



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

Anna Kawamoto, Jean-François Le Galliard, Arnaud Badiane

► To cite this version:

Anna Kawamoto, Jean-François Le Galliard, Arnaud Badiane. The role of social costs as a mechanism enforcing the honesty of ultraviolet-reflecting signals in a lizard. *Biological Journal of the Linnean Society*, 2021, 133 (4), pp.1126-1138. 10.1093/biolinnean/blab008 . hal-03376443

HAL Id: hal-03376443

<https://cnrs.hal.science/hal-03376443>

Submitted on 13 Oct 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

Anna Kawamoto*¹, Jean-François Le Galliard^{1,2}, Arnaud Badiane*¹

¹ Sorbonne Université, CNRS, IRD, INRA, Institut d'écologie et des sciences de l'environnement (IEES), 4 Place Jussieu, 75005 Paris, France.

² Centre de recherche en écologie expérimentale et prédictive (CEREEP-Ecotron IleDeFrance), Département de biologie, Ecole Normale Supérieure, CNRS, PSL Research University, UMS 3194, 11 chemin de Busseau, 77140 Saint-Pierre-lès-Nemours, France

* Both authors contributed equally to this work

Corresponding author: Anna Kawamoto - annakaw423@gmail.com

Short title: Social costs of an ultraviolet signal

Abstract

According to animal signalling theory, social costs, for example induced by aggression from conspecifics, are one of the mechanisms maintaining signal honesty. While our understanding of signal evolution has much improved for pigment-based colours, the mechanisms maintaining the honesty of structural colour signals, such as ultraviolet (UV), remain elusive. Here, we used the common lizard *Zootoca vivipara* to test whether the honesty of UV signals displayed on male throats is under social control. To do so, we staged dyadic agonistic interactions between non-manipulated focal males and opponents of either larger or smaller body size. We used either control or manipulated UV signals to create small cheaters with UV-enhanced throats, large cheaters with UV-reduced throats, and their respective controls. In support of a conventional signal hypothesis, focal males were aggressive towards large cheaters and became submissive when these large cheaters retaliated, and were less submissive against small cheaters. However, that focal males were not more aggressive towards small cheaters contradicts our initial predictions. We then confirmed that male UV coloration and bite force were good predictors of contest outcomes in control conditions. Overall, we provide partial evidence suggesting that social costs enforce UV signal honesty in common lizards.

Key words: Animal communication – Deception – Male competition – Ultraviolet – *Zootoca vivipara*

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Introduction

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

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

1
2
3 67 mismatch between their opponent's quality and signalling level (Rohwer & Rohwer, 1978). In
4
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,
10
11 71 thus leading Bachmann *et al.* (2017) to call for adequately designed studies to reduce this
12
13 72 research bias.
14
15
16

17 73 Colour signals constitute a diverse class of signals and result from different colour-
18
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
30
31 80 colours, especially melanin-based black or white coloration (Møller, 1987; Martín &
32
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
36
37 83 (Ligon & McGraw, 2016), and of pigment-based colours potentially costly to produce (Martín
38
39 84 & Forsman, 1997).
40
41
42
43

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
47
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
51
52 89 evidence is still lacking (Fitzpatrick, 1998; Kemp & Rutowski, 2007; Kemp, Herberstein, &
53
54 90 Grether, 2012; Kemp & Grether, 2015; White, 2020). UV signals have also been suggested to
55
56 91 function as conventional signals especially in lizards, but hard proof is still needed to confirm
57
58
59
60

1
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
6
7 94 male agonistic contests. They found that males were less aggressive and more submissive
8
9 95 against cheaters than against honest males, thus rejecting a conventional signal hypothesis in
10
11 96 this species. In blue tits (*Cyanistes caeruleus*), three important studies suggested that the UV
12
13 97 coloration displayed on male crowns may function as conventional signals during male
14
15 98 contests (Alonso-Alvarez *et al.*, 2004; Poesel *et al.*, 2007; Rémy *et al.*, 2010). These,
16
17 99 however, are not conclusive since they were designed to explore the role of UV signals during
18
19 100 agonistic interactions rather than to test whether social costs enforced their honesty.
20
21
22
23

24 101 To identify social costs of colour signals, researchers must experimentally create out-of-
25
26 102 equilibrium colour signals to simulate cheating individuals and examine whether these
27
28 103 cheaters receive more aggression than honest signallers during agonistic interactions (Ligon &
29
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.*,
37
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;
47
48 113 Names *et al.*, 2019). Body size is thus a cue widely used by lizards to extract information on
49
50 114 male quality (we use the terms ‘signal’ and ‘cue’ as defined in Bradbury & Vehrencamp,
51
52 115 2011).
53
54
55
56
57
58
59
60

Here, we first determined whether or not male-induced social costs are associated with dishonest UV signals in this species, and then investigated the relative importance of male UV signals, bite force and body size during male agonistic contests. To do so, we designed dyadic agonistic encounters between non-manipulated focal males and opponents that were either smaller or larger than focal males, with either a control (i.e. honest) or a manipulated (i.e. cheaters) UV-reflecting throat. To disrupt the correlation between UV signal and quality, we used lizards of different body size. Our rationale was that precise quality traits advertised by UV signals are not completely known yet in this species, but body size is a well-known cue of male quality that correlates with UV signals in this and other lizards species (Bonnaïffé *et al.*, 2018). Specifically, small opponents were either UV-control or UV-enhanced so as to create cheaters of lower quality (i.e. small) with high signalling level. Large opponents were either UV-control or UV-reduced so as to create cheaters of higher quality (i.e. large) with a low signalling level. If the UV-reflecting throat functions as socially enforced conventional signals, we predict that cheaters will pay the cost of their dishonesty in the form of received aggression from focal males. We thus expected focal males to behave more aggressively and be less submissive against cheaters than against honest opponents.

Material and Methods

Study species

The common lizard (*Zootoca vivipara*) is a small lacertid inhabiting humid habitats across Eurasia (Massot *et al.*, 1992). In our study site, adult males usually emerge from hibernation in March. The emergence of females starts approximately 3-4 weeks later in the beginning of April, depending on weather conditions, and marks the beginning of the mating season (Massot *et al.*, 1992). During the mating season, males chase away other males to ensure access to females and there is endurance competition among males to find mates (Heulin, 1988). Adult common lizards occupy overlapping home-ranges and are polygynandrous, with

both sexes having multiple sexual partners (Laloi *et al.*, 2004; Fitze *et al.*, 2005). Adult males have a conspicuous belly ranging from yellow to red, interspersed with numerous black spots (Martin *et al.*, 2013; San-Jose *et al.*, 2017). In females, ventral coloration is duller, from cream to orange, with fewer black spots than males and extends more on the throat (Bauwens, 1987; Cote *et al.*, 2008). In addition, the ventral and throat coloration have a secondary reflectance peak in the UV, which is especially pronounced in males, particularly on their throat (Martin *et al.*, 2013).

Sampling and measurements

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

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

recorded reflectance spectra relative to a white diffuse standard (WS1; Ocean Optics Inc.) and a dark reading. We set integration time to 9, scans to average to 10, and boxcar width to 10. For data acquisition, we hand-held the probe over the centre of the targeted colour patch with a 90° angle between the probe and the skin surface (i.e. coincident normal recording geometry, Anderson & Prager, 2006). An entomological pin attached to the tip of the probe allowed us to maintain a constant distance of 3 mm between the tip of the probe and the skin surface. We always aimed the probe at a skin area larger than 1.5 mm in diameter that did not contain any black spot to avoid spectral contamination (Badiane *et al.*, 2017). We later processed spectral data in R v.3.3.2 (R Development Core Team, 2017) using the package *pavo* 2.0 (Maia *et al.*, 2019). We cropped each spectrum between 300–700 nm, smoothed them using a loess smooth span of 0.2, and averaged the two replicates recorded for each body region. Then, we extracted two UV-related colorimetric variables from the throat spectra, namely spectral intensity (i.e. $R_{300-700}$), and UV chroma (i.e. $R_{300-400}/R_{300-700}$).

Following measurement, we placed the lizards individually in opaque terraria (25x15.5x15 cm) layered with soil substrate, and equipped with a shelter (7,6 x 15,2 x 15,1 cm, ExoTerra) and a small water dish (Petri dish ~5 cm in diameter). An incandescent bulb (25 W) and white light UV-B neon tubes (Reptisun 10.0 UVB, Zoomed) provided heat and light following a 10/14-h dark-light schedule. We provided food three times a week (300–400 mg of live house crickets, *Acheta domesticus*) and water *ad libitum*. Lizards were housed for a total of 18 days, including 10 days of acclimation to the laboratory conditions during which we waited the lizards' first moult to occur as it marks the onset of sexual activity (Laloi *et al.*, 2011), and 8 days of experiment.

Colour manipulation and behavioural assays

Behavioural assays took place in a temperature-controlled room maintained at 21°C using two neutral arenas to eliminate any resident-intruder effect (Martin *et al.*, 2015, 2016). Arenas

1
2
3 191 were composed of a large opaque plastic terrarium (75x50x40 cm) with one transparent wall
4
5 192 to allow video recording, and contained a layer of blond peat as substrate. Two removable
6
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
10
11 195 served as solitary holding areas to allow acclimation to the neutral arena, and were each
12
13 196 equipped with a 25-W heat bulb placed 15 cm above a shelter (Exoterra Inc.) that also acted
14
15 197 as basking spot. In the central compartment, we placed another 30-W heat bulb 15 cm above a
16
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
26
27 203 distance to create visual isolation. Two digital SLR cameras (Nikon D500 and Nikon D5300)
28
29 204 mounted on tripods recorded the experiments in high definition from a lateral, slightly
30
31 205 elevated point of view, through the transparent wall of the arena.
32
33
34
35
36

37 206 To test the hypothesis that male-induced social costs are associated with dishonest UV
38
39 207 signals in common lizards, we staged dyadic encounters using 59 adult male common lizards
40
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
48
49 212 in SVL and were either UV-control or UV-enhanced. Large opponents (60-63 mm in SVL), in
50
51 213 contrast, were either UV-control or UV-reduced. This study design allowed us to create a
52
53 214 mismatch between UV signalling level and body size, and ultimately with male quality since
54
55 215 body size is a primary predictor of fighting ability and male contest outcome in lizards
56
57
58
59
60

(Carpenter, 1995; Karsten *et al.*, 2009; Baird, 2013; Names *et al.*, 2019). Focal males were always 3-6 mm larger ($\beta = 4.21 \text{ mm} \pm 0.41$, $p < 0.001$) and 1-5 mm smaller ($\beta = -2.84 \text{ mm} \pm 0.42$, $p < 0.001$) than their small and large opponents, respectively. There were no significant differences in body size and body mass between small controls and small cheaters (SVL: $\beta = -0.38 \text{ mm} \pm 0.66$, $p = 0.978$; body mass: $\beta = -0.21 \text{ mm} \pm 0.21$, $p = 0.846$), nor between large controls and large cheaters (SVL: $\beta = 0.30 \pm 0.68$, $p = 0.991$; body mass: $\beta = 0.37 \pm 0.22$, $p = 0.465$).

To reduce the UV reflectance within the natural range of variation, we used UV-blocking (290-400 nm) inorganic agents (zinc oxide and titanium dioxide) mixed with a fat combination of petroleum jelly and liquid paraffin (respectively, 6:4:50:40 for 100 g). Large males of the control group were treated with the fat combination and large males of the UV-reduced treatment were treated with the fat combination mixed with the inorganic agents (Figure 1). The spectral curve of this UV-reduction corresponded well with the spectra obtained in previous studies (Martin *et al.*, 2016; Badiane *et al.*, 2020). We applied both mixtures using a thin paintbrush on the lizards' throat, from the tip of the jaw to the collar scale row. To enhance throat UV reflectance, we used a light orange Edding 4500 T-shirt marker pen (colour code 016) that reflects in the UV range. This marker is similar to those previously used to enhance UV-blue coloration in birds and lizards (Kurvers *et al.*, 2010; Rémy *et al.*, 2010; Names *et al.*, 2019), except that we used light orange instead of light blue in our study because it better matches the natural throat colour of male common lizards. To facilitate the marker application on the lizards' throat, we dismantled the marker and pressed the ink reservoir so as to deposit a drop of water-based ink on a plate, then we dipped the tip of a forceps into the droplet and spread it on the lizards' throat from the tip of the jaw to the collar scale row. We then let it dry for a few minutes before starting the experiments. Small lizards from the UV-enhanced group were treated with this marker pen while small lizards

from the UV-control group were not treated at all (Figure 1). As Figure 1 illustrates, our UV-enhancing treatment augmented throat reflectance in UV but also in the orange part of the spectrum, and spectral shape looked somewhat artificial. This marker pen, however, produced the best spectral shape of all the different marker pens and paintings we have tried.

Each focal male participated in four dyadic encounters against four different males from the four treatments (i.e. small cheaters, small controls, large cheaters, and large controls) presented in a random sequence. We chose the opponent so as to standardize the size difference between focal and opponent males, such that the largest focal males encountered the largest opponents from both the small and large size categories, and the smallest focal males faced the smallest opponents of both size categories. We designed the experiment such that focal males participated to encounters only once every two days, and opponents not more than once a day. We performed a total of 116 trials during 8 days with a maximum of 16 trials per day (8 trials per arena per day) during the activity period of the lizards from 09:00 to 17:00. Most males from the paired interactions had no prior knowledge of each other because they were hosted in separate enclosures during all their lives, except for 14 tests (12%) for which both males came from the same 100-m² enclosure. However, in 12 out of these 14 encounters, both males were entering their first reproductive season (almost 2 years old) and had therefore not competed in the past. The two remaining contests both involved a sexually mature male (almost 3 years old) against a newly sexually mature male (almost 2 years old), and had therefore never competed against each other. In the light of this, it is unlikely that prior knowledge due to sexual competition among the males impacted our results.

Before each experiment, we removed the participating males from their home terrarium, manipulated their throat coloration, and randomly placed each male in one of the two compartments of the neutral arena. We allowed a first 10-min acclimation period with the shelters and basking spot in both compartments. After 10 min, we removed the shelters from

the compartments and allowed another 10-min acclimation period without shelters to force them to be active, leaving the heat bulb turned on for thermoregulation. After this 20-min acclimation period with and without shelters (and without observers), the experiment started as we removed the opaque walls to reveal the central area and immediately turned the heat bulbs from the two compartments off, such that the only basking spot left is the wooden plate at the centre of the arena. We turned the video camera on and left the room to prevent any observer-induced disturbance. The experiment lasted 20 min as the two males behaved and competed for the basking spot. Next, a single observer, blind to the experimental treatments, used Jwatcher (Blumstein & Daniel, 2007) to analyse the lizards' behaviours from all the video recordings to avoid any observer effect.

We recorded each time a lizard performed any of the behaviours described in Table 1 (Martin *et al.*, 2016; Names *et al.*, 2019). We assigned a coefficient to each of these behaviours to give more weight to the most aggressive behaviours, since they are more likely to be costly for the opponent (Carazo, Font, & Desfilis, 2008; Abalos *et al.*, 2016). Although an obvious hierarchy exists between behaviours with regard to contest escalation, there still is some degree to which coefficient assignment can be subjective and arbitrary. Hence, in addition to the first set of coefficients we consider as most relevant, we assigned two more sets of coefficients to examine how coefficient assignment may influence our results. We thus calculated three versions of the aggression score and three versions of the submission score as indicated in Table 1. In addition, we recorded basking duration, that is the time spent basking on the wooden plate, because males competed over a unique basking spot. We also recorded the duration of wall-scratching behaviour for each male. This behaviour consists of males scratching the walls of the arena to try to escape and may be due to stress as a consequence of laboratory conditions (de Fraipont 2000, Rozen-Rechels 2018). It may also be triggered by a

1
2
3 290 male fleeing from another male. None of the contests resulted in observable injuries and all
4
5 291 males were released to their semi-natural outdoor enclosures after the 8 days of experiment.
6
7 292 *Statistical analyses*
8
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*
15
16
17 296 First, to test whether or not social costs are imposed on dishonest male UV signals, we
18
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
22
23 299 males corresponded to UV-control males while cheaters corresponded to manipulated males
24
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
28
29 302 for focal males: the three versions of aggression score, the three versions of submission score,
30
31 303 basking duration, and duration of wall-scratching behaviour. We included male ID and trial
32
33 304 order as random intercepts in these models. We considered trial order as random because we
34
35 305 were not interested in the effects of trial order *per se*; however, we also ran these models with
36
37 306 trial order as fixed factor and present the results from post-hoc Tukey tests when significant.
38
39 307 We included the additive effects of opponent size and opponent honesty as well as their two-
40
41 308 way interactions, and the additive effect of bite force as fixed effects. When the interaction
42
43 309 was significant, we split our data set according to the “opponent size” category to explore the
44
45 310 interaction. To reduce the impact of influential values (detected with Cook’s distances) and
46
47 311 improve our models, we performed an alpha-winsorisation with a 0.03 trim on the submission
48
49 312 score and wall-scratching behaviour. For all the models described above, we checked the
50
51 313 model assumptions using the *performance* R package (Lüdtke *et al.*, 2020). We used a
52
53 314 squared-root transformation for wall-scratching behaviour to comply with these assumptions.
54
55
56
57
58
59
60

All continuous variables assuming a Gaussian distribution were centred and scaled prior to analyses to ease result interpretations (Schielzeth, 2010).

Determinants of male contests

Next, to explore the role of body size, bite force, and throat UV reflectance during male agonistic contests, we analysed only interactions between focal males and control opponents from both size categories, thus excluding the cheaters. We used linear mixed-effects models (LMMs) and generalized linear mixed-effects models (GLMMs) to test the additive effects of bite force, UV chroma, spectral intensity, opponent body size, opponent UV chroma, and opponent spectral intensity on the three versions of aggression score, the three versions of submission score, basking duration, and duration of wall-scratching behaviour. We included the same random intercepts as above. We used the *lme4* R package (Bates *et al.*, 2015) to perform GLMMs on count variables assuming a negative binomial distribution for the aggression score and a Poisson distribution for the submission score. For the remaining response variables (i.e. basking duration, and wall-scratching duration), we assumed a Gaussian distribution and used LMMs as implemented in the *nlme* R package (Pinheiro *et al.*, 2019). To reduce the impact of influential values (detected with Cook's distances) and improve our models, we performed an alpha-winsorisation with a 0.03 trim on the submission score and wall-scratching behaviour. We proceeded with a model selection and conditional averaging procedure as implemented in the *MuMin* R package (Bartoń, 2019), using the functions *dredge* and *model.avg*. This model selection procedure allowed us to select the best models ($\Delta AICc < 2$) from all possible combinations of predictors, including a null model without any predictor.

Results

Social costs on dishonest UV signals

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

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

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

362 *Determinants of male contests in control interactions*

In control interactions, males with a higher aggression score (calculated with the first set of coefficients) had a significantly higher bite force ($\beta = 0.29 \pm 0.11$, $p = 0.010$). This result was corroborated when we used both alternative aggression scores. In addition, focal males were more submissive (submission score calculated with the first set of coefficients) against opponents with a high throat spectral intensity ($\beta = 0.28 \pm 0.12$, $p = 0.023$). When we used the two alternative versions of the aggression score, however, none of the predictors were significant. We also found that males with a higher bite force tended to spend more time on the basking spot than males with lower bite force ($\beta = 0.31 \pm 0.16$, $p = 0.059$). Focal males spending more time performing wall-scratching behaviours had higher throat spectral intensity ($\beta = 0.47 \pm 0.17$, $p = 0.006$). Statistics are fully reported in Supp. Info. S2. When we included trial order as fixed instead of random factor, all the above results were qualitatively similar, and we found that the submission score was lower during the third trial than during 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 trial ($\beta = -1.19 \pm 0.27$, $p < 0.001$).

Discussion

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

Social costs on dishonest UV signals

1
2
3 388 We provide partial evidence that the UV components of the UV-reflecting throat of common
4
5 389 lizards may function as conventional signals enforced by male-induced social costs. The story
6
7 390 becomes more complex than expected when we examine the aggression and submission
8
9 391 scores. On one hand, large males with UV-reduced throats received more aggressions but also
10
11 392 triggered more submissive behaviours in focal males. This result suggests that, for large
12
13 393 males, downplaying UV signals is costlier than being honest since these large UV-reduced
14
15 394 cheaters are more likely to be challenged by the smaller focal males. When the focal males
16
17 395 challenge the large cheaters, the latter may retaliate since, after all, they are larger and more
18
19 396 likely to win fights, and focal males end up being more submissive. Hence, under this
20
21 397 scenario, what seemed to be a contradictory result at first glance may in fact be coherent and
22
23 398 support the idea that UV signals function as conventional signals in this species. Although
24
25 399 large males pose a serious threat to smaller males, if a large male signals low condition, it
26
27 400 may pay-off for smaller males to challenge this large male and gain a fitness advantage (e.g.
28
29 401 access to resources and/or females). Unexpectedly, small UV-enhanced cheaters did not
30
31 402 receive more aggression from the focal males compared to their honest counterparts.
32
33 403 However, that focal males behaved less submissively against small cheaters aligns with the
34
35 404 predictions of a conventional signal hypothesis.
36
37
38
39
40
41

42 405 In the case of conventional signals, social costs are either imposed to individuals that
43
44 406 signal above a given threshold intensity or penalize the mismatch between the sender's quality
45
46 407 or behaviour and its signalling level. Signal honesty can therefore be maintained only if these
47
48 408 costs exceed the benefits of cheating (Searcy & Nowicki, 2005; Bradbury & Vehrencamp,
49
50 409 2011). However, some degree of deception may still arise and pay off as long as the signal
51
52 410 remains honest to some degree (Adams & Mesterton-Gibbons, 1995; Carazo & Font, 2014).
53
54 411 Individuals can either be exclusively honest or exclusively dishonest, or switch from one
55
56 412 strategy to another according to the situation they find themselves into, depending on whether
57
58
59
60

the signal is very labile and can change rapidly or not (Akçay, Campbell, & Beecher, 2013; Wilson & Angilletta, 2015; Ligon & McGraw, 2016). In common lizards, the UV-reflecting coloration on males' throat does not seem to change rapidly (Bonnaffé *et al.*, 2018), thus leaving little room for "occasional" cheating. Retaliation or punishment rules taking the form of physical and non-physical aggressions are the main mechanisms maintaining the honesty of conventional signals (Martin & Forsman, 1997; Tibbetts & Izzo, 2010; Tibbetts, 2014; Wilson & Angilletta, 2015; Ligon & McGraw, 2016). In this regard, the different behaviours measured in our study do not have the same weight as evidence of socially imposed costs. Our aggression score is the most meaningful factor here because it is the most likely to inflict a cost (e.g. injury) on the opponent. Overall, social costs taking the form of physical aggression may be quite high in common lizards, as 43% of our staged encounters (50 out of 116) escalated to the point of a male biting another male at least once. Although we cannot estimate the cost-benefit balance of cheating in our study, the risk of injury due to physical aggression is high and should not be neglected in this species (Le Galliard *et al.*, 2005). On top of this, other behavioural processes, for instance in the form of non-physical aggression and/or spatial dominance, not necessarily measured, may increase the impact of social costs. Our submission score may therefore capture the reaction to such behaviours and give us hints on whether or not social costs exist. Altogether, our results seem to indicate that cheating is generally more costly than being honest, although it is not always clear-cut.

In fact, the inconsistencies in our results involved almost exclusively interactions between focal males and small opponents, as small UV-enhanced cheaters did not receive more aggression from focal males. A possible interpretation may simply be that cheating is more likely to pay off for a small male that exaggerates its UV signal than for a large male that downplays its signal. However, in the context of male-male competition, we would expect social costs to prevent low-quality males from signalling high quality, and gain

438 advantage in terms of resources and/or access to females over males that are actually of higher
439 quality (e.g. Molles & Vehrencamp, 2001). Another hypothesis may be that smaller males
440 generally behave in a non-threatening way when they face larger males, for example by
441 avoiding being close to larger opponent. Therefore, focal males would not need to show any
442 sign of aggression and spatial occupancy, perhaps captured in our submission score, may be
443 enough to affirm dominance. Alternatively, if focal males are more aggressive towards any
444 opponent that signals above a given threshold intensity, and that small honest males are
445 already signalling close to or above that threshold, we would not see any difference in terms
446 of aggression score between small UV-enhanced cheaters and their honest counterparts.

447 However, in this context, we would not expect to find differences in the submission
448 score as we did here. This also raises the possibility that our results were obscured by our UV
449 manipulation protocol. While the experimental reduction of the UV reflectance within the
450 natural range of variation has been previously validated in the common lizard (Martin *et al.*,
451 2016; Badiane *et al.*, 2020) and other lizard species (Martin *et al.*, 2015; Names *et al.*, 2019),
452 it is much more difficult to enhance UV reflectance. To the best of our knowledge, only a
453 handful of studies have experimentally augmented the UV coloration of animals, mostly in
454 the blue tit *Cyanistes caeruleus* (Poesel *et al.*, 2007; Rémy *et al.*, 2010) and one study in the
455 common wall lizard *Podarcis muralis* (Names *et al.*, 2019). In these and our study, whether or
456 not these UV-enhanced patches can be considered to be within the natural range of variation
457 remains debatable, since spectral shape can look artificial. In addition, our marker pen did not
458 only increase reflectance in the UV range but also in the orange part of the spectrum (idem, to
459 a lesser extent, with the UV reduction treatment) and this may set a limit to results'
460 interpretations since we do not know how this may have influenced the outcome of our
461 behavioural experiments. It is therefore possible that the focal males did not consider the UV-
462 enhanced throat of small cheaters as a high signalling level, but simply as an 'odd' signal. For

example, the increased orange coloration on the throat may somewhat resemble female's throats (Martin *et al.*, 2013) and thus confuse the receivers. In addition, we cannot exclude that the artificial light orange colour faded to some extent during the experiment, although not completely (pers. obs.). Future studies should investigate adequate methods to enhance "naturally" UV coloration so that research on UV signalling may take a step forward.

Determinants of male contests

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

Conclusion

Overall, our study highlights that UV coloration of male throat plays a role during male contests, both from the point of view of the signaller, as it correlates with the signaller's

1
2
3 488 behaviour, and from the perspective of the receiver since receivers adjust their behaviour
4
5 489 based on these signals. Therefore, our study confirms the importance of UV coloration as
6
7 490 predictors of male contest outcomes in the common lizard (Martin *et al.*, 2016). However, we
8
9 491 can only provide partial evidence that social costs maintain the honesty of UV-reflecting
10
11 492 signals. This is because we observed different patterns of physical and non-physical
12
13 493 aggression in the face of deception in situations where focal males faced small opponents than
14
15 494 with large opponents. Although not entirely conclusive, this suggests that UV signals can be
16
17 495 honest thanks to context-dependent social costs imposed by rival males during male-male
18
19 496 competition. Future work should keep investigating these avenues of signal honesty with UV
20
21 497 signals to improve our understanding of animal communication at large.
22
23
24
25

26 498 **Research data**

27
28 499 All data used in this study will be made freely available on the public repository Zenodo.
29
30

31 500 **Acknowledgements**

32
33 501 We are thankful to Bruno Malhao for helping us build the two experimental arenas and Simon
34
35 502 Chollet for lending the plasma lamps. This study is part of the project UVSIGNAL funded by
36
37 503 a Marie Sklodowska-Curie fellowship (European program Horizon 2020) attributed to Arnaud
38
39 504 Badiane. This work has benefited from technical and human resources provided by CEREEP-
40
41 505 Ecotron IleDeFrance (CNRS/ENS UMS 3194) as well as financial support from the Regional
42
43 506 Council of Ile-de-France under the DIM Program R2DS bearing the reference I-05-098/R. It
44
45 507 has received a support under the program" Investissements d'Avenir" launched by the French
46
47 508 government and implemented by ANR with the reference ANR-11-INBS-0001 AnaEE France
48
49 509 and ANR-10-IDEX-0001-02 PSL. The capture, handling, and experimentation on the animals
50
51 510 in this study was authorized by the Ministère de l'Enseignement Supérieur, de la Recherche et
52
53 511 de l'Innovation (ref. APAFIS#19642-2019030616456029v4), and by the Direction
54
55 512 départementale de la protection des populations (ref. 2017-01666).
56
57
58
59
60

References

- Abalos J, Pérez i de Lanuza G, Carazo P & Font E. 2016. The role of male coloration in the outcome of staged contests in the European common wall lizard (*Podarcis muralis*). *Behaviour* **153**: 607–631.
- Adams ES & Mesterton-Gibbons M. 1995. The cost of threat displays and the stability of deceptive communication. *Journal of Theoretical Biology* **175**: 405–421.
- Akçay Ç, Campbell SE & Beecher MD. 2013. Individual differences affect honest signalling in a songbird. *Proceedings of the Royal Society B: Biological Sciences* **281**.
- Alonso-Alvarez C, Bertrand S, Devevey G, Gaillard M, Prost J, Faivre B & Sorci G. 2004. An experimental test of the dose-dependent effect of carotenoids and immune activation on sexual signals and antioxidant activity. *American Naturalist* **164**: 651–659.
- Anderson S & Prager M. 2006. Quantifying colors. In: Hill GE, McGraw KJ, eds. *Bird coloration: Volume 1, mechanisms and measurements.*, 41–89.
- Bachmann JC, Cortesi F, Hall MD, Marshall NJ, Salzburger W & Gante HF. 2017. Real-time social selection maintains honesty of a dynamic visual signal in cooperative fish. *Evolution Letters* **1**: 269–278.
- Badiane A, Pérez i de Lanuza G, García-Custodio M del C, Carazo P & Font E. 2017. Colour patch size and measurement error using reflectance spectrophotometry. *Methods in Ecology and Evolution* **8**: 1585–1593.
- Badiane A, Martin M, Meylan S, Richard M, Decencièrre Ferrandière B & Le Galliard JF. 2020. Male ultraviolet reflectance and female mating history influence female mate choice and male mating success in a polyandrous lizard. *Biological Journal of the Linnean Society* **130**: 586–598.
- Baird TA. 2013. Lizards and other reptiles as model systems for the study of contest behaviour. In: Hardy IC, Briffa M, eds. *Animal Contests.*, 258–286.

- 538 **Bartoń K. 2019.** ‘MuMin’: Multi-model inference.
- 539 **Bates D, Maechler M, Bolker B & Walker S. 2015.** Fitting linear mixed-effects models
540 using lme4. *Journal of statistical software* **67**: 1–48.
- 541 **Bauwens D. 1987.** Sex recognition by males of the lizard *Lacerta vivipara*: an introductory
542 study. *Amphibia-Reptilia* **8**: 49–57.
- 543 **Beani L & Turillazzi S. 1999.** Stripes display in hover-wasps (Vespidae: Stenogastrinae): A
544 socially costly status badge. *Animal Behaviour* **57**: 1233–1239.
- 545 **Blumstein DT & Daniel JC. 2007.** Quantifying behavior the Jwatcher way.
- 546 **Bonnaffé W, Martin M, Mugabo M, Meylan S & Le Galliard J. 2018.** Ontogenetic
547 trajectories of body coloration reveal its function as a multicomponent nonsenescent signal.
548 *Ecology and Evolution* **8**: ece3.4369.
- 549 **Bradbury JW & Vehrencamp SL. 2011.** *Principles of animal communication*. Sinauer
550 Association Press Sunderland.
- 551 **Carazo P & Font E. 2014.** ‘Communication breakdown’: The evolution of signal
552 unreliability and deception. *Animal Behaviour* **87**: 17–22.
- 553 **Carazo P, Font E & Desfilis E. 2008.** Beyond ‘nasty neighbours’ and ‘dear enemies’?
554 Individual recognition by scent marks in a lizard (*Podarcis hispanica*). *Animal Behaviour* **76**:
555 1953–1963.
- 556 **Carpenter GC. 1995.** Modeling Dominance : the Influence of size, coloration, and
557 experience on dominance relations in tree lizards (*Urosaurus ornatus*). *Herpetological*
558 *Monographs* **9**: 88–101.
- 559 **Cote J, Le Galliard JF, Rossi JM & Fitze PS. 2008.** Environmentally induced changes in
560 carotenoid-based coloration of female lizards: a comment on Vercken et al. *Journal of*
561 *Evolutionary Biology* **21**: 1165–1172.
- 562 **Fitze PS, Le Galliard JF, Federici P, Richard M & Clobert J. 2005.** Conflict over

- multiple-partner mating between males and females of the polygynandrous common lizards.
Evolution **59**: 2451–2459.
- Fitze PS & Le Galliard JF. 2008.** Operational sex ratio, sexual conflict and the intensity of sexual selection. *Ecology Letters* **11**: 432–439.
- Fitzpatrick S. 1998.** Colour schemes for birds: Structural coloration and signals of quality in feathers. *Annales Zoologici Fennici* **35**: 67–77.
- de Fraipont M, Colbert J, John-Alder H & Meylan S. 2000.** Increased pre-natal maternal corticosterone promotes in common of offspring philopatry lizards *Lacerta vivipara*. *Journal of Animal Ecology* **69**: 404–413.
- Le Galliard JF, Fitze PS, Ferrière R & Clobert J. 2005.** Sex ratio bias, male aggression, and population collapse in lizards. *Proceedings of the National Academy of Sciences* **102**: 18231–18236.
- Grafen A. 1990.** Biological signals as handicaps. *Journal of Theoretical Biology* **144**: 517–546.
- Guilford T & Dawkins MS. 1995.** What are conventional signals? *Animal Behaviour* **49**: 1689–1695.
- Heulin B. 1988.** Observations sur l'organisation de la reproduction et sur les comportements sexuels et agonistiques chez *Lacerta vivipara*. *Vie et milieu* **38**: 177–187.
- Higham JP. 2014.** How does honest costly signaling work? *Behavioral Ecology* **25**: 8–11.
- Hurd PL. 1997.** Is signalling of fighting ability costlier for weaker individuals? *Journal of Theoretical Biology* **184**: 83–88.
- Hurd PL & Enquist M. 2005.** A strategic taxonomy of biological communication. *Animal Behaviour* **70**: 1155–1170.
- Husak JF, Lappin KA, Fox SF & Lemos-Espinal JA. 2006.** Bite-Force Performance Predicts Dominance in Male Venerable Collared Lizards (*Crotaphytus antiquus*). *Copeia*

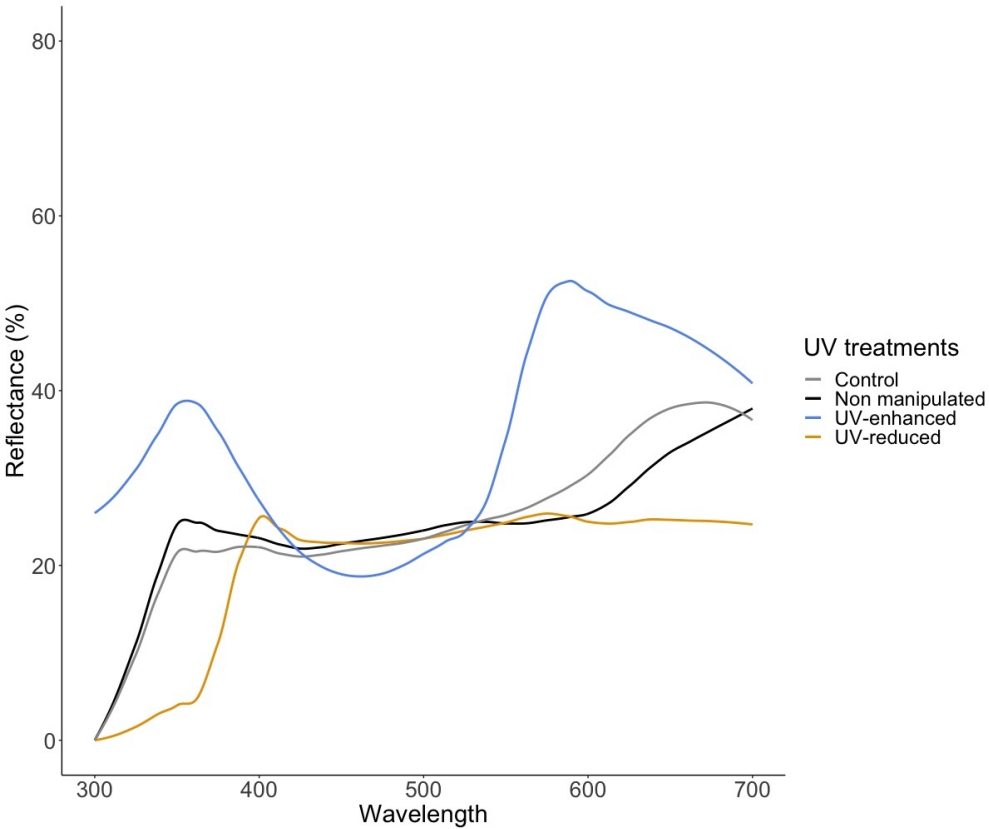
- 588 **2006**: 301–306.
- 589 **Huyghe K, Vanhooydonck B, Scheers H, Molina-Borja M & Van Damme R. 2005.**
- 590 Morphology, performance and fighting capacity in male lizards, *Gallotia galloti*. *Functional*
- 591 *Ecology* **19**: 800–807.
- 592 **Johnstone RA & Norris K. 1993.** Badges of status and the cost of aggression. *Behavioral*
- 593 *Ecology and Sociobiology* **32**: 127:134.
- 594 **Karsten KB, Andriamandimbiarisoa LN, Fox SF & Raxworthy CJ. 2009.** Sexual
- 595 selection on body size and secondary sexual characters in 2 closely related, sympatric
- 596 chameleons in Madagascar. *Behavioral Ecology* **20**: 1079–1088.
- 597 **Kemp DJ & Grether GF. 2015.** Integrating functional and evolutionary approaches to the
- 598 study of color-based animal signals. In: *Animal Signaling and Function: An Integrative*
- 599 *Approach.*, 111–140.
- 600 **Kemp DJ, Herberstein ME & Grether GF. 2012.** Unraveling the true complexity of costly
- 601 color signaling. *Behavioral Ecology* **23**: 233–236.
- 602 **Kemp DJ & Rutowski RL. 2007.** Condition dependence, quantitative genetics, and the
- 603 potential signal content of iridescent ultraviolet butterfly coloration. *Evolution* **61**: 168–183.
- 604 **Kurvers RHJM, Delhey K, Roberts ML & Peters A. 2010.** No consistent female
- 605 preference for higher crown UV reflectance in Blue Tits *Cyanistes caeruleus*: A mate choice
- 606 experiment. *Ibis* **152**: 393–396.
- 607 **Laloi D, Richard M, Lecomte J, Massot M & Clobert J. 2004.** Multiple paternity in
- 608 clutches of common lizard *Lacerta vivipara*: Data from microsatellite markers. *Molecular*
- 609 *Ecology* **13**: 719–723.
- 610 **Laloi D, Eizaguirre C, Fédérici P & Massot M. 2011.** Female choice for heterozygous
- 611 mates changes along successive matings in a lizard. *Behavioural Processes* **88**: 149–154.
- 612 **Lappin AK & Husak JF. 2005.** Weapon performance, not size, determines mating success

- and potential reproductive output in the collared lizard (*Crotaphytus collaris*). *American Naturalist* **166**: 426–436.
- Lappin AK & Jones MEH. 2014.** Reliable quantification of bite-force performance requires use of appropriate biting substrate and standardization of bite out-lever. *The Journal of Experimental Biology* **217**: 4303–4312.
- Ligon RA & McGraw KJ. 2016.** Social costs enforce honesty of a dynamic signal of motivation. *Proceedings of the Royal Society B: Biological Sciences* **283**.
- Lüdecke D, Makowski D, Waggoner P & Patil I. 2020.** Performance: Assessment of regression models performance, CRAN, R package.
- Maia R, Gruson H, Endler JA & White TE. 2019.** pavo 2: new tools for the spectral and spatial analysis of colour in R. *Methods in Ecology and Evolution* **10**: 1097–1107.
- Martin M, Meylan S, Gomez D & Le Galliard JF. 2013.** Ultraviolet and carotenoid-based coloration in the viviparous lizard *Zootoca vivipara* (Squamata: Lacertidae) in relation to age, sex, and morphology. *Biological Journal of the Linnean Society* **110**: 128–141.
- Martin M, Meylan S, Perret S & Le Galliard JF. 2015.** UV coloration influences spatial dominance but not agonistic behaviors in male wall lizards. *Behavioral Ecology and Sociobiology* **69**: 1483–1491.
- Martin M, Meylan S, Haussy C, Decenci re B, Perret S & Le Galliard JF. 2016.** UV color determines the issue of conflicts but does not covary with individual quality in a lizard. *Behavioral Ecology* **27**: 262–270.
- Mart n J & Forsman A. 1997.** Social costs and development of nuptial coloration in male *Psammodromus algirus* lizards : an experiment. *Behavioral Ecology* **10**: 396–400.
- Massot M, Clobert J, Pilorge T, Lecomte J & Barbault R. 1992.** Density dependence in the common lizard: demographic consequences of a density manipulation. *Ecology* **73**: 1742–1756.

- 638 **Maynard Smith J & Harper D. 2003.** *Animal signals*. New York: Oxford University Press.
- 639 **Møller AP. 1987.** Variation in badge size in male house sparrows *Passer domesticus*:
 640 evidence for status signalling. *Animal Behaviour* **35**: 1637–1644.
- 641 **Molles LE & Vehrencamp SL. 2001.** Songbird cheaters pay a retaliation cost: Evidence for
 642 auditory conventional signals. *Proceedings of the Royal Society B: Biological Sciences* **268**:
 643 2013–2019.
- 644 **Names G, Martin M, Badiane A & Le Galliard JF. 2019.** The relative importance of body
 645 size and UV coloration in influencing male-male competition in a lacertid lizard. *Behavioral*
 646 *Ecology and Sociobiology* **73**: 98.
- 647 **Pinheiro J, Bates D, DebRoy S, Sarkar D & RCoreTeam. 2019.** nlme: Linear and
 648 nonlinear mixed effects models.
- 649 **Poesel A, Peters A, Dabelsteen T, Darden SK & Delhey K. 2007.** Territorial responses of
 650 male blue tits, *Cyanistes caeruleus*, to UV-manipulated neighbours. *Journal of Ornithology*
 651 **148**: 179–187.
- 652 **Qvarnstrom A. 1997.** Experimentally increased badge size increases male competition and
 653 reduces male parental care in the collared flycatcher. *Proceedings of the Royal Society B:*
 654 *Biological Sciences* **264**: 1225–1231.
- 655 **R Development Core Team. 2017.** R: A language and environment for statistical computing.
- 656 **Rémy A, Grégoire A, Perret P & Doutrelant C. 2010.** Mediating male-male interactions:
 657 The role of the UV blue crest coloration in blue tits. *Behavioral Ecology and Sociobiology* **64**:
 658 1839–1847.
- 659 **Rohwer S & Rohwer FC. 1978.** Status signalling in Harris Sparrows. *Animal Behaviour* **26**:
 660 1012–1022.
- 661 **Roulin A. 2016.** Condition-dependence, pleiotropy and the handicap principle of sexual
 662 selection in melanin-based colouration. *Biological Reviews* **91**: 328–348.

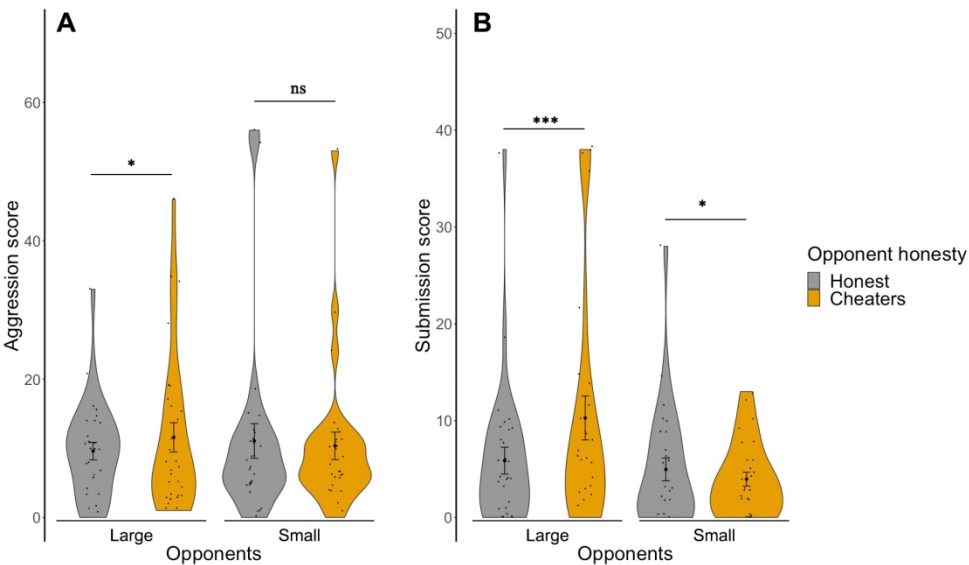
- 663 **Rozen-Rechels D, Badiane A, Agostini S, Meylan S & Le Galliard J. 2020.** Water
664 restriction induces behavioral fight but impairs thermoregulation in a dry-skinned ectotherm.
665 *Oikos* **129**: 572–584.
- 666 **Rozen-Rechels D, Dupoué A, Meylan S, Decencière B, Guingand S & Le Galliard JF.**
667 **2018.** Water restriction in viviparous lizards causes transgenerational effects on behavioral
668 anxiety and immediate effects on exploration behavior. *Behavioral Ecology and Sociobiology*
669 **72**.
- 670 **San-Jose LM, Huyghe K, Schuerch J & Fitze PS. 2017.** More melanized males bite
671 stronger but run slower: potential performance trade-offs related to melanin-based coloration.
672 *Biological Journal of the Linnean Society* **122**: 184–196.
- 673 **San-Jose LM & Roulin A. 2018.** Toward understanding the repeated occurrence of
674 associations between melanin-based coloration and multiple phenotypes. *The American*
675 *Naturalist* **192**: 111–130.
- 676 **Schielzeth H. 2010.** Simple means to improve the interpretability of regression coefficients.
677 *Methods in Ecology and Evolution* **1**: 103–113.
- 678 **Searcy W & Nowicki S. 2005.** *The evolution of animal communication: reliability and*
679 *deception in signaling systems*.
- 680 **Shawkey MD & D’Alba L. 2017.** Interactions between colour-producing mechanisms and
681 their effects on the integumentary colour palette. *Philosophical Transactions of the Royal*
682 *Society B: Biological Sciences* **372**: 20160536.
- 683 **Stapley J & Whiting MJ. 2006.** Ultraviolet signals fighting ability in a lizard. *Biology*
684 *Letters* **2**: 169–172.
- 685 **Svensson PA & Wong BBM. 2011.** Carotenoid-based signals in behavioural ecology: A
686 review. *Behaviour* **148**: 131–189.
- 687 **Tibbetts EA. 2014.** The evolution of honest communication: Integrating social and

- 688 physiological costs of ornamentation. *Integrative and Comparative Biology* **54**: 578–590.
- 689 **Tibbetts EA & Izzo A. 2010.** Social punishment of dishonest signalers caused by mismatch
690 between signal and behavior. *Current Biology* **20**: 1637–1640.
- 691 **Vehrencamp SL. 2001.** Is song-type matching a conventional signal of aggressive intentions?
692 *Proceedings of the Royal Society B: Biological Sciences* **268**: 1637–1642.
- 693 **Weaver RJ, Koch RE & Hill GE. 2017.** What maintains signal honesty in animal colour
694 displays used in mate choice? *Philosophical Transactions of the Royal Society of London B:*
695 *Biological Sciences* **372**: 20160343.
- 696 **Webster MS, Ligon RA & Leighton GM. 2018.** Social costs are an underappreciated force
697 for honest signalling in animal aggregations. *Animal Behaviour* **143**: 167–176.
- 698 **White TE. 2020.** Structural colours reflect individual quality : a meta-analysis. *Biology*
699 *Letters* **16**: 20200001.
- 700 **Whiting MJ, Nagy K a & Bateman PW. 2003.** Evolution and maintenance of social status-
701 signaling badges. In: *Lizard social behavior.*, 47—82.
- 702 **Wilson RS & Angilletta MJ. 2015.** Dishonest signaling during aggressive interactions:
703 Theory and Empirical Evidence. In: *Animal Signaling and Function: An Integrative*
704 *Approach.*, 205–227.
- 705 **Zahavi A. 1975.** Mate selection - A selection for a handicap. *Journal of Theoretical Biology*
706 **53**: 205–214.



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 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
	Burly	Number of times a lizard burly 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

Supplementary information S1 - Social costs on dishonest UV signals

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

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

Supplementary information S2 – Contest outcome in control interactions

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

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

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

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

Table S3. Conditional model-averaged coefficient ($\beta \pm se$), p -value, and sum of weights (sw) 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