The role of claw colouration in fiddler crabs' mate choice: Private communication channel or handicap?

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Declarations of interest: none

Abstract

Colour cues play an important role in sexual selection and conspecific recognition. Literature shows that conspecifics might enjoy their everyday chat, without ever worrying about occasional eavesdroppers (e.g., predators), when information interchange evolves into a private communication channel. Yet, when signalling is converted into foraging cues by predators, their prey must pay the due cost for sustaining conversation. For that matter, fiddler crabs draw attention for having flashy enlarged claws that could potentially attract the attention of many predators. Surprisingly, the costs associated with claw colouration in fiddler crabs are still poorly understood and have never been studied in American species. Here, we initially examine whether hypertrophied claws of American thin-fingered fiddler crabs (*Leptuca leptodactyla*) reflect UV-light and how conspecific females react to these cues. Then we test two alternative hypotheses concerning the role of claw colouration in fiddler crabs' mate choice: a) that claw

colouration evolved into a private communication channel, which could have significantly lowered signalling costs for males; b) that claw colouration is conspicuous to potential reproductive partners, as well as to predators, making colour signalling by males very costly (i.e., a handicap). Thereafter, we measured the reflectance spectra from several enlarged claws and modelled their chromatic contrast against the background spectrum, considering the visual systems of conspecific fiddler crabs and two kinds of predators (foxes and plovers). We also tested female conspecifics' preference towards enlarged claws that reflected UV-light or other colour cues, by artificially altering claw colouration. Our results show a clear female preference for UV reflecting males. We also found that natural enlarged claws should be highly detectable by avian predators, refuting the private communication channel hypothesis. Furthermore, since female fiddler crabs select the most flamboyant claws from the sandy background, claw colouration in fiddler crabs can be understood as an honest signal.

Keywords: Animal communication; *Cerdocyon thous*; *Charadrius collaris*; colour vision; handicap principle; ocypodidae; runaway selection; signal honesty; spectrophotometry; ultraviolet signal.

HIGHLIGHTS

1) The hypertrophied claws of male *Leptuca leptodactyla* reflect UV light.
2) Female fiddler crabs display a natural preference for UV light cues.
3) Male enlarged claws are conspicuous to birds and crabs, but cryptic to mammals.
4) Conspicuous claws function as handicaps and may honestly signal individual quality.
5) Our data refute the presence of a private communication channel in *L. leptodactyla*.

INTRODUCTION

The evolution of animal colouration has been associated with numerous functional drivers, such as social signalling, antipredator defence, parasitic exploitation, thermoregulation, and protective colouration (Cuthill et al. 2017). Among these drivers, the use of colour signals for intra and interspecific recognition, intrasexual competition, and mate choice have received special attention from researchers that study different animal taxa (Higham and Winter 2015). Yet, when we consider the study of the functional significance of colouration, an especially colourful group that has received far less attention, at least when compared to other arthropods (e.g., insects and spiders), is Brachyura (crabs) (Caro 2018), a promising taxon on which to test some key evolutionary drivers of external appearance (Zeil and Hemmi 2006; Caro 2018).

Among Brachyura, fiddler crabs have attracted the scientific interest for some time, and, for that matter, it is a group that already offers a substantial theoretical framework on which working hypotheses may be formulated. To wit, literature has established these animals present an array of agonistic and sexual visual displays based on size (Oliveira and Custodio 1998), posture (Schöne 1968; Murai and Backwell 2006), movement (Byers et al. 2010) and colour (Detto 2007) cues. Such visual cues are thought to relay information concerning individual reproductive status (Crane 1975) and quality (Latruffe et al. 1999), and to allow intra and interspecific recognition (Dyson et al. 2020).

Typically, male fiddler crabs have a brightly coloured (Dyson and Backwell 2016) and hypertrophied claw that can be used either as a weapon, in male-male disputes, or as an ornament, for female attraction (Crane 1975). Since fiddler crabs express two different kinds of visual pigments, which are responsible for absorbing light in the UV (300-400 nm) and visible (400-700 nm) light range (Horch et al. 2002; Jordão et al. 2007), they are expected to see UV cues and to show a dichromatic colour discrimination (Jacobs 2018). Behavioural

experiments, conducted on banana fiddler crabs (*Austruca mjoebergi*), suggest that colour (UV light included), but not brightness, is important for conspecific reckoning and mate choice (Detto et al. 2006; Detto 2007; Detto and Backwell 2009; Dyson et al. 2020).

The adaptive value of UV light reflection in fiddler crabs, however, is still poorly understood and might be attributed to different ecological interactions. For instance, Detto and Backwell (2009) hypothesize that, if UV reflection enhances male conspicuity, increasing their detectability by female fiddler crabs, the trait should have been fixed in the population. On one hand, the argument of Detto and Backwell (2009) seems to follow Fisher's runaway selection hypothesis (see Henshaw and Jones 2020), according to which a secondary sexual trait expressed in one sex should become correlated with a preference for the trait in the other sex. On the other hand, UV reflection could also be understood as a handicap that attracts the attention of predators and warrants signal honesty about individual quality to reproductive partners (Zahavi 1975). Bright colourations (which also include UV reflection) has been pointed out as honest indicators of low parasite loads (Hamilton and Zuk 1982) or, in a more general sense, good genes (Andersson et al. 1998). Yet, these possibilities remain to be tested in fiddler crabs.

Another explanation, not yet formally scrutinized in fiddler crabs, is that ultraviolet reflection could also result from a trade-off between the advantages of intraspecific conspicuous signalling and the disadvantages of predator attraction. Fish subjected to these conditions have been reported to develop UV light reflection, which could yield a private communication channel (i.e., wherein a species produces a signal that is detected by conspecifics but not predators; see Cummings et al. 2003). In fiddler crabs' list of predators we might find species that are completely insensitive to the UV light spectrum, such as crab-eating foxes (*Cerdocyon thous*), and others which detect UV light very well, such as collared plovers (*Charadrius collaris*) and many crabs species.

101 Recently, a taxonomic review of family Ocypodidae Rafinesque, 1815 (Crustacea:
102 Brachyura) divided fiddler crabs' former taxon (i.e., *Uca*) in 11 different genera (Shih et al.
103 2016). The endemic genera from the Americas (*Leptuca*, *Minuca*, *Petruca* and *Uca*) now
104 encompass 57 species, approximately 55% of fiddler crabs' current species. Among all 104
105 fiddler crab species, only three (*Austruca mjoebergi*, *Tubuca signata* and *Tubuca capricornis*),
106 all from Australia, already had the utility of their claw colouration examined (Detto et al. 2006;
107 Detto 2007; Detto and Backwell 2009; Dyson et al. 2020). More surprisingly, *Leptuca*, fiddler
108 crabs' most heavily studied taxon (Nabout et al. 2010), and the richest genus in Ocypodidae
109 family, enclosing almost one third of all fiddler crab species (i.e., 30 species according to Shih
110 et al. 2016), has not yet been explored with respect to the ecological pressures shaping its claw
111 colouration.

112 Hence, at first, we test two competing hypotheses regarding the functional significance
113 of fiddler crabs' enlarged claw colour, using *Leptuca leptodactyla* as an experimental model.
114 (I) We hypothesize that hypertrophied claw colouration plays a part in a private communication
115 channel, through which fiddler crabs exchange social/reproductive signals that are not
116 detectable by their predators. We predict our results will show that colour contrast between
117 enlarged claws and the sandy background is significantly perceptible to fiddler crabs' visual
118 system, while imperceptible to the visual systems of their potential predators. (II) As an
119 alternative hypothesis, we propose that the conspicuity of enlarged claws works as a handicap
120 (see Zahavi 1975), imposing to male fiddler crabs the heavy cost of enhancing predator
121 attraction, while also honestly advertising their presence and quality to potential female mates.
122 In this case, we predict our results will show the more noticeable an enlarged claw is for a
123 reproductive partner, the more conspicuous it should also be for predators.

124 In addition, we also test a third hypothesis regarding the role that UV light reflectance
125 exerts on female mate choice. (III) We hypothesize that UV reflection from enlarged claws will

be the major colour signal considered by females in their decision making. In case our third hypothesis is correct, we expect our behavioural results to demonstrate females prefer males that reflect UV light, as already shown for Australian species (Detto and Backwell 2009).

METHODS

Choice of Study Species and Study Site

Just a few reports have examined the biology of the thin-fingered fiddler crabs (*Leptuca leptodactyla*; Figure 1) (Nabout et al. 2010), which populations spread throughout the Western Atlantic: Caribbean, Venezuela to Brazil, eastern Yucatan Peninsula (Mexico), south-eastern Florida (USA). The present study took place at a mangrove area, in which a population of thin-fingered fiddler crabs (*L. leptodactyla*) naturally occurs, showing a rainy tropical climate, with rains extending from February to September, and temperatures ranging from 21°C (min.) to 30°C (max.), with a mean temperature of 26°C, and predominant vegetation comprised of sandy coastal plains and mangroves. The area is located within a hydrographic basin, in which unconsolidated sand and gravel composes the fluvial flatland, that is subject to periodical flooding. At the study site, substrate becomes exposed during the low tides, revealing hundreds of burrows, in which *L. leptodactyla* and other crab species live.

Mate Choice Experiments

We conducted experiments throughout the low tides, and our experimental procedures were adapted from Detto et al. (2006), Detto (2007) and Detto and Backwell (2009). Before the beginning of each experimental session, we delimited a squared shaped arena (30 cm^2) on the same sandy substrate in which the animals built their burrows, foraged and mate. For that, we displaced all the animals, obstructed their burrows, and drew a square in the sand.

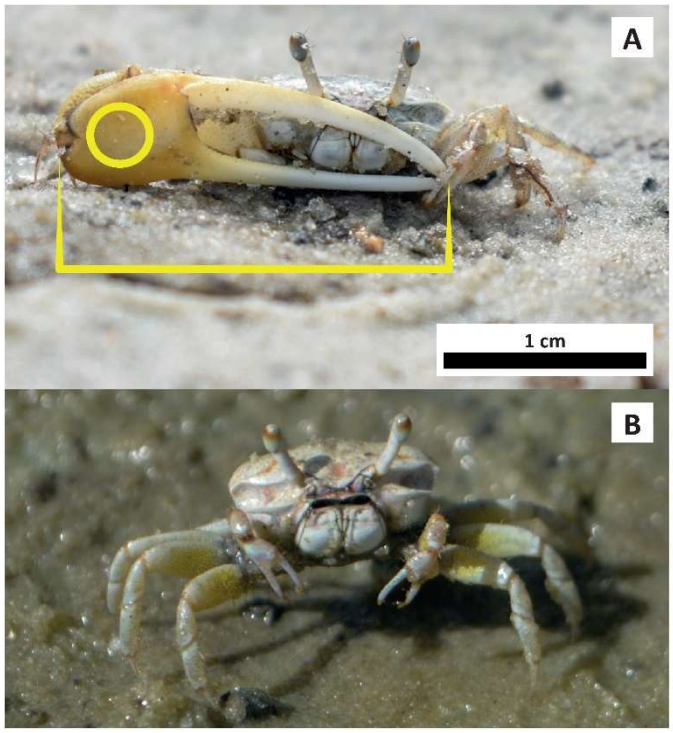

Figure 1. Male (A) and female (B) specimens of thin-fingered fiddler crabs (*Leptuca leptodactyla*). Yellow callipers indicate how male hypertrophied claws were sized, while the yellow circle indicates where the reflectance spectra (colour) of male hypertrophied claws were measured.

Then, we captured a few male fiddler crabs (*L. leptodactyla*) and measured the length (Figure 1) of their hypertrophied claws (chelae) with a calliper, from the base of their palm (propodus) to their fingertip (dactyl), assigning the crabs to different groups according to their claw's size. The maximal acceptable intragroup difference was established at 0.1 cm. From a same group, we randomly chose a set of four size-matched male crabs and subjected each animal to one of the experimental treatments described in Table 1. We decided to use white, yellow, and orange paints because white is *L. leptodactyla*'s carapace colour, while different shades of yellow and orange are the most frequent colouration found on their hypertrophied claws. We also decided to use blue paint to represent a kind of unfamiliar colour that is not expressed by *L. leptodactyla*, or any other species found in the same crab community, but that can be found on species of fiddler crabs of other geographical regions. In experiment 1, irrespective of their experimental treatment, males' posterior carapaces were also treated with

165 white paint and/or sunblock (Table 1), to control for any chemical cues that could be
166 transmitted to the females. Males' posterior carapaces were not viewable from females'
167 location.
168
169 Table 1. Treatments to which male thin-fingered fiddler crabs (*Leptuca leptodactyla*) were assigned in
170 experiments 1 and 2. All paints were acquired from Acrilex (Matte Ink for Crafts) and sunblock was acquired
171 from Natura (Fotoequilibrio SPF 60).

Experimental group	Treatment (claw)		Treatment (posterior carapace)	
	Sunblock	Paint	Sunblock	White paint
Experiment 1				
Control	No	No	Yes	Yes
Sunblock	Yes	No	No	Yes
White claw	No	White paint	Yes	No
Yellow claw	No	Bright yellow paint	Yes	No
Experiment 2				
White claw	No	White paint	No	No
Yellow claw	No	Yellow ocher paint	No	No
Orange claw	No	Orange paint	No	No
Blue claw	No	Blue paint	No	No

172
173 Once painted by the experimenters, males were attached to nylon threads through their
174 posterior carapaces, with superglue, while the other end of the threads were tied to nails,
175 anchoring the crabs to the arena's substrate, one male crab at each corner, facing each other, at
176 12 cm from the centre. Anchoring prevented males from moving, but still allowed them to
177 move their locomotory appendages and to wave their claws, although waving displays
178 following capture were not observed. We always randomized treatment positioning between
179 different sets of size-matched males.
180 Consecutively, we captured a female crab (*L. leptodactyla*), placed it at the centre of
181 the arena, under a transparent cup, and kept it there, habituating, for one minute. After
182 habituation, we lifted the cup and observed the female's behaviour for three minutes, unless it

183 spent less time making a valid choice (i.e., slowly approaching a male by less than two
184 centimetres) or evading the arena. We considered females to have evaded the arena when, as
185 soon as the cup was lifted, they quickly ran towards one of the males and left the arena, or they
186 left the arena without approaching any male. Females that spent three minutes without making
187 a valid choice or evading the arena were replaced by another one. Females were tested only
188 once, being freed right away, however, each set of four size-matched males was presented to
189 several females, until we recorded three female valid choices. After that, the set of males was
190 released and replaced by a new group of four sized-matched males, and so on. Prior to their
191 liberation, males were released from their nylon threads.

192 In experiment 1, we tested if females choose male conspecifics according to the
193 presence of UV reflection. While in experiment 2, we tested if females showed any sensory
194 bias towards any specific claw colouration (e.g., acquainted, and unacquainted colours),
195 irrespective of UV cues. In experiment 1 we used 20 groups of males (totalling 80 males) and
196 a total of 206 females (146 evasions and 60 female choices), while in experiment 2 we used 20
197 groups of males (80 males), having tested a total of 168 females (108 female evasions and 60
198 female choices). These sample sizes are in accordance with what has been stablished by
199 previous published studies (Detto et al. 2006; Detto 2007; Detto and Backwell 2009).

200 Our research protocol adheres to the ASAB/ABS guidelines for the use of animals in
201 research and is in accordance with institutional guidelines and local legislation.

202 *Spectral Measurements*

203 We used a USB4000-UV-VIS (Ocean Optics, Inc.) spectrophotometer connected to a
204 light source (DH2000-BAL; Ocean Optics, Inc.) through a bifurcated optic probe (QR450-7-
205 XSR; Ocean Optics, Inc.). The tip of the optic probe was coupled to a custom-made probe
206 holder, to reduce the sampling area (1 mm of diameter; Appendix 1). The system was calibrated
207 using a WS-1-SL (Ocean Optics, Inc.), as the white standard, and by turning the light source

208 off, as the black standard. All measurements were taken at a fixed angle (90º) and distance (5
209 mm) from stimuli, with help of the SpectraSuite software (Ocean Optics, Inc.), in which boxcar
210 width and number of spectra averaged were set to 5 and 10, respectively.

211 Forty male fiddler crabs were, randomly, collected in the study area and brought to the
212 laboratory, to have the natural colour of their hypertrophied claws registered (Figure 1). These
213 data confirmed that the chosen population reflected UV light, and stablished that there was a
214 natural variation among hypertrophied claw spectra. Using a shovel, we collected a sample of
215 the study site's sediment and carefully caried it to the laboratory to avoid disaggregation. Using
216 the above-mentioned procedure, we also measured the reflectance spectrum of the outmost
217 sediment layer (Figure 2).

218 In a subsequent opportunity, in order to characterize the effect that each experimental
219 treatment (Table 1) had on the reflectance spectra of male claws, we captured six additional
220 crabs, measured their natural colouration, as described previously, and covered their
221 hypertrophied claws with one of the following products: 1) sunblock (Natura Fotoequilibrio
222 SPF 60); 2) white paint (Matte Ink for Crafts, Acrilex); 3) bright yellow paint (Matte Ink for
223 Crafts, Acrilex); 4) yellow ochre paint (Matte Ink for Crafts, Acrilex); 5) orange paint (Matte
224 Ink for Crafts, Acrilex); 6) blue paint (Matte Ink for Crafts, Acrilex). Males' claw colourations
225 were remeasured after treatment (Figure 3). All paints completely blocked UV light
226 reflectance, in the same way sunblock did.

227 *Visual Modelling*

228 To determine how fiddler crabs and their predators (e.g. collared plovers - *Charadrius*
229 *collaris*; and crab-eating foxes - *Cerdocyon thous*) visualize the colouration of male claws
230 against the sandy substrate, we applied the receptor noise (RNL) model of colour
231 discrimination (Vorobyev and Osorio 1998) to determine the chromatic contrasts (ΔS) between
232 the reflectance spectrum of the sandy background and claws' natural colourations, according

to the visual system of fiddler crabs, birds and mammals. It is important to note that the RNL model only considers chromatic information, disregarding achromatic cues. Modelling was conducted in pavo 2.0 (Maia et al. 2019), a R package for spectral analysis of colour.

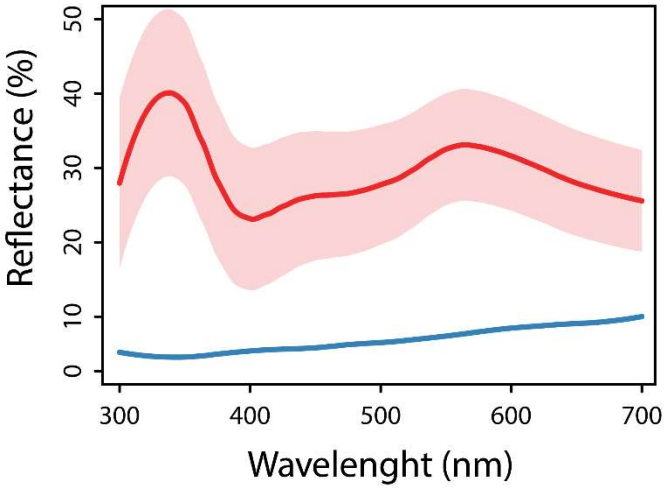

Figure 2. Natural reflectance spectra measured from a set of 40 male thin-fingered fiddler crabs' (*Leptuca leptodactyla*) hypertrophied claws. Average spectrum and variation (maximal and minimum values) are indicated by the red line and its adjoining shaded pink area, respectively. The blue line represents the sandy background reflectance spectrum.

Initially, we estimated the absolute amount of light captured by the photoreceptors of each observer ('Q_i' – quantum catch), considering three factors: 1) the reflectance spectrum of the object (i.e., male claw) or background (i.e., sandy substrate); 2) the illuminant spectrum of incident light (i.e., natural light shining on the study site); 3) the observer's visual sensitivity curves. We compared the natural reflectance spectra collected from 40 animals, as described previously, with the reflectance spectrum collected from the sandy background (Figure 2). A 'bluesky' illuminant spectrum, provided by pavo 2.0's library, was used. Since estimation of receptor sensitivities do not affect model results too seriously (Olsson et al. 2018), we used available spectral sensitivities from the Atlantic Mangrove Fiddler Crab (*Leptuca thayeri*: 430 nm, 520 nm; Horch et al. 2002), the Blue Tit (*Cyanistes caeruleus*: 372 nm, 453 nm, 539 nm, 607 nm; Hart and Hunt 2007) and the Island Fox (*Urocyon littoralis*: 432 nm, 555 nm; Jacobs

et al. 1993), as proxies for crab, bird, and mammal vision, respectively. We set the remaining parameters to default (i.e., trans = 'ideal', vonkries = FALSE, scale = 1), with the following exceptions: for bird visual system we set *trans* = 'bluetit', considering *Cyanistes caeruleus* already known ocular transmission (Hart et al. 2000); since we required absolute quantum catches, instead of relative quantum catches, we set *relative* = FALSE.

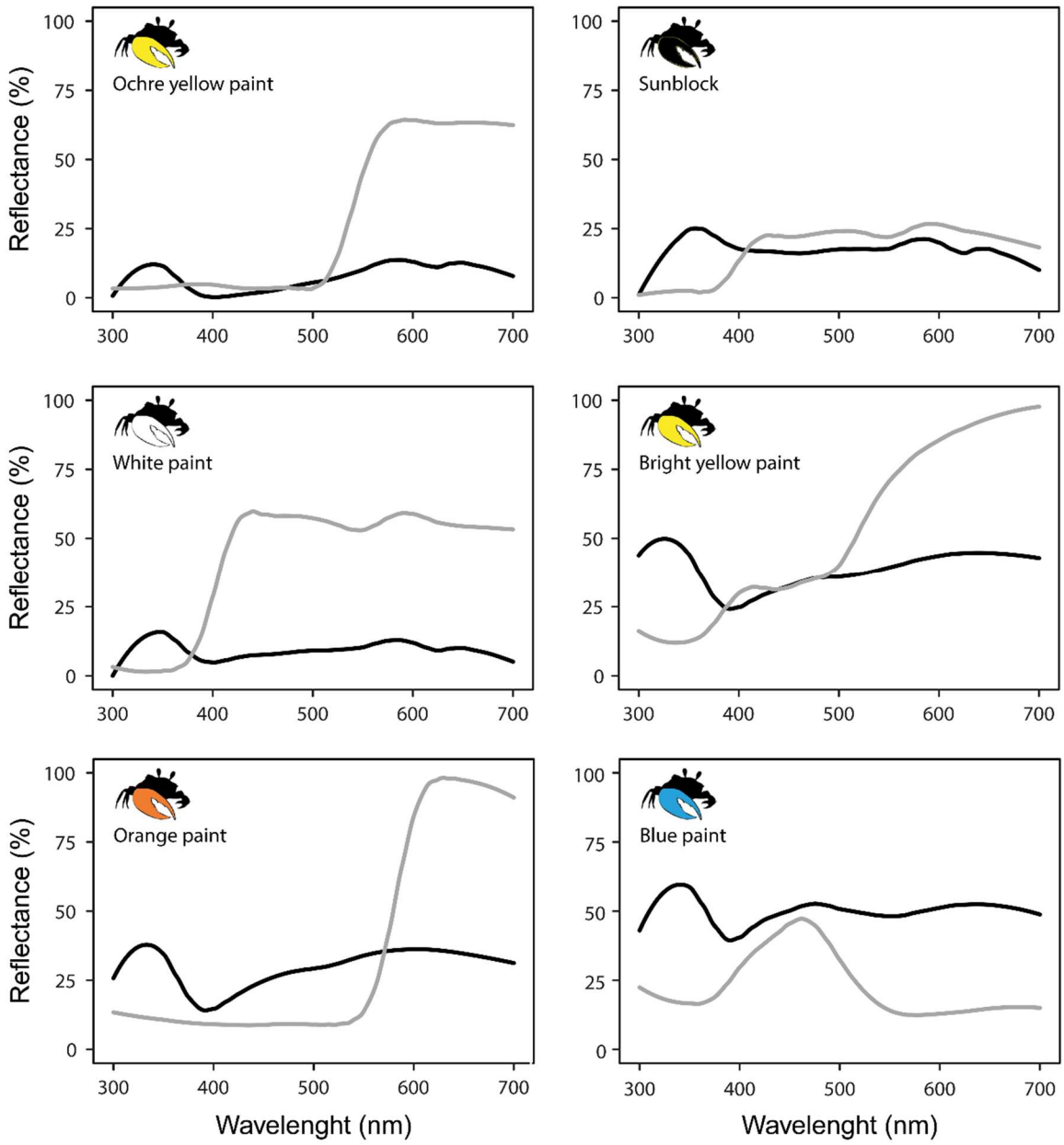

Figure 3. Reflectance spectra measured from the enlarged claws of six male thin-fingered fiddler crabs (*Leptuca leptodactyla*) subjected to different experimental treatments (detailed in Table 1). Natural spectra (before treatment) are represented by black lines, while grey lines indicate claws' spectra after treatments.

In addition, when calculating the chromatic contrasts (ΔS) for each kind of observer, we ran the RNL model and compared Q_i information of each individual crab with that of the sandy background, setting parameters to default (i.e., photoreceptor noise set as 'neural', weber = 0.1, weber.ref = 'longest') and including specific cone densities for the visual systems of fiddler crabs [n = c(1:1); no data available in literature], birds (*Cyanistes caeruleus*) [n = c(1:1.9:2.7:2.7); following Hart et al. 2000] and mammals (*Canis lupus familiaris*) [n = c(1:10); following Mowat et al. 2008]. The ΔS output, between an object an its background, was given in units of just noticeable difference (JND). Following Siddiqi et al., (2004), we adopted three levels of detectability for the observers' visual systems modelled in this study: cryptic (ΔS < 1 JND), detectable (1 JND ≤ ΔS ≤ 3 JND) and highly detectable (ΔS > 3 JND). The higher the chromatic contrast, the higher the colour difference between a male claw and the sandy background, favouring their detectability.

Statistics

Owing to the non-parametric nature of our visual modelling results and behavioural data (Shapiro-Wilk, $P < 0.05$), chromatic contrast values generated by our visual model for different observers (i.e. crabs, birds and mammals) were compared through Kruskal-Wallis tests, with Dunn's post hoc test and Bonferroni correction, while a Generalized linear model (Poisson model GZLM using a log link) was used to compare the different treatments of experiments 1 and 2. The Poisson model was described by ratio rate (RR) and confidence interval (CI). All analyses were run on R statistics (R Core Team, 2017), and assumed $\alpha = 0.05$.

RESULTS

Visual Modelling

The output of our visual model (Figure 4), in which the natural colouration of 40 males was compared to the sandy substrate's colour, shows that claws of *L. leptodactyla* produce

colour signals that vary from cryptic (ΔS < 1) to highly detectable (ΔS > 3 JND), according to the eye of the beholder. When taking colour cues into consideration, all measured enlarged claws were expected to be completely camouflaged against the sand when seen by mammalian predators, since all data points have fallen in the darker grey area of Figure 4 (i.e., below the detectability threshold of 1 JND). In contrast, for avian predators every claw should be deemed detectable against the sandy substrate, with one half falling in the lighter grey area (i.e., detectable) and another half falling in the white area (i.e., highly detectable).

For fiddler crabs' conspecifics (e.g., females) the great majority (82.5%) of enlarged claws have fallen in the darker grey area of Figure 4, which indicates that 33 males, out of 40, should not be able to attract the attention of females based on the colour of their claws alone. Seven out of 40 enlarged claws (17.5%), however, have fallen in the lighter grey area of detectability, while no claws were able to reach the white area of high detectability. These seven most conspicuous claws (hereafter referred as "the remarkable seven"), considering fiddler crabs visual system, were also responsible for reaching high chromatic contrast values for bird vision.

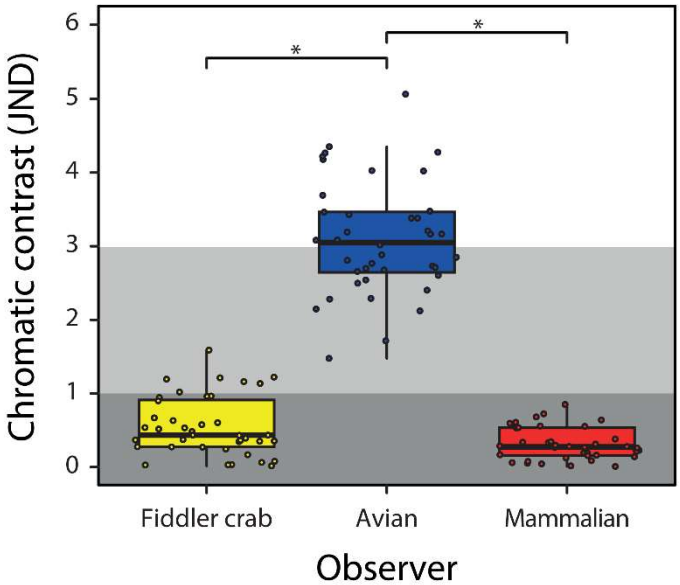

Figure 4. Chromatic contrast (ΔS) between the natural reflectance spectra measured from the hypertrophied claws of 40 male thin-fingered fiddler crabs (*Leptuca leptodactyla*) and the sandy substrate's reflectance spectrum, modelled according to the visual systems of different observers. Dots represent individual values of chromatic

contrast (in unit s of JND). Medians (black thick horizontal lines), interquartile ranges (boxes) and variability outside the upper and lower quartiles (whiskers) are also indicated. Thresholds of detectability are signalled by different grey areas. Dots that fall in the darker grey area are not detectable (ΔS < 1 JND), while dots that fall in the lighter grey area or white area are, respectively, detectable (1 JND ≤ ΔS ≤ 3 JND) and highly detectable (ΔS > 3 JND). Bars with asterisks indicate statistically significant difference between observers.

When we statistically compared chromatic contrast values generated by our visual model there was a significant difference in perceptual performance between different observers (Kruskal-Wallis: $\chi 2_{(2)} = 82.751$; $P < 0.0001$; Figure 4), in which birds statistically outperformed fiddler crabs (Dunn's test: $P < 0.0001$) and mammals (Dunn's test: $P < 0.0001$), while these last two observers did not differ from each other (Dunn's test: $P = 0.091$).

Mate Choice Experiments

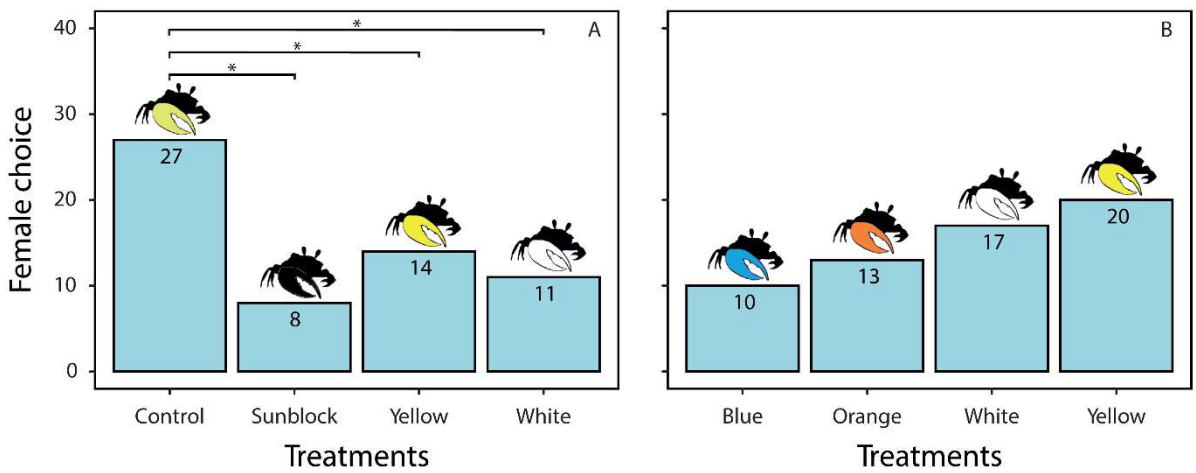

Figure 5. Mate choice by female thin-fingered fiddler crabs (*Leptuca leptodactyla*), when subjected to conditions of experiments 1 (A) and 2 (B). Treatments' details are given in Table 1. Bars with asterisks indicate statistically significant difference between treatments.

In Experiment 1, the Poisson model (GZLM) indicated that claw colouration influenced females preference ($\chi^2 = 12.928$; $P = 0.004$; Figure 5a), favouring males showing UV light reflection (i.e. males with claws of natural colouration) when compared to males that had their UV light reflection depleted by sunblock ($RR = 0.2962$ [0.1 - 0.6]; $P = 0.002$), white paint (RR

323 = 0.4074 [0.19 - 0.79]; P = 0.012), or yellow paint (RR = 0.5185 [0.26 - 0.97]; P = 0.046).
324 While in Experiment 2, the Poisson model (GZLM) revealed no indication of a female sensory
325 bias (χ^2 = 3.9329; P = 0.2688; Figure 5b) being directed towards any specific claw colouration,
326 when UV light reflection was depleted in all available treatments.
327

328 **DISCUSSION**

329 Our spectrophotometric data confirmed that the hypertrophied cheliped of thin-fingered
330 fiddler crabs (*Leptuca leptodactyla*) significantly reflects UV light, while our behavioural
331 results have proven that *L. leptodactyla* is also capable of discriminating the UV cues generated
332 by conspecifics, which corroborates electrophysiological data gathered in a close species
333 (*Leptuca thayeri* - Horch, 2002). Our findings parallel what has been found in an Australian
334 species, the banana fiddler crab (*Austruca mjoebergi*), to which UV light reflection and
335 preference has been associated with Fisherian explanations (Detto and Backwell 2009).

336 Yet, concerning non-UV cues, our data reveals a crucial difference in colour preference
337 between Australian (*A. mjoebergi*) and American (*L. leptodactyla*) fiddler crabs. In the absence
338 of ultraviolet information, while female Australian fiddler crabs are attracted by enlarged
339 yellow (Detto et al. 2006; Dyson et al. 2020) and orange claws (Dyson et al. 2020), female
340 American fiddler crabs present no sensory bias to any hypertrophied claw colouration
341 whatsoever, as shown by our second experiment.

342 *The Role of Claw Colouration in Fiddler Crabs*

343 *The private communication channel hypothesis*

344 On one hand, our visual modelling results do not support the existence of a private
345 communication channel (Cummings et al. 2003), through which fiddler crabs could
346 communicate without being seen by avian predators. In fact, our data show the opposite of
347 what we predicted in our first hypothesis. Birds, which are responsible for most predation

348 pressure suffered by fiddler crabs (Ribeiro et al. 2019), should outperform female fiddler crabs
349 in using colour to identify males' hypertrophied claws on the sandy substrate.

350 It is not surprising that our modelling data also predicts that mammalian predators
351 should not detect enlarged claws at all. Contrary to birds, that are highly visually oriented,
352 relying primarily on their tetrachromatic colour vision (i.e., can compare the activity of four
353 different kinds of photoreceptors to derive colour information) and UV light sensitivity, most
354 mammals are dichromats (i.e., use only two different kinds of photoreceptors to generate their
355 colour sense, like human colour-blind) and are not usually sensitive to the UV light spectrum
356 (Sherry 2016; Jacobs 2018). Although fiddler crabs also have a dichromatic colour vision, they
357 diverge from most mammals in having a good sensitivity to the UV light range, which should
358 allow them to detect UV signals reflected from, at least, some of the enlarged chelipeds.

359 *The handicap principle hypothesis*

360 On the other hand, when considering our behavioural and visual modelling data, both
361 seem to corroborate our second and third hypotheses. Previous allegations that male
362 hypertrophied chelae would assist fiddler crab detection by humans (Jordão and Oliveira 2001),
363 in addition to our modelling results predicting that birds should pose a threat to male fiddler
364 crabs, demonstrate that males' hypertrophied claws might be regarded as handicaps (Zahavi
365 1975). According to Zahavi's point of view (Zahavi and Zahavi 1997), the simple act of bearing
366 a handicap (i.e., flamboyant claw) and not having been captured by predators would prove an
367 individual's quality to their potential mates, as they propose it would happen with peacocks
368 and other species displaying bright colourations. So, we could speculate that just a few high-
369 quality males (i.e., "the remarkable seven") should be able break claw crypticity and pay the
370 costs for socio-sexual advertisement (i.e., honest signal), coping with the resulting
371 enhancement in bird predation pressure.

372 Another, not mutually exclusive, possibility would be that colourful chelipeds could
373 serve as anti-predatory honest signalling. In an exquisite behavioural study, Bildstein et al
374 (1989) showed that the enlarged claw of male fiddler crabs reduces the likelihood of their
375 capture by relatively large avian predators (i.e., white ibises), enhancing the chances that
376 declawed males, or females, have of being chosen instead. These results are also in line with
377 Zahavi's handicap principle, since white ibises would be choosing to attack prey that could not
378 convey reliable proofs of their quality (i.e., fiddle crabs with small, or absent, chelae), in the
379 same way wolves prefer to attack gazelles that run instead of jumping (Zahavi and Zahavi
380 1997).

381 *Fisherian hypotheses*

382 Female choice in fiddler crabs might be linked to direct (i.e., resources, protection) and
383 indirect (i.e., better sperm, good genes) benefits that are supplied by the males. A good example
384 of direct benefits, that might be explored by females, is the existing relation between size of
385 hypertrophied claws and quality of male burrows, with larger males occupying larger, safer,
386 and more thermally stable burrows (Christy 1987). Concerning the potential indirect benefits
387 of female choice, two dominant hypotheses have been recognized, Fisher's runaway selection
388 hypothesis and the good-genes hypothesis (Anderson 1994).

389 Although our study has not evaluated if there is a genetic correlation between UV
390 reflection by male claws and females' preference for UV cues, another way of interpreting our
391 data would be that a Fisherian runaway selection is under action in fiddler crabs, selecting a
392 strong female preference for UV colouration in correlation with a strong UV reflection by
393 males' hypertrophied claws. According to the runaway hypotheses, in which a self-reinforcing
394 process of ever-elaborating traits and preferences would take place, the mean values of traits
395 and preferences would increase, while their variances and correlation should approach a stable
396 equilibrium (Henshaw and Jones 2020). Our data, however, does not seem to support Detto

397 and Backwell (2009) Fisherian hypothesis, in which selection for UV reflection could be
398 explained by the enhancement of male conspicuity with female concomitant attraction. Even
399 though we have shown there to be a clear preference for UV signals among half of female
400 fiddler crab population, our visual models predict that only the claws of a very few males (i.e.,
401 17.5% of the population) would be conspicuous to their mates, whilst the remaining of them
402 would be regarded as cryptic or poorly detectable, something that goes against the logic of
403 Fisher's classical runaway selection hypothesis.

404 Nevertheless, a recent reinterpretation of Fisher's original mathematical model predicts
405 the occurrence of two qualitatively different outcomes, besides the classical runaway:
406 explosive runaway and fizzle away (Henshaw and Jones 2020).

407 According to the explosive runaway possibility, in case a large variance in preference
408 overcame fiddler crab's female population, with some females showing a huge preference for
409 male UV reflection while others could not care less about the same male trait, selection could
410 be so strong that extreme outliers (i.e., those few males with conspicuous claws) in the original
411 distributions could be strongly favoured, leading to a super exponentially increase in both the
412 means and variances of traits and preferences, that could reach absurd values in very few
413 generations. When we take the behavioural data from our first experiment and split every
414 female into two categories, we can see that half of them choose an UV-reflecting male (n =
415 27), while the other half does not (n = 33). If Henshaw and Jones (2020) correction of Fisher's
416 mathematical model is accurate, this observed variance in female's preference for UV signals
417 should start an ultra-rapid selection process with explosive increase in enlarged claws UV
418 conspicuity, something that we also have not encountered in our sample.

419 At last, we conclude that the third Fisherian possible outcome, the fizzle away selection,
420 in which variation in both traits and preferences would converge to zero, while the means of
421 both traits and preferences would plateau after an initial period of increase (Henshaw and Jones

2020), also does not fit our results, inasmuch as we have shown variation to take place both on female preference for UV signals and UV reflectance by male enlarged claws.

Only further experimentation testing, for example, if there is a hereditarian cooccurrence between a higher UV reflection in males and a higher UV preference in related females, or how physiological attributes of male fiddler crabs correlate with their colour signals, especially if female choice leads to offspring of superior viability, can give us more conclusive answers about the evolution of UV reflection on fiddler crabs in light of Fisher's and the good-genes hypotheses.

Conclusions

We failed to prove the existence of a UV private communication channel related to fiddler crabs' enlarged claw colouration. Our data endorse the view that male enlarged UV-reflecting chelae function as handicaps and might honestly signal quality to potential mates and predators. We also have shown that, similarly to Australian fiddler crabs, American fiddler crabs produce, discriminate, and prefer UV light signals. Would female preference for UV signals and UV reflection by male enlarged claws be widespread traits within fiddler crabs? Have the trait and the preference evolved only once, a long time ago, before the split of Gelasiminae into the Indo-West Pacific and American groups (Shih et al. 2016)? Or, instead, are they more recent acquisitions that have been independently selected in the American and Indo-West Pacific branches through convergent evolution? Future studies investigating traits and preferences in additional species of fiddler crabs can shed more light on how the evolution of UV signalling happened in this group.

ACKNOWLEDGMENT

We are deeply indebted to J. Medeiros and L. V. Silva, for helping with the logistics of the project. We would also like to thank H. R. Silva, M. S. Capitulo, J. B. C. Neto and B. A. Souza

for assistance in data collection. This manuscript was verified by an English native speaker (G.W. Erickson). This study was financed in part by the Coordenacao de Aperfeicoamento de Pessoal de Nivel Superior – Brasil CAPES (Finance Codes 001 and 043/2012), by Conselho Nacional de Desenvolvimento Cientifico e Tecnologico – Brasil (CNPq) (Finance Codes 478222/2006-8 and 474392/2013-9) and by Programa de Apoio aos Nucleos de Excelencia – FAPERN/CNPq (Finance Code 25674/2009). An Undergraduate Scientific Initiation Scholarship was granted to R.S.G., M.Sc. Scholarships were granted to D.J.A.S. and M.F.E., and a Researcher Scholarship was granted to D.M.A.P., all by Conselho Nacional de Desenvolvimento Cientifico e Tecnologico – Brasil CNPq.

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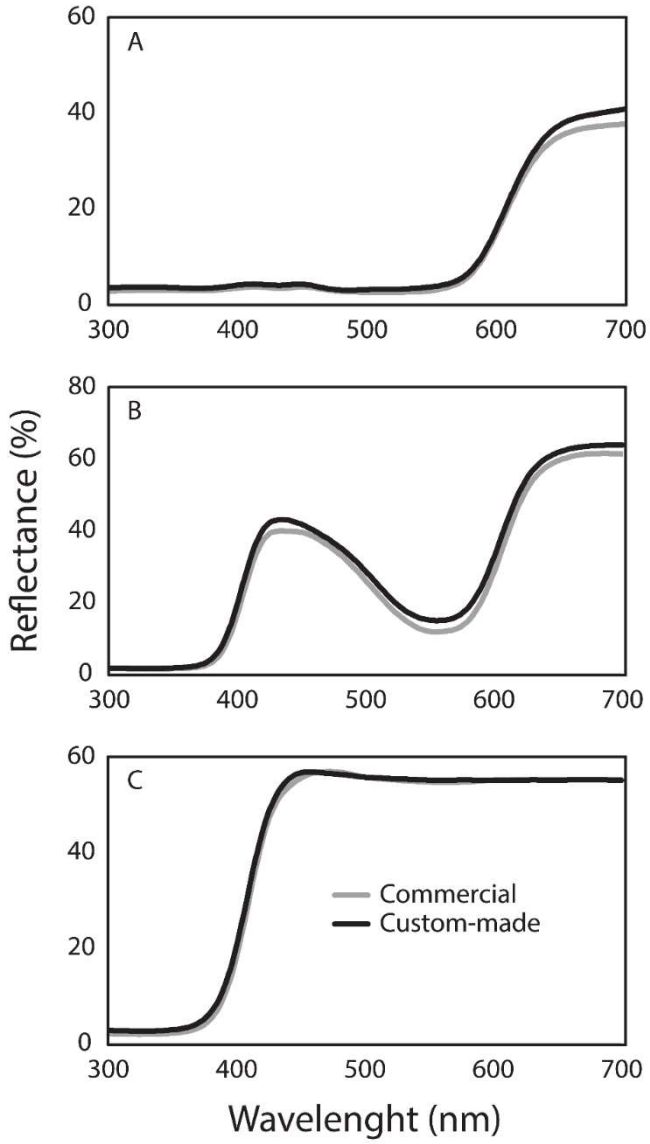
APPENDIX



Appendix 1. Reflectance spectra, of three different natural surfaces, measured with aid of either a commercial reflectance probe holder (RPH-1, Ocean Optics Inc., Dunedin, Florida) or a custom-made, 3D printed,

reflectance probe holder. A) Petal of *Delonix regia* (Bojer ex Hook.) Raf.; B) Petal of *Catharanthus roseus* (L.) G.Don; C) Petal of *Plumeria pudica* Jacq.