

The role of social costs as a mechanism enforcing the honesty of ultraviolet-reflecting signals in a lizard

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3 1 **The role of social costs as a mechanism enforcing the honesty of ultraviolet signals in a**
4
5 2 **lizard**

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35 15 **Short title:** Social costs of an ultraviolet signal
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3 19 **Abstract**
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5 20 According to animal signalling theory, social costs, for example induced by aggression from
6
7 21 conspecifics, are one of the mechanisms maintaining signal honesty. While our understanding
8
9 22 of signal evolution has much improved for pigment-based colours, the mechanisms
10
11 23 maintaining the honesty of structural colour signals, such as ultraviolet (UV), remain elusive.
12
13 24 Here, we used the common lizard *Zootoca vivipara* to test whether the honesty of UV signals
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15 25 displayed on male throats is under social control. To do so, we staged dyadic agonistic
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17 26 interactions between non-manipulated focal males and opponents of either larger or smaller
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19 27 body size. We used either control or manipulated UV signals to create small cheaters with
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21 28 UV-enhanced throats, large cheaters with UV-reduced throats, and their respective controls.
22
23 29 In support of a conventional signal hypothesis, focal males were aggressive towards large
24
25 30 cheaters and became submissive when these large cheaters retaliated, and were less
26
27 31 submissive against small cheaters. However, that focal males were not more aggressive
28
29 32 towards small cheaters contradicts our initial predictions. We then confirmed that male UV
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31 33 coloration and bite force were good predictors of contest outcomes in control conditions.
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33 34 Overall, we provide partial evidence suggesting that social costs enforce UV signal honesty in
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35 35 common lizards.
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44 37 **Key words:** Animal communication – Deception – Male competition – Ultraviolet – *Zootoca*
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46 38 *vivipara*
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42 **Introduction**

43 Animals use an astounding variety of signals to communicate with one another and these
44 signals constitute the backbone of animal social interactions. To be evolutionarily stable,
45 signals must confer net fitness benefits to both senders and receivers and this condition can be
46 achieved only if signals are honest on average (Maynard Smith & Harper, 2003; Searcy &
47 Nowicki, 2005; Bradbury & Vehrencamp, 2011). When the interests of senders and receivers
48 diverge, mechanisms enforcing signal honesty are required to prevent low-quality individuals
49 from dishonestly signalling high quality (Searcy & Nowicki, 2005). For example, differential
50 costs conditional on the sender's quality may be associated with the signal to ensure its
51 honesty (Searcy & Nowicki, 2005; Bradbury & Vehrencamp, 2011; Higham, 2014). These
52 costs may be a direct consequence of signal production and/or maintenance (i.e. physiological
53 costs, Zahavi, 1975; Grafen, 1990; Higham, 2014; Webster, Ligon, & Leighton, 2018), or
54 may be imposed by receivers, for example in the form of retaliation or punishment during
55 social interactions (i.e. social costs, Johnstone & Norris, 1993; Guilford & Dawkins, 1995;
56 Bradbury & Vehrencamp, 2011; Bachmann *et al.*, 2017).

57 Conventional signals, sometimes referred to as badges of status in the context of male
58 competition, fall in the second category (Hurd, 1997; Whiting, Nagy, & Bateman, 2003;
59 Bradbury & Vehrencamp, 2011). They are linked to the advertised quality based on an
60 arbitrary convention (Guilford & Dawkins, 1995; Hurd & Enquist, 2005) and are often
61 associated with socially imposed costs during agonistic interactions (Higham, 2014; Weaver,
62 Koch, & Hill, 2017). Tibbetts (2014) and Webster *et al.* (2018) further highlight that
63 physiological and social costs need not be mutually exclusive in maintaining honest signalling
64 and argue that, regardless of whether physiological costs exist or not, social costs are likely to
65 arise during aggressive interactions. This is because receivers are more likely to attack when
66 rivals have similar signalling level as their own (Tibbetts, 2014), and/or when they discern a

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3 67 mismatch between their opponent's quality and signalling level (Rohwer & Rohwer, 1978). In
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5 68 both cases, cheating becomes particularly costly for low-quality individuals because of the
6
7 69 increased risk of injury due to physical attacks (Tibbetts, 2014). In spite of this, most studies
8
9 70 investigating honest signalling focused on physiological costs and very few on social costs,
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11 71 thus leading Bachmann *et al.* (2017) to call for adequately designed studies to reduce this
12
13 72 research bias.
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16
17 73 Colour signals constitute a diverse class of signals and result from different colour-
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19 74 producing mechanisms including pigmentary and structural components (Shawkey & D'Alba,
20
21 75 2017). Recent evidence has much improved our understanding of the signalling role and
22
23 76 evolution of pigment-based colours such as melanin- and carotenoid-based colours (Svensson
24
25 77 & Wong, 2011; Roulin, 2016; Weaver *et al.*, 2017; San-Jose & Roulin, 2018). In fact, most
26
27 78 conventional signals described so far are colour signals (but see Molles & Vehrencamp, 2001;
28
29 79 Vehrencamp, 2001) displayed during male-male competition that involve pigment-based
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31 80 colours, especially melanin-based black or white coloration (Møller, 1987; Martín &
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33 81 Forsman, 1997; Qvarnstrom, 1997; Beani & Turillazzi, 1999; Ligon & McGraw, 2016;
34
35 82 Bachmann *et al.*, 2017). Social costs can also maintain the honesty of rapid colour change
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37 83 (Ligon & McGraw, 2016), and of pigment-based colours potentially costly to produce (Martín
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39 84 & Forsman, 1997).
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44 85 The costs maintaining the honesty of structural colour signals, including ultraviolet
45
46 86 (UV) signals, are yet to be uncovered. Some lines of argument suggest that assembling the
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48 87 dermal, light-scattering nanoscale structures composing structural coloration could pose
49
50 88 developmental challenges, which could ultimately maintain signal honesty but robust
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52 89 evidence is still lacking (Fitzpatrick, 1998; Kemp & Rutowski, 2007; Kemp, Herberstein, &
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54 90 Grether, 2012; Kemp & Grether, 2015; White, 2020). UV signals have also been suggested to
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56 91 function as conventional signals especially in lizards, but hard proof is still needed to confirm
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2
3 92 this hypothesis (Whiting *et al.*, 2003; Stapley & Whiting, 2006). Names *et al.* (2019)
4
5 93 manipulated the UV-blue patches of male common wall lizards (*Podarcis muralis*) during
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7 94 male agonistic contests. They found that males were less aggressive and more submissive
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10 95 against cheaters than against honest males, thus rejecting a conventional signal hypothesis in
11
12 96 this species. In blue tits (*Cyanistes caeruleus*), three important studies suggested that the UV
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14 97 coloration displayed on male crowns may function as conventional signals during male
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16 98 contests (Alonso-Alvarez *et al.*, 2004; Poesel *et al.*, 2007; Rémy *et al.*, 2010). These,
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18 99 however, are not conclusive since they were designed to explore the role of UV signals during
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21 100 agonistic interactions rather than to test whether social costs enforced their honesty.
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24 101 To identify social costs of colour signals, researchers must experimentally create out-of-
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26 102 equilibrium colour signals to simulate cheating individuals and examine whether these
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28 103 cheaters receive more aggression than honest signallers during agonistic interactions (Ligon &
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30 104 McGraw, 2016; Bachmann *et al.*, 2017; Names *et al.*, 2019). In this study, we used the
31
32 105 common lizard *Zootoca vivipara* to investigate whether or not socially imposed costs
33
34 106 maintain the honesty of UV signals. Male common lizards display UV-reflecting signals on
35
36 107 their throat (Martin *et al.*, 2013) that play a role during male-male competition (Martin *et al.*,
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38 108 2016) and female mate choice (Badiane *et al.*, 2020). In addition, UV chroma on male throat
39
40 109 increases with age and body size (Bonnaffé *et al.*, 2018). Altogether, these results strongly
41
42 110 suggest that male UV-reflecting throats might signal male quality in *Z. vivipara*. Furthermore,
43
44 111 body size is one of the best predictors of male contest outcome in lizards with larger lizards
45
46 112 more likely to win fights than smaller ones (Carpenter, 1995; Fitze & Le Galliard, 2008;
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48 113 Names *et al.*, 2019). Body size is thus a cue widely used by lizards to extract information on
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50 114 male quality (we use the terms ‘signal’ and ‘cue’ as defined in Bradbury & Vehrencamp,
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52 115 2011).
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3 116 Here, we first determined whether or not male-induced social costs are associated with
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5 117 dishonest UV signals in this species, and then investigated the relative importance of male UV
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7 118 signals, bite force and body size during male agonistic contests. To do so, we designed dyadic
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9 119 agonistic encounters between non-manipulated focal males and opponents that were either
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11 120 smaller or larger than focal males, with either a control (i.e. honest) or a manipulated (i.e.
12
13 121 cheaters) UV-reflecting throat. To disrupt the correlation between UV signal and quality, we
14
15 122 used lizards of different body size. Our rationale was that precise quality traits advertised by
16
17 123 UV signals are not completely known yet in this species, but body size is a well-known cue of
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19 124 male quality that correlates with UV signals in this and other lizards species (Bonnaffé *et al.*,
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21 125 2018). Specifically, small opponents were either UV-control or UV-enhanced so as to create
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23 126 cheaters of lower quality (i.e. small) with high signalling level. Large opponents were either
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25 127 UV-control or UV-reduced so as to create cheaters of higher quality (i.e. large) with a low
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27 128 signalling level. If the UV-reflecting throat functions as socially enforced conventional
28
29 129 signals, we predict that cheaters will pay the cost of their dishonesty in the form of received
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31 130 aggression from focal males. We thus expected focal males to behave more aggressively and
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33 131 be less submissive against cheaters than against honest opponents.
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40 **Material and Methods**

41 *Study species*

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43 134 The common lizard (*Zootoca vivipara*) is a small lacertid inhabiting humid habitats across
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45 135 Eurasia (Massot *et al.*, 1992). In our study site, adult males usually emerge from hibernation
46
47 136 in March. The emergence of females starts approximately 3-4 weeks later in the beginning of
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49 137 April, depending on weather conditions, and marks the beginning of the mating season
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51 138 (Massot *et al.*, 1992). During the mating season, males chase away other males to ensure
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53 139 access to females and there is endurance competition among males to find mates (Heulin,
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55 140 1988). Adult common lizards occupy overlapping home-ranges and are polygynandrous, with
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1
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3 141 both sexes having multiple sexual partners (Laloi *et al.*, 2004; Fitze *et al.*, 2005). Adult males
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5 142 have a conspicuous belly ranging from yellow to red, interspersed with numerous black spots
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7 143 (Martin *et al.*, 2013; San-Jose *et al.*, 2017). In females, ventral coloration is duller, from
8
9 144 cream to orange, with fewer black spots than males and extends more on the throat (Bauwens,
10
11 145 1987; Cote *et al.*, 2008). In addition, the ventral and throat coloration have a secondary
12
13 146 reflectance peak in the UV, which is especially pronounced in males, particularly on their
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15 147 throat (Martin *et al.*, 2013).

148 *Sampling and measurements*

149 On March 19th 2019, we captured 59 adult males by hand at the Centre de Recherche en
150 Ecologie Expérimentale et Prédictive (CEREEP-Ecotron Ile-De-France, 48°17'N, 2°41'E),
151 where a captive population of common lizards is maintained in separate 100-m² enclosures
152 under natural, outdoor environmental conditions. We brought the lizards to the laboratory,
153 measured their snout-vent length (SVL) with a ruler (± 1 mm), and their body mass using a
154 digital scale (± 1 mg). We also measured bite force, which provides a good proxy for fighting
155 ability and whole-organism performance in lizards (Huyghe *et al.*, 2005; Lappin & Husak,
156 2005). To do so, we used a purpose-built bite force meter constructed from a modified Sauter
157 25N digital force gauge. We retained the maximum score out of three bite force
158 measurements and made sure that the lizards had a body temperature comprised between
159 30°C and 35°C when biting (Lappin & Jones, 2014), since their preferred body temperature is
160 around 32-34°C (Rozen-Rechels *et al.*, 2020).

161 We obtained reflectance spectra from the throat and belly of each male (two replicates
162 per body region) using a USB-2000 diode-array spectrophotometer with a R400-7-UV/VIS
163 reading-illumination probe (Ocean Optics Inc.) and a notebook computer running OceanView
164 (Ocean Optics Inc.). We took reflectance readings in a darkened room using an HL-2000
165 Halogen-Deuterium light source (Ocean Optics Inc.) for full spectrum illumination. We

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3 166 recorded reflectance spectra relative to a white diffuse standard (WS1; Ocean Optics Inc.) and
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5 167 a dark reading. We set integration time to 9, scans to average to 10, and boxcar width to 10.
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7 168 For data acquisition, we hand-held the probe over the centre of the targeted colour patch with
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9 169 a 90° angle between the probe and the skin surface (i.e. coincident normal recording
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11 170 geometry, Anderson & Prager, 2006). An entomological pin attached to the tip of the probe
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13 171 allowed us to maintain a constant distance of 3 mm between the tip of the probe and the skin
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15 172 surface. We always aimed the probe at a skin area larger than 1.5 mm in diameter that did not
16
17 173 contain any black spot to avoid spectral contamination (Badiane *et al.*, 2017). We later
18
19 174 processed spectral data in R v.3.3.2 (R Development Core Team, 2017) using the package
20
21 175 *pavo* 2.0 (Maia *et al.*, 2019). We cropped each spectrum between 300-700 nm, smoothed
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23 176 them using a loess smooth span of 0.2, and averaged the two replicates recorded for each
24
25 177 body region. Then, we extracted two UV-related colorimetric variables from the throat
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27 178 spectra, namely spectral intensity (i.e. $R_{300-700}$), and UV chroma (i.e. $R_{300-400}/R_{300-700}$).
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33 179 Following measurement, we placed the lizards individually in opaque terraria
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35 180 (25x15.5x15 cm) layered with soil substrate, and equipped with a shelter (7,6 x 15,2 x 15,1
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37 181 cm, ExoTerra) and a small water dish (Petri dish ~5 cm in diameter). An incandescent bulb
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39 182 (25 W) and white light UV-B neon tubes (Reptisun 10.0 UVB, Zoomed) provided heat and
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41 183 light following a 10/14-h dark-light schedule. We provided food three times a week (300-400
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43 184 mg of live house crickets, *Acheta domesticus*) and water *ad libitum*. Lizards were housed for a
44
45 185 total of 18 days, including 10 days of acclimation to the laboratory conditions during which
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47 186 we waited the lizards' first moult to occur as it marks the onset of sexual activity (Laloi *et al.*,
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49 187 2011), and 8 days of experiment.
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53 188 *Colour manipulation and behavioural assays*

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55 189 Behavioural assays took place in a temperature-controlled room maintained at 21°C using two
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57 190 neutral arenas to eliminate any resident-intruder effect (Martin *et al.*, 2015, 2016). Arenas
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3 191 were composed of a large opaque plastic terrarium (75x50x40 cm) with one transparent wall
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5 192 to allow video recording, and contained a layer of blond peat as substrate. Two removable
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7 193 opaque plastic walls divided the arena into two equally-sized compartments on both sides and
8
9 194 a larger compartment at the centre. The two compartments at the extremities of the arena
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11 195 served as solitary holding areas to allow acclimation to the neutral arena, and were each
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13 196 equipped with a 25-W heat bulb placed 15 cm above a shelter (Exoterra Inc.) that also acted
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15 197 as basking spot. In the central compartment, we placed another 30-W heat bulb 15 cm above a
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17 198 wooden basking spot (12x8x1.5 cm). We illuminated the arenas with a light-emitting plasma
18
19 199 fixture (Gavita Pro 270° GROW LEP) placed 80 cm above the bottom of the arena. This light
20
21 200 source reproduces almost exactly the full spectrum of the sun, including UVB and UVA
22
23 201 thanks to a UV transmitting glass filter, and is thus ideal to examine the role of UV signals
24
25 202 during laboratory experiments. White, opaque curtains surrounded the two arenas at a 1-m
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27 203 distance to create visual isolation. Two digital SLR cameras (Nikon D500 and Nikon D5300)
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29 204 mounted on tripods recorded the experiments in high definition from a lateral, slightly
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31 205 elevated point of view, through the transparent wall of the arena.
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37 206 To test the hypothesis that male-induced social costs are associated with dishonest UV
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39 207 signals in common lizards, we staged dyadic encounters using 59 adult male common lizards
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41 208 (SVL, range = 50-63, mean = 57; body mass, range = 2.4-5.3 , mean = 3.8). Each dyadic
42
43 209 interaction was unique and involved medium-sized (56-60 mm in SVL), non-manipulated
44
45 210 focal males (n = 29), which faced opponents of either larger (n = 15) or smaller size (n = 15)
46
47 211 with control or manipulated throat UV reflectance. Small opponents ranged from 50-55 mm
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49 212 in SVL and were either UV-control or UV-enhanced. Large opponents (60-63 mm in SVL), in
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51 213 contrast, were either UV-control or UV-reduced. This study design allowed us to create a
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53 214 mismatch between UV signalling level and body size, and ultimately with male quality since
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55 215 body size is a primary predictor of fighting ability and male contest outcome in lizards
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3 216 (Carpenter, 1995; Karsten *et al.*, 2009; Baird, 2013; Names *et al.*, 2019). Focal males were
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5 217 always 3-6 mm larger ($\beta = 4.21 \text{ mm} \pm 0.41$, $p < 0.001$) and 1-5 mm smaller ($\beta = -2.84 \text{ mm} \pm$
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7 218 0.42 , $p < 0.001$) than their small and large opponents, respectively. There were no significant
8
9 219 differences in body size and body mass between small controls and small cheaters (SVL: $\beta = -$
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11 220 $0.38 \text{ mm} \pm 0.66$, $p = 0.978$; body mass: $\beta = -0.21 \text{ mm} \pm 0.21$, $p = 0.846$), nor between large
12
13 221 controls and large cheaters (SVL: $\beta = 0.30 \pm 0.68$, $p = 0.991$; body mass: $\beta = 0.37 \pm 0.22$, $p =$
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15 222 0.465).

19
20 223 To reduce the UV reflectance within the natural range of variation, we used UV-
21
22 224 blocking (290-400 nm) inorganic agents (zinc oxide and titanium dioxide) mixed with a fat
23
24 225 combination of petroleum jelly and liquid paraffin (respectively, 6:4:50:40 for 100 g). Large
25
26 226 males of the control group were treated with the fat combination and large males of the UV-
27
28 227 reduced treatment were treated with the fat combination mixed with the inorganic agents
29
30 228 (Figure 1). The spectral curve of this UV-reduction corresponded well with the spectra
31
32 229 obtained in previous studies (Martin *et al.*, 2016; Badiane *et al.*, 2020). We applied both
33
34 230 mixtures using a thin paintbrush on the lizards' throat, from the tip of the jaw to the collar
35
36 231 scale row. To enhance throat UV reflectance, we used a light orange Edding 4500 T-shirt
37
38 232 marker pen (colour code 016) that reflects in the UV range. This marker is similar to those
39
40 233 previously used to enhance UV-blue coloration in birds and lizards (Kurvers *et al.*, 2010;
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42 234 Rémy *et al.*, 2010; Names *et al.*, 2019), except that we used light orange instead of light blue
43
44 235 in our study because it better matches the natural throat colour of male common lizards. To
45
46 236 facilitate the marker application on the lizards' throat, we dismantled the marker and pressed
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48 237 the ink reservoir so as to deposit a drop of water-based ink on a plate, then we dipped the tip
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50 238 of a forceps into the droplet and spread it on the lizards' throat from the tip of the jaw to the
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52 239 collar scale row. We then let it dry for a few minutes before starting the experiments. Small
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54 240 lizards from the UV-enhanced group were treated with this marker pen while small lizards
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3 241 from the UV-control group were not treated at all (Figure 1). As Figure 1 illustrates, our UV-
4
5 242 enhancing treatment augmented throat reflectance in UV but also in the orange part of the
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7 243 spectrum, and spectral shape looked somewhat artificial. This marker pen, however, produced
8
9 244 the best spectral shape of all the different marker pens and paintings we have tried.
10
11

12 245 Each focal male participated in four dyadic encounters against four different males from
13
14 246 the four treatments (i.e. small cheaters, small controls, large cheaters, and large controls)
15
16 247 presented in a random sequence. We chose the opponent so as to standardize the size
17
18 248 difference between focal and opponent males, such that the largest focal males encountered
19
20 249 the largest opponents from both the small and large size categories, and the smallest focal
21
22 250 males faced the smallest opponents of both size categories. We designed the experiment such
23
24 251 that focal males participated to encounters only once every two days, and opponents not more
25
26 252 than once a day. We performed a total of 116 trials during 8 days with a maximum of 16 trials
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28 253 per day (8 trials per arena per day) during the activity period of the lizards from 09:00 to
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30 254 17:00. Most males from the paired interactions had no prior knowledge of each other because
31
32 255 they were hosted in separate enclosures during all their lives, except for 14 tests (12%) for
33
34 256 which both males came from the same 100-m² enclosure. However, in 12 out of these 14
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36 257 encounters, both males were entering their first reproductive season (almost 2 years old) and
37
38 258 had therefore not competed in the past. The two remaining contests both involved a sexually
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40 259 mature male (almost 3 years old) against a newly sexually mature male (almost 2 years old),
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42 260 and had therefore never competed against each other. In the light of this, it is unlikely that
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44 261 prior knowledge due to sexual competition among the males impacted our results.
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51 262 Before each experiment, we removed the participating males from their home terrarium,
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53 263 manipulated their throat coloration, and randomly placed each male in one of the two
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55 264 compartments of the neutral arena. We allowed a first 10-min acclimation period with the
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57 265 shelters and basking spot in both compartments. After 10 min, we removed the shelters from
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3 266 the compartments and allowed another 10-min acclimation period without shelters to force
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5 267 them to be active, leaving the heat bulb turned on for thermoregulation. After this 20-min
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7 268 acclimation period with and without shelters (and without observers), the experiment started
8
9 269 as we removed the opaque walls to reveal the central area and immediately turned the heat
10
11 270 bulbs from the two compartments off, such that the only basking spot left is the wooden plate
12
13 271 at the centre of the arena. We turned the video camera on and left the room to prevent any
14
15 272 observer-induced disturbance. The experiment lasted 20 min as the two males behaved and
16
17 273 competed for the basking spot. Next, a single observer, blind to the experimental treatments,
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19 274 used Jwatcher (Blumstein & Daniel, 2007) to analyse the lizards' behaviours from all the
20
21 275 video recordings to avoid any observer effect.
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26 276 We recorded each time a lizard performed any of the behaviours described in Table 1
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28 277 (Martin *et al.*, 2016; Names *et al.*, 2019). We assigned a coefficient to each of these
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30 278 behaviours to give more weight to the most aggressive behaviours, since they are more likely
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32 279 to be costly for the opponent (Carazo, Font, & Desfilis, 2008; Abalos *et al.*, 2016). Although
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34 280 an obvious hierarchy exists between behaviours with regard to contest escalation, there still is
35
36 281 some degree to which coefficient assignment can be subjective and arbitrary. Hence, in
37
38 282 addition to the first set of coefficients we consider as most relevant, we assigned two more
39
40 283 sets of coefficients to examine how coefficient assignment may influence our results. We thus
41
42 284 calculated three versions of the aggression score and three versions of the submission score as
43
44 285 indicated in Table 1. In addition, we recorded basking duration, that is the time spent basking
45
46 286 on the wooden plate, because males competed over a unique basking spot. We also recorded
47
48 287 the duration of wall-scratching behaviour for each male. This behaviour consists of males
49
50 288 scratching the walls of the arena to try to escape and may be due to stress as a consequence of
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52 289 laboratory conditions (de Fraipont 2000, Rozen-Rechels 2018). It may also be triggered by a
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3 290 male fleeing from another male. None of the contests resulted in observable injuries and all
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5 291 males were released to their semi-natural outdoor enclosures after the 8 days of experiment.

6
7
8 292 *Statistical analyses*

9
10 293 We used R v.3.3.2 (R Development Core Team, 2017) to perform two complementary set of
11
12 294 statistical analyses of the behavioural data.

13
14 295 *Social costs on dishonest UV signals*

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16
17 296 First, to test whether or not social costs are imposed on dishonest male UV signals, we
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19 297 calculated two categorical variables named ‘opponent size’ with two levels (‘large’ and
20
21 298 ‘small’) and named ‘opponent honesty’ with two levels (‘honest’ and ‘cheaters’). Honest
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23 299 males corresponded to UV-control males while cheaters corresponded to manipulated males
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25 300 from both the UV-reduced and UV-enhanced treatment groups. Then, we ran LMMs for
26
27 301 Gaussian variables and GLMMs for Poisson variables using the following response variables
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29 302 for focal males: the three versions of aggression score, the three versions of submission score,
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31 303 basking duration, and duration of wall-scratching behaviour. We included male ID and trial
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33 304 order as random intercepts in these models. We considered trial order as random because we
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35 305 were not interested in the effects of trial order *per se*; however, we also ran these models with
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37 306 trial order as fixed factor and present the results from post-hoc Tukey tests when significant.
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39 307 We included the additive effects of opponent size and opponent honesty as well as their two-
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41 308 way interactions, and the additive effect of bite force as fixed effects. When the interaction
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43 309 was significant, we split our data set according to the “opponent size” category to explore the
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45 310 interaction. To reduce the impact of influential values (detected with Cook’s distances) and
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47 311 improve our models, we performed an alpha-winsorisation with a 0.03 trim on the submission
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49 312 score and wall-scratching behaviour. For all the models described above, we checked the
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51 313 model assumptions using the *performance* R package (Lüdtke *et al.*, 2020). We used a
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53 314 squared-root transformation for wall-scratching behaviour to comply with these assumptions.
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3 315 All continuous variables assuming a Gaussian distribution were centred and scaled prior to
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5 316 analyses to ease result interpretations (Schielzeth, 2010).

7 317 *Determinants of male contests*

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10 318 Next, to explore the role of body size, bite force, and throat UV reflectance during male
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12 319 agonistic contests, we analysed only interactions between focal males and control opponents
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14 320 from both size categories, thus excluding the cheaters. We used linear mixed-effects models
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16 321 (LMMs) and generalized linear mixed-effects models (GLMMs) to test the additive effects of
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18 322 bite force, UV chroma, spectral intensity, opponent body size, opponent UV chroma, and
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20 323 opponent spectral intensity on the three versions of aggression score, the three versions of
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22 324 submission score, basking duration, and duration of wall-scratching behaviour. We included
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24 325 the same random intercepts as above. We used the *lme4* R package (Bates *et al.*, 2015) to
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26 326 perform GLMMs on count variables assuming a negative binomial distribution for the
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28 327 aggression score and a Poisson distribution for the submission score. For the remaining
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30 328 response variables (i.e. basking duration, and wall-scratching duration), we assumed a
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32 329 Gaussian distribution and used LMMs as implemented in the *nlme* R package (Pinheiro *et al.*,
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34 330 2019). To reduce the impact of influential values (detected with Cook's distances) and
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36 331 improve our models, we performed an alpha-winsorisation with a 0.03 trim on the submission
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38 332 score and wall-scratching behaviour. We proceeded with a model selection and conditional
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40 333 averaging procedure as implemented in the *MuMin* R package (Bartoń, 2019), using the
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42 334 functions *dredge* and *model.avg*. This model selection procedure allowed us to select the best
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44 335 models ($\Delta AICc < 2$) from all possible combinations of predictors, including a null model
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46 336 without any predictor.

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53 337 **Results**

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56 338 *Social costs on dishonest UV signals*
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3 339 We found that the two-way interaction between opponent size and opponent honesty
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5 340 influenced significantly the aggression score of focal males ($\beta = -0.33 \pm 0.12$, $p = 0.005$). In
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7 341 conflicts with smaller males, opponent honesty did not significantly explain the aggression
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9 342 score of focal males, though the tendency was a smaller aggression score of focal males (UV-
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11 343 enhanced cheaters: $\beta = -0.15 \pm 0.09$, $p = 0.075$). In conflicts with larger males, focal males
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13 344 were significantly more aggressive (by 1.2 units on average) towards UV-reduced cheaters
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15 345 than towards honest opponents ($\beta = 0.18 \pm 0.08$, $p = 0.021$, Figure 2A). When the two
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17 346 alternative versions of the aggression score were used, the results were qualitatively similar.

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22 347 Furthermore, our analyses revealed that the two-way interaction between opponent size
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24 348 and opponent honesty best explained the submission score of focal males ($\beta = -0.73 \pm 0.16$, p
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26 349 < 0.001). More precisely, focal males were less submissive (by 1.4 units of submission score
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28 350 on average) against small cheaters (UV-enhanced) than against small honest males ($\beta = -0.33$
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30 351 ± 0.13 , $p = 0.012$), but more submissive (by 1.7 units on average) against large cheaters (UV-
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32 352 reduced) than against large honest males ($\beta = 0.50 \pm 0.11$, $p < 0.001$; Figure 2B). When the
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34 353 two alternative versions of the submission score were used, results were qualitatively similar
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36 354 except that we did not find that focal males were less submissive against small cheaters (UV-
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38 355 enhanced).

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43 356 Moreover, treatment factors did significantly explain the time focal males spent at the
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45 357 basking spot, nor the time spent performing wall-scratching behaviours. Statistics are fully
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47 358 reported in Supp. Info. S1. When we included trial order as fixed instead of random factor, all
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49 359 the above results were qualitatively similar, and we found that aggression ratio was lower
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51 360 during the second trial than during the first ($\beta = -0.24 \pm 0.08$, $p = 0.025$) and the third ($\beta = -$
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53 361 0.26 ± 0.09 , $p = 0.013$).

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57 362 *Determinants of male contests in control interactions*
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3 363 In control interactions, males with a higher aggression score (calculated with the first set of
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5 364 coefficients) had a significantly higher bite force ($\beta = 0.29 \pm 0.11$, $p = 0.010$). This result was
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7 365 corroborated when we used both alternative aggression scores. In addition, focal males were
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9 366 more submissive (submission score calculated with the first set of coefficients) against
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11 367 opponents with a high throat spectral intensity ($\beta = 0.28 \pm 0.12$, $p = 0.023$). When we used the
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13 368 two alternative versions of the aggression score, however, none of the predictors were
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15 369 significant. We also found that males with a higher bite force tended to spend more time on
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17 370 the basking spot than males with lower bite force ($\beta = 0.31 \pm 0.16$, $p = 0.059$). Focal males
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19 371 spending more time performing wall-scratching behaviours had higher throat spectral
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21 372 intensity ($\beta = 0.47 \pm 0.17$, $p = 0.006$). Statistics are fully reported in Supp. Info. S2. When we
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23 373 included trial order as fixed instead of random factor, all the above results were qualitatively
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25 374 similar, and we found that the submission score was lower during the third trial than during
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27 375 the first ($\beta = -0.55 \pm 0.19$, $p = 0.017$), the second ($\beta = -0.92 \pm 0.25$, $p = 0.002$), and the fourth
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29 376 trial ($\beta = -1.19 \pm 0.27$, $p < 0.001$).

377 **Discussion**

378 Our results revealed partial evidence that socially imposed costs may enforce the honesty of
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40 379 UV-reflecting signals in male common lizards *Z. vivipara*. In support of the hypothesis of
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42 380 social costs, focal males were more aggressive against large UV-reduced cheaters than against
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44 381 large honest opponents, and were less submissive against small UV-enhanced cheaters than
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46 382 against small honest opponents. However, inconsistently with this hypothesis, focal males
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48 383 were not more aggressive against small UV enhanced cheaters than against small honest
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50 384 opponents and were more submissive against large UV-reduced cheaters than against large
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52 385 honest opponents. In addition to this, our analyses excluding manipulated males indicated that
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54 386 male bite force is an important predictor of male contest outcome.

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59 387 *Social costs on dishonest UV signals*
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3 388 We provide partial evidence that the UV components of the UV-reflecting throat of common
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5 389 lizards may function as conventional signals enforced by male-induced social costs. The story
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7 390 becomes more complex than expected when we examine the aggression and submission
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9 391 scores. On one hand, large males with UV-reduced throats received more aggressions but also
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11 392 triggered more submissive behaviours in focal males. This result suggests that, for large
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13 393 males, downplaying UV signals is costlier than being honest since these large UV-reduced
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15 394 cheaters are more likely to be challenged by the smaller focal males. When the focal males
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17 395 challenge the large cheaters, the latter may retaliate since, after all, they are larger and more
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19 396 likely to win fights, and focal males end up being more submissive. Hence, under this
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21 397 scenario, what seemed to be a contradictory result at first glance may in fact be coherent and
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23 398 support the idea that UV signals function as conventional signals in this species. Although
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25 399 large males pose a serious threat to smaller males, if a large male signals low condition, it
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27 400 may pay-off for smaller males to challenge this large male and gain a fitness advantage (e.g.
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29 401 access to resources and/or females). Unexpectedly, small UV-enhanced cheaters did not
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31 402 receive more aggression from the focal males compared to their honest counterparts.
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33 403 However, that focal males behaved less submissively against small cheaters aligns with the
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35 404 predictions of a conventional signal hypothesis.
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42 405 In the case of conventional signals, social costs are either imposed to individuals that
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44 406 signal above a given threshold intensity or penalize the mismatch between the sender's quality
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46 407 or behaviour and its signalling level. Signal honesty can therefore be maintained only if these
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48 408 costs exceed the benefits of cheating (Searcy & Nowicki, 2005; Bradbury & Vehrencamp,
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50 409 2011). However, some degree of deception may still arise and pay off as long as the signal
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52 410 remains honest to some degree (Adams & Mesterton-Gibbons, 1995; Carazo & Font, 2014).
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54 411 Individuals can either be exclusively honest or exclusively dishonest, or switch from one
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56 412 strategy to another according to the situation they find themselves into, depending on whether
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3 413 the signal is very labile and can change rapidly or not (Akçay, Campbell, & Beecher, 2013;
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5 414 Wilson & Angilletta, 2015; Ligon & McGraw, 2016). In common lizards, the UV-reflecting
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7 415 coloration on males' throat does not seem to change rapidly (Bonnaffé *et al.*, 2018), thus
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9 416 leaving little room for “occasional” cheating. Retaliation or punishment rules taking the form
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11 417 of physical and non-physical aggressions are the main mechanisms maintaining the honesty of
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13 418 conventional signals (Martín & Forsman, 1997; Tibbetts & Izzo, 2010; Tibbetts, 2014;
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15 419 Wilson & Angilletta, 2015; Ligon & McGraw, 2016). In this regard, the different behaviours
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17 420 measured in our study do not have the same weight as evidence of socially imposed costs. Our
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19 421 aggression score is the most meaningful factor here because it is the most likely to inflict a
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21 422 cost (e.g. injury) on the opponent. Overall, social costs taking the form of physical aggression
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23 423 may be quite high in common lizards, as 43% of our staged encounters (50 out of 116)
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25 424 escalated to the point of a male biting another male at least once. Although we cannot
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27 425 estimate the cost-benefit balance of cheating in our study, the risk of injury due to physical
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29 426 aggression is high and should not be neglected in this species (Le Galliard *et al.*, 2005). On
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31 427 top of this, other behavioural processes, for instance in the form of non-physical aggression
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33 428 and/or spatial dominance, not necessarily measured, may increase the impact of social costs.
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35 429 Our submission score may therefore capture the reaction to such behaviours and give us hints
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37 430 on whether or not social costs exist. Altogether, our results seem to indicate that cheating is
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39 431 generally more costly than being honest, although it is not always clear-cut.

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47 432 In fact, the inconsistencies in our results involved almost exclusively interactions
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49 433 between focal males and small opponents, as small UV-enhanced cheaters did not receive
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51 434 more aggression from focal males. A possible interpretation may simply be that cheating is
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53 435 more likely to pay off for a small male that exaggerates its UV signal than for a large male
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55 436 that downplays its signal. However, in the context of male-male competition, we would
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57 437 expect social costs to prevent low-quality males from signalling high quality, and gain
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3 438 advantage in terms of resources and/or access to females over males that are actually of higher
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5 439 quality (e.g. Molles & Vehrencamp, 2001). Another hypothesis may be that smaller males
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7 440 generally behave in a non-threatening way when they face larger males, for example by
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9 441 avoiding being close to larger opponent. Therefore, focal males would not need to show any
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11 442 sign of aggression and spatial occupancy, perhaps captured in our submission score, may be
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13 443 enough to affirm dominance. Alternatively, if focal males are more aggressive towards any
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15 444 opponent that signals above a given threshold intensity, and that small honest males are
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17 445 already signalling close to or above that threshold, we would not see any difference in terms
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19 446 of aggression score between small UV-enhanced cheaters and their honest counterparts.
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24 447 However, in this context, we would not expect to find differences in the submission
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26 448 score as we did here. This also raises the possibility that our results were obscured by our UV
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28 449 manipulation protocol. While the experimental reduction of the UV reflectance within the
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30 450 natural range of variation has been previously validated in the common lizard (Martin *et al.*,
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32 451 2016; Badiane *et al.*, 2020) and other lizard species (Martin *et al.*, 2015; Names *et al.*, 2019),
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34 452 it is much more difficult to enhance UV reflectance. To the best of our knowledge, only a
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36 453 handful of studies have experimentally augmented the UV coloration of animals, mostly in
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38 454 the blue tit *Cyanistes caeruleus* (Poesel *et al.*, 2007; Rémy *et al.*, 2010) and one study in the
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40 455 common wall lizard *Podarcis muralis* (Names *et al.*, 2019). In these and our study, whether or
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42 456 not these UV-enhanced patches can be considered to be within the natural range of variation
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44 457 remains debatable, since spectral shape can look artificial. In addition, our marker pen did not
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46 458 only increase reflectance in the UV range but also in the orange part of the spectrum (*idem*, to
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48 459 a lesser extent, with the UV reduction treatment) and this may set a limit to results'
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50 460 interpretations since we do not know how this may have influenced the outcome of our
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52 461 behavioural experiments. It is therefore possible that the focal males did not consider the UV-
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54 462 enhanced throat of small cheaters as a high signalling level, but simply as an 'odd' signal. For
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3 463 example, the increased orange coloration on the throat may somewhat resemble female's
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5 464 throats (Martin *et al.*, 2013) and thus confuse the receivers. In addition, we cannot exclude
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7 465 that the artificial light orange colour faded to some extent during the experiment, although not
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10 466 completely (pers. obs.). Future studies should investigate adequate methods to enhance
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12 467 “naturally” UV coloration so that research on UV signalling may take a step forward.

14 468 *Determinants of male contests*

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17 469 To further explore the individual determinants of male contests, we focused exclusively on
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19 470 encounters between focal and honest males. We found that aggression score correlated
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21 471 positively with male bite force, thus providing evidence that bite force is a good proxy of
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23 472 male dominance. Bite force has been previously linked with male dominance (Husak *et al.*,
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25 473 2006), male mating success (Lappin & Husak, 2005), and male fighting capacity (Huyghe *et*
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27 474 *al.*, 2005) in lizards. Moreover, our results revealed that focal males were more submissive
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29 475 against opponents with high throat intensity on one hand, but focal males with high throat
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31 476 intensity spent more time performing wall-scratching behaviour on the other. It may seem
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33 477 contradictory if we interpret wall-scratching behaviour as a submissive behaviour, which
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35 478 could well be the case, but it could also be linked with individual stress unrelated to the
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37 479 opponent behaviour (de Fraipont *et al.*, 2000; Rozen-Rechels *et al.*, 2018). Nevertheless, the
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39 480 results from this first part of the analyses were somewhat sensitive to the different set of
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41 481 coefficients used to calculate the aggression and submission scores. Hence, the robustness of
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43 482 these results is somewhat challenged, and this should lead behavioural ecologists and
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45 483 ethologists to take the effects of weighted behaviours into account when behavioural scores
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47 484 are calculated.

53 485 *Conclusion*

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56 486 Overall, our study highlights that UV coloration of male throat plays a role during male
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58 487 contests, both from the point of view of the signaller, as it correlates with the signaller's
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3 488 behaviour, and from the perspective of the receiver since receivers adjust their behaviour
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5 489 based on these signals. Therefore, our study confirms the importance of UV coloration as
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7 490 predictors of male contest outcomes in the common lizard (Martin *et al.*, 2016). However, we
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9 491 can only provide partial evidence that social costs maintain the honesty of UV-reflecting
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11 492 signals. This is because we observed different patterns of physical and non-physical
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13 493 aggression in the face of deception in situations where focal males faced small opponents than
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15 494 with large opponents. Although not entirely conclusive, this suggests that UV signals can be
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17 495 honest thanks to context-dependent social costs imposed by rival males during male-male
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19 496 competition. Future work should keep investigating these avenues of signal honesty with UV
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21 497 signals to improve our understanding of animal communication at large.
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25 26 498 **Research data**

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28 499 All data used in this study will be made freely available on the public repository Zenodo.
29

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32
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34
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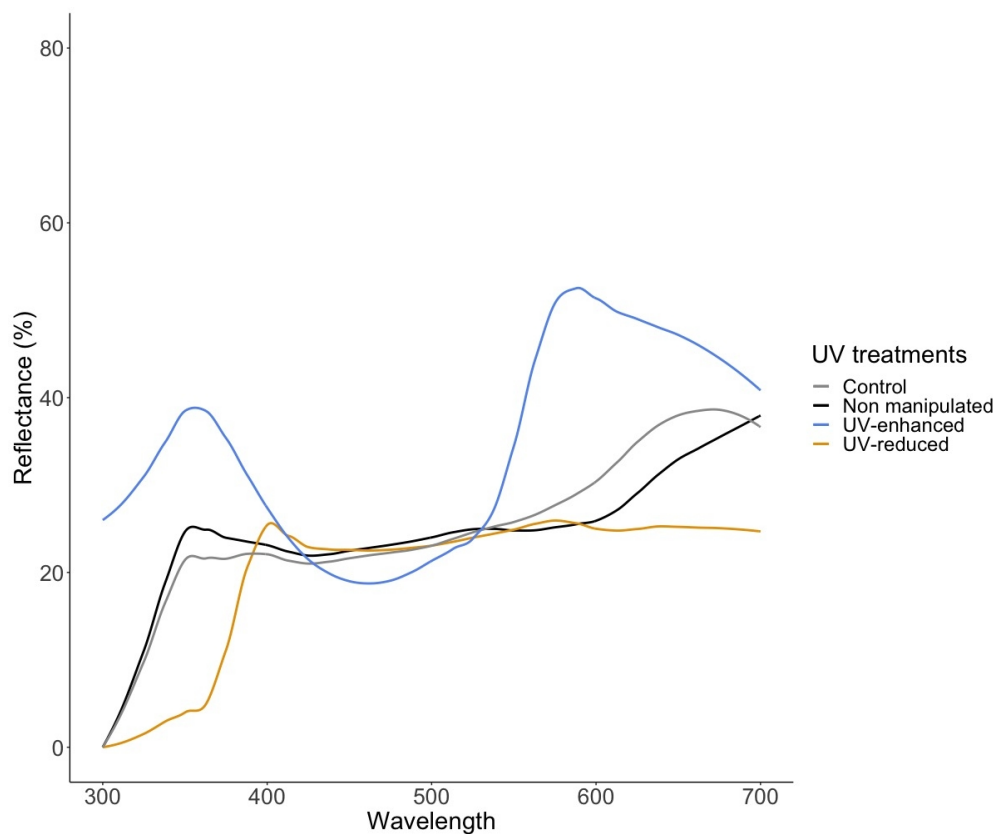
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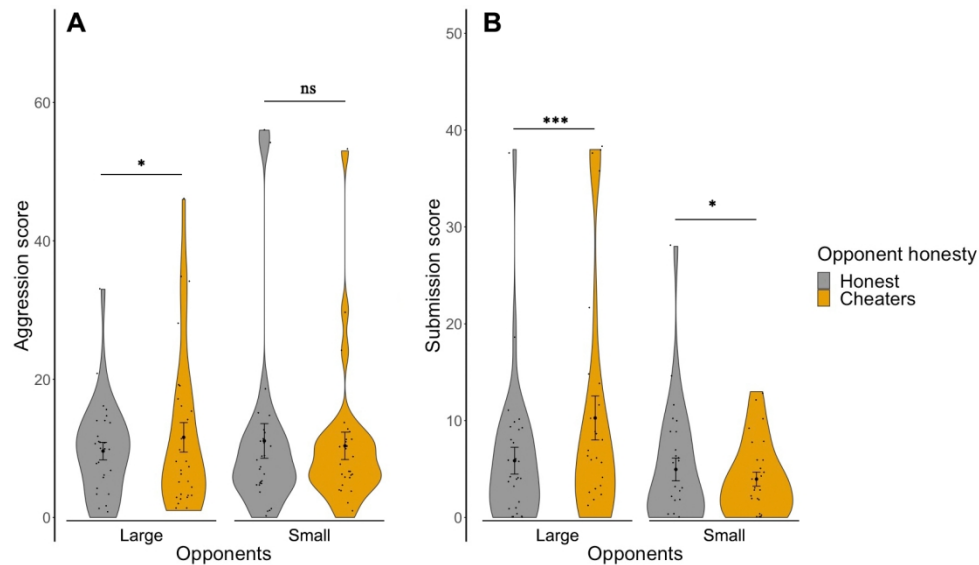
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Reflectance spectra resulting from the different UV treatments of our experimental UV treatments applied on a single individual so that the spectral variations represented are only due to the experimental treatments.

Small cheaters were UV-enhanced using a light orange marker pen. Small honest males were not manipulated. Large cheaters were UV-reduced using a mix of UV-blocking inorganic agents and a fat solution. Large honest males were treated with a fat solution only.

423x352mm (72 x 72 DPI)



Violin plots including the mean and standard errors of the aggression score (A) and the submission score (B) of focal males according to the opponent body size and UV treatment. Aggression and submission scores were calculated by adding the aggressive and submissive behaviours, respectively, weighted by their coefficient (coef.1 from table 1). UV signals were reduced in large cheaters but enhanced in small cheaters. Levels of significance are indicated ($p < 0.05$ *, $p < 0.01$ **, $p < 0.001$ ***).

625x352mm (72 x 72 DPI)

Table 1: List and descriptions of the different behaviours displayed by male *Zootoca vivipara* and their associated coefficient used to calculate scores. Coef.1 corresponds to the first set of coefficients that we assigned to the behaviours and consider as the most realistic ranking. Coef.2 and Coef.3 are two additional sets of coefficients that vary slightly from Coef.1 to examine how coefficient assignment affect our results.

Scores	Behaviours	Description	Coef.1	Coef.2	Coef.3
Aggression score	Approach	Reduce distance with rival	1	1	1
	Chase	Quickly follows fleeing rival	2	2	2
	Lunge	Hits rival with closed mouth	3	3	3
	Retaliation	Lunge in response to rival approach or lunge	3	3	3
	Bite	Holds rival for < 2 s	4	3	4
	Bite hold	Holds rival for > 2 s	5	3	4
Submission score	Tail wagging	Wagging movements of the tail	1	1	1
	Burry	Number of times a lizard burry itself into the soil substrate	2	1	2
	Escape	Rapid movement away from the rival	3	1	2
Other variables	Basking duration	Time spent basking on the wooden spot	-	-	-
	Wall-scratching duration	Time spent scratching the walls of the arena	-	-	-

The role of social costs as a mechanism enforcing the honesty of ultraviolet signals in a lizard

1 **Supplementary information S1 - Social costs on dishonest UV signals**

2

3 Test statistics resulting from our models performed to investigate whether social costs are
 4 associated with signal honesty. Estimates \pm standard error and the p-value of each predictor
 5 are indicated. These models took the form $response \sim opponent\ size * opponent\ honesty +$
 6 $bite\ force + random\ intercept\ factors$. Random factors were always the ID of focal males and
 7 trial order. The term ‘interaction’ means the two-way interaction between ‘opponent size’ and
 8 ‘opponent honesty’. Levels of significance are indicated (* < 0.05 , ** < 0.01 , *** < 0.001).

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10 Table S1. Coefficient for each predictor and response variable.

Predictors	Aggression score	Submission score	Basking duration	Wall-scratching duration
Bite Force	0.18 ± 0.11 P = 0.101	-0.05 ± 0.14 P = 0.710	0.12 ± 0.12 P = 0.334	0.12 ± 0.15 P = 0.418
Opponent honesty	0.20 ± 0.08 P = 0.012*	0.51 ± 0.10 P < 0.001***	-0.39 ± 0.23 P = 0.100	-0.17 ± 0.19 P = 0.385
Opponent size	0.22 ± 0.09 P = 0.009**	-0.22 ± 0.12 P = 0.055	-0.29 ± 0.24 P = 0.218	-0.16 ± 0.20 P = 0.411
Interaction	-0.33 ± 0.12 P = 0.004**	-0.73 ± 0.16 P < 0.001***	0.60 ± 0.33 P = 0.077	0.19 ± 0.28 P = 0.499

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14 **Supplementary information S2 – Contest outcome in control interactions**

15 Results of the model selection procedure taking into account only the interactions between
 16 focal males and control opponents and excluding manipulated opponents. Table S2 provides
 17 the best models ($\Delta AICc < 2$) and the null model for each response variable obtained from our
 18 model selection procedure involving a total of 64 models. We also provide the AICc score,

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The role of social costs as a mechanism enforcing the honesty of ultraviolet signals in a lizard

19 the $\Delta AICc$, and the weight of each one of the best models. Table S3 summarises the
 20 conditional model averaging and indicates the estimates \pm the adjusted standard error and the
 21 p value of each predictor. When the predictor *Null* is indicated, it corresponds to the null
 22 model in which no predictors were added. These models were in the form $response \sim$
 23 $predictors + random\ intercept\ factors$. Random factors were always ID of the focal male and
 24 trial order.

26 Table S2. Best models for each response variable.

Response	Predictors	AICc	$\Delta AICc$	Weight
Aggression score	Bite Force	374.07	0.00	0.16
	Bite Force + UV _{chroma}	375.30	1.23	0.09
	Bite Force + Opponent UV _{intensity}	375.61	1.44	0.08
	Bite Force + UV _{intensity}	375.71	1.64	0.07
	<i>Null</i>	377.81	3.74	0.02
Submission score	Opponent UV _{intensity}	348.57	0.00	0.23
	Opponent UV _{intensity} + UV _{intensity}	350.36	1.78	0.09
	<i>Null</i>	354.55	5.98	0.01
Basking duration	Opponent UV _{chroma} + Bite Force	154.89	0.00	0.09
	Opponent UV _{chroma} + Bite Force + UV _{intensity}	155.62	0.73	0.06
	Bite Force	155.72	0.83	0.06
	Bite Force + Opponent Body Size	156.16	1.28	0.05
	Bite Force + UV _{intensity}	156.24	1.35	0.05
	Bite Force + Opponent Body Size + UV _{intensity}	156.77	1.89	0.04
	Opponent UV _{chroma}	156.85	1.96	0.03
<i>Null</i>	157.20	2.32	0.03	
Wall- scratching duration	UV _{intensity}	136.69	0.00	0.18
	Opponent Body Size + UV _{intensity}	138.05	1.36	0.09
	UV _{chroma} + UV _{intensity}	138.27	1.58	0.08
	<i>Null</i>	140.44	3.75	0.03

28 Table S3. Conditional model-averaged coefficient ($\beta \pm se$), p -value, and sum of weights (sw)
 29 for each predictor and response variable.

The role of social costs as a mechanism enforcing the honesty of ultraviolet signals in a lizard

Predictors	Aggression score	Submission score	Basking duration	Wall-scratching duration
UV _{chroma}	0.15 ± 0.12	-0.11 ± 0.23	0.12 ± 0.17	-0.21 ± 0.17
	P = 0.249	P = 0.626	P = 0.503	P = 0.218
	sw = 0.36	sw = 0.23	sw = 0.26	sw = 0.30
UV _{intensity}	0.08 ± 0.11	0.24 ± 0.23	-0.22 ± 0.17	0.47 ± 0.17
	P = 0.452	P = 0.297	P = 0.183	P = 0.006**
	sw = 0.27	sw = 0.29	sw = 0.43	sw = 0.87
Opponent UV _{chroma}	0.04 ± 0.14	-0.04 ± 0.15	-0.19 ± 0.14	0.08 ± 0.20
	P = 0.771	P = 0.818	P = 0.186	P = 0.682
	sw = 0.23	sw = 0.23	sw = 0.47	sw = 0.25
Opponent UV _{intensity}	0.13 ± 0.14	0.26 ± 0.12	-0.06 ± 0.14	0.05 ± 0.11
	P = 0.357	P = 0.038*	P = 0.652	P = 0.641
	sw = 0.30	sw = 0.94	sw = 0.23	sw = 0.22
Opponent size	0.11 ± 0.28	-0.24 ± 0.20	-0.19 ± 0.31	-0.34 ± 0.25
	P = 0.703	P = 0.239	P = 0.554	P = 0.167
	sw = 0.23	sw = 0.25	sw = 0.33	sw = 0.32
Bite Force	0.29 ± 0.11	-0.06 ± 0.24	0.31 ± 0.16	0.04 ± 0.17
	P = 0.010*	P = 0.812	P = 0.059	P = 0.838
	sw = 0.84	sw = 0.23	sw = 0.66	sw = 0.22

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