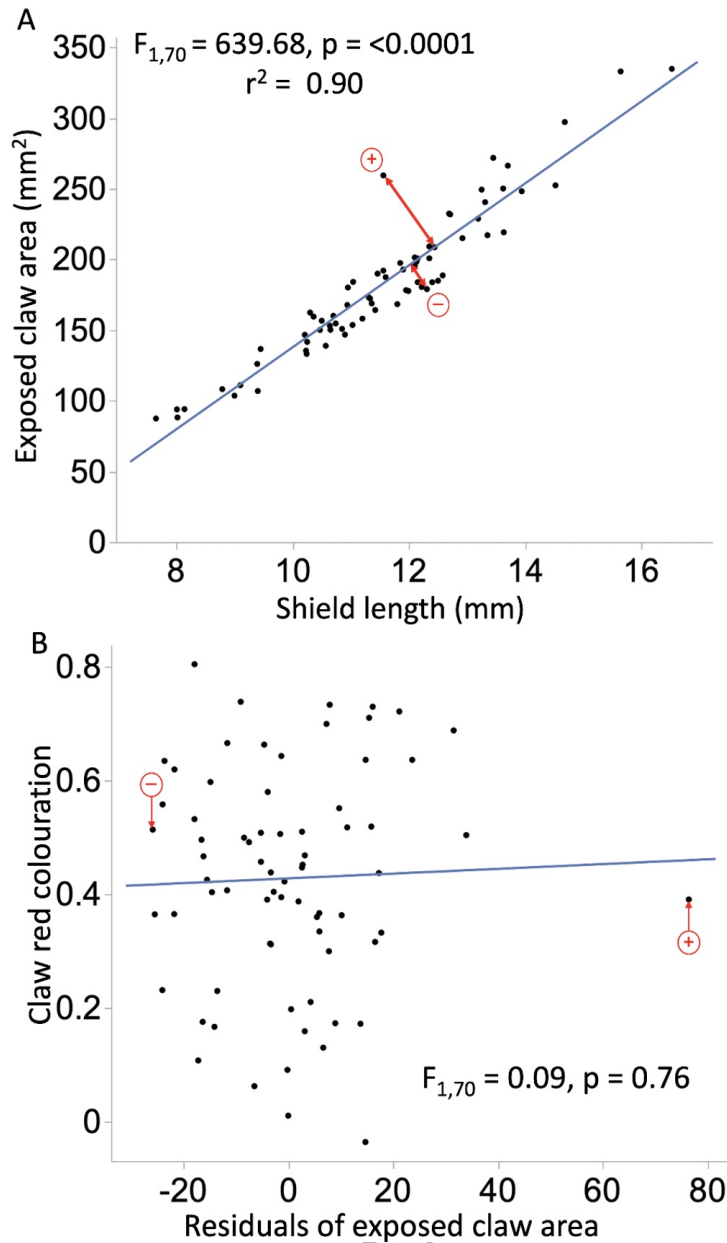


Figure 4. (A) Linear regression of exposed claw area (mm²) against overall body size (shield length in mm) for $N = 72$ individuals. Red arrows show residuals (most positive and most negative) for difference from the predicted line. (B) Linear regression of red colouration of exposed claws against residuals of exposed claw area. Related data points highlighted in (A) and (B) for reference.

Table 1. Competing hypotheses for pattern of red colouration.

	<i>Explanation</i>	<i>Supported?</i>
<i>Adaptive</i>		
Intraspecific signal	Selected to convey information to conspecifics (e.g., signaller's RHP)	Yes
Interspecific signal	Selected to convey information to heterospecifics (e.g., signaller's toxicity)	Unlikely¹
Camouflage	Selected to help individual evade predators by blending with background	Unlikely¹
UV protection	Selected to absorb sunlight at damaging wavelengths	Unlikely¹
<i>Non-adaptive</i>		
Direct environmental impact of exposure	Due to greater exposure to external elements (e.g., weather, sand abrasion, salinity, or sunlight) outside of architecture	Unclear
By-product of selection for another trait	Selection on a trait other than red colouration incidentally gives rise to this colour pattern	Unclear

¹ Years of natural history observations and accumulated knowledge on the study system suggest that these explanations are logically quite unlikely (see Discussion). Nevertheless, further explicit tests, especially experimental tests of these and other hypotheses, would be valuable.