

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

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19 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*

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 & Enguist, 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

mismatch between their opponent's quality and signalling level (Rohwer & Rohwer, 1978). In
both cases, cheating becomes particularly costly for low-quality individuals because of the
increased risk of injury due to physical attacks (Tibbetts, 2014). In spite of this, most studies
investigating honest signalling focused on physiological costs and very few on social costs,
thus leading Bachmann *et al.* (2017) to call for adequately designed studies to reduce this
research bias.

Colour signals constitute a diverse class of signals and result from different colour-producing mechanisms including pigmentary and structural components (Shawkey & D'Alba, 2017). Recent evidence has much improved our understanding of the signalling role and evolution of pigment-based colours such as melanin- and carotenoid-based colours (Svensson & Wong, 2011; Roulin, 2016; Weaver et al., 2017; San-Jose & Roulin, 2018). In fact, most conventional signals described so far are colour signals (but see Molles & Vehrencamp, 2001; Vehrencamp, 2001) displayed during male-male competition that involve pigment-based colours, especially melanin-based black or white coloration (Møller, 1987; Martín & Forsman, 1997; Qvarnstrom, 1997; Beani & Turillazzi, 1999; Ligon & McGraw, 2016; Bachmann et al., 2017). Social costs can also maintain the honesty of rapid colour change (Ligon & McGraw, 2016), and of pigment-based colours potentially costly to produce (Martín & Forsman, 1997).

The costs maintaining the honesty of structural colour signals, including ultraviolet (UV) signals, are yet to be uncovered. Some lines of argument suggest that assembling the dermal, light-scattering nanoscale structures composing structural coloration could pose developmental challenges, which could ultimately maintain signal honesty but robust evidence is still lacking (Fitzpatrick, 1998; Kemp & Rutowski, 2007; Kemp, Herberstein, & Grether, 2012; Kemp & Grether, 2015; White, 2020). UV signals have also been suggested to function as conventional signals especially in lizards, but hard proof is still needed to confirm

this hypothesis (Whiting et al., 2003; Stapley & Whiting, 2006). Names et al. (2019) manipulated the UV-blue patches of male common wall lizards (Podarcis muralis) during male agonistic contests. They found that males were less aggressive and more submissive against cheaters than against honest males, thus rejecting a conventional signal hypothesis in this species. In blue tits (Cvanistes caeruleus), three important studies suggested that the UV coloration displayed on male crowns may function as conventional signals during male contests (Alonso-Alvarez et al., 2004; Poesel et al., 2007; Rémy et al., 2010). These, however, are not conclusive since they were designed to explore the role of UV signals during agonistic interactions rather than to test whether social costs enforced their honesty. To identify social costs of colour signals, researchers must experimentally create out-ofequilibrium colour signals to simulate cheating individuals and examine whether these cheaters receive more aggression than honest signallers during agonistic interactions (Ligon & McGraw, 2016; Bachmann et al., 2017; Names et al., 2019). In this study, we used the common lizard Zootoca vivipara to investigate whether or not socially imposed costs maintain the honesty of UV signals. Male common lizards display UV-reflecting signals on their throat (Martin et al., 2013) that play a role during male-male competition (Martin et al., 2016) and female mate choice (Badiane et al., 2020). In addition, UV chroma on male throat increases with age and body size (Bonnaffé et al., 2018). Altogether, these results strongly suggest that male UV-reflecting throats might signal male quality in Z. vivipara. Furthermore, body size is one of the best predictors of male contest outcome in lizards with larger lizards more likely to win fights than smaller ones (Carpenter, 1995; Fitze & Le Galliard, 2008; Names et al., 2019). Body size is thus a cue widely used by lizards to extract information on male quality (we use the terms 'signal' and 'cue' as defined in Bradbury & Vehrencamp, 2011).

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 rational 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 (Bonnaffé 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.

132 Material and Methods

133 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).

148 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 $(\pm 1 \text{ mm})$, 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

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

were composed of a large opaque plastic terrarium (75x50x40 cm) with one transparent wall to allow video recording, and contained a layer of blond peat as substrate. Two removable opaque plastic walls divided the arena into two equally-sized compartments on both sides and a larger compartment at the centre. The two compartments at the extremities of the arena served as solitary holding areas to allow acclimation to the neutral arena, and were each equipped with a 25-W heat bulb placed 15 cm above a shelter (Exoterra Inc.) that also acted as basking spot. In the central compartment, we placed another 30-W heat bulb 15 cm above a wooden basking spot (12x8x1.5 cm). We illuminated the arenas with a light-emitting plasma fixture (Gavita Pro 270^e GROW LEP) placed 80 cm above the bottom of the arena. This light source reproduces almost exactly the full spectrum of the sun, including UVB and UVA thanks to a UV transmitting glass filter, and is thus ideal to examine the role of UV signals during laboratory experiments. White, opaque curtains surrounded the two arenas at a 1-m distance to create visual isolation. Two digital SLR cameras (Nikon D500 and Nikon D5300) mounted on tripods recorded the experiments in high definition from a lateral, slightly elevated point of view, through the transparent wall of the arena. To test the hypothesis that male-induced social costs are associated with dishonest UV signals in common lizards, we staged dyadic encounters using 59 adult male common lizards (SVL, range = 50-63, mean = 57; body mass, range = 2.4-5.3, mean = 3.8). Each dyadic interaction was unique and involved medium-sized (56-60 mm in SVL), non-manipulated focal males (n = 29), which faced opponents of either larger (n = 15) or smaller size (n = 15) with control or manipulated throat UV reflectance. Small opponents ranged from 50-55 mm

in SVL and were either UV-control or UV-enhanced. Large opponents (60-63 mm in SVL), in
contrast, were either UV-control or UV-reduced. This study design allowed us to create a

mismatch between UV signalling level and body size, and ultimately with male quality since

215 body size is a primary predictor of fighting ability and male contest outcome in lizards

216	(Carpenter, 1995; Karsten et al., 2009; Baird, 2013; Names et al., 2019). Focal males were
217	always 3-6 mm larger (β = 4.21 mm \pm 0.41, p < 0.001) and 1-5 mm smaller (β = -2.84 mm \pm
218	0.42, $p < 0.001$) than their small and large opponents, respectively. There were no significant
219	differences in body size and body mass between small controls and small cheaters (SVL: β = -
220	$0.38 \text{ mm} \pm 0.66, \text{ p} = 0.978$; body mass: $\beta = -0.21 \text{ mm} \pm 0.21, \text{ p} = 0.846$), nor between large
221	controls and large cheaters (SVL: $\beta = 0.30 \pm 0.68$, p = 0.991; body mass: $\beta = 0.37 \pm 0.22$, p =
222	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

male fleeing from another male. None of the contests resulted in observable injuries and all
 males were released to their semi-natural outdoor enclosures after the 8 days of experiment.
 Statistical analyses

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

295 Social costs on dishonest UV signals

First, to test whether or not social costs are imposed on dishonest male UV signals, we calculated two categorical variables named 'opponent size' with two levels ('large' and 'small') and named 'opponent honesty' with two levels ('honest' and 'cheaters'). Honest males corresponded to UV-control males while cheaters corresponded to manipulated males from both the UV-reduced and UV-enhanced treatment groups. Then, we ran LMMs for Gaussian variables and GLMMs for Poisson variables using the following response variables for focal males: the three versions of aggression score, the three versions of submission score, basking duration, and duration of wall-scratching behaviour. We included male ID and trial order as random intercepts in these models. We considered trial order as random because we were not interested in the effects of trial order per se; however, we also ran these models with trial order as fixed factor and present the results from post-hoc Tukey tests when significant. We included the additive effects of opponent size and opponent honesty as well as their twoway interactions, and the additive effect of bite force as fixed effects. When the interaction was significant, we split our data set according to the "opponent size" category to explore the interaction. 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. For all the models described above, we checked the model assumptions using the *performance* R package (Lüdecke *et al.*, 2020). We used a squared-root transformation for wall-scratching behaviour to comply with these assumptions.

Biological Journal of the Linnean Society

Page 14 of 35

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

317 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

338 Social costs on dishonest UV signals

Page 15 of 35

We found that the two-way interaction between opponent size and opponent honesty influenced significantly the aggression score of focal males ($\beta = -0.33 \pm 0.12$, p = 0.005). In conflicts with smaller males, opponent honesty did not significantly explain the aggression score of focal males, though the tendency was a smaller aggression score of focal males (UV-enhanced cheaters: $\beta = -0.15 \pm 0.09$, p = 0.075). In conflicts with larger males, focal males were significantly more aggressive (by 1.2 units on average) towards UV-reduced cheaters than towards honest opponents ($\beta = 0.18 \pm 0.08$, p = 0.021, Figure 2A). When the two alternative versions of the aggression score were used, the results were qualitatively similar. Furthermore, our analyses revealed that the two-way interaction between opponent size and opponent honesty best explained the submission score of focal males ($\beta = -0.73 \pm 0.16$, p < 0.001). More precisely, focal males were less submissive (by 1.4 units of submission score on average) against small cheaters (UV-enhanced) than against small honest males ($\beta = -0.33$ ± 0.13 , p = 0.012), but more submissive (by 1.7 units on average) against large cheaters (UV-reduced) than against large honest males ($\beta = 0.50 \pm 0.11$, p < 0.001; Figure 2B). When the two alternative versions of the submission score were used, results were qualitatively similar except that we did not find that focal males were less submissive against small cheaters (UV-enhanced).

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

opponents with a high throat spectral intensity ($\beta = 0.28 \pm 0.12$, p = 0.023). When we used the

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

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

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

male bite force is an important predictor of male contest outcome.

honest opponents. In addition to this, our analyses excluding manipulated males indicated that

more submissive (submission score calculated with the first set of coefficients) against

two alternative versions of the aggression score, however, none of the predictors were

spending more time performing wall-scratching behaviours had higher throat spectral

Discussion

387 Social costs on dishonest UV signals

trial ($\beta = -1.19 \pm 0.27$, p < 0.001).

Page 17 of 35

We provide partial evidence that the UV components of the UV-reflecting throat of common lizards may function as conventional signals enforced by male-induced social costs. The story becomes more complex than expected when we examine the aggression and submission scores. On one hand, large males with UV-reduced throats received more aggressions but also triggered more submissive behaviours in focal males. This result suggests that, for large males, downplaying UV signals is costlier than being honest since these large UV-reduced cheaters are more likely to be challenged by the smaller focal males. When the focal males challenge the large cheaters, the latter may retaliate since, after all, they are larger and more likely to win fights, and focal males end up being more submissive. Hence, under this scenario, what seemed to be a contradictory result at first glance may in fact be coherent and support the idea that UV signals function as conventional signals in this species. Although large males pose a serious threat to smaller males, if a large male signals low condition, it may pay-off for smaller males to challenge this large male and gain a fitness advantage (e.g. access to resources and/or females). Unexpectedly, small UV-enhanced cheaters did not receive more aggression from the focal males compared to their honest counterparts. However, that focal males behaved less submissively against small cheaters aligns with the predictions of a conventional signal hypothesis.

In the case of conventional signals, social costs are either imposed to individuals that signal above a given threshold intensity or penalize the mismatch between the sender's quality or behaviour and its signalling level. Signal honesty can therefore be maintained only if these costs exceed the benefits of cheating (Searcy & Nowicki, 2005; Bradbury & Vehrencamp, 2011). However, some degree of deception may still arise and pay off as long as the signal remains honest to some degree (Adams & Mesterton-Gibbons, 1995; Carazo & Font, 2014). Individuals can either be exclusively honest or exclusively dishonest, or switch from one strategy to another according to the situation they find themselves into, depending on whether

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 (Martín & 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

Biological Journal of the Linnean Society

advantage in terms of resources and/or access to females over males that are actually of higher quality (e.g. Molles & Vehrencamp, 2001). Another hypothesis may be that smaller males generally behave in a non-threatening way when they face larger males, for example by avoiding being close to larger opponent. Therefore, focal males would not need to show any sign of aggression and spatial occupancy, perhaps captured in our submission score, may be enough to affirm dominance. Alternatively, if focal males are more aggressive towards any opponent that signals above a given threshold intensity, and that small honest males are already signalling close to or above that threshold, we would not see any difference in terms of aggression score between small UV-enhanced cheaters and their honest counterparts. However, in this context, we would not expect to find differences in the submission score as we did here. This also raises the possibility that our results were obscured by our UV manipulation protocol. While the experimental reduction of the UV reflectance within the natural range of variation has been previously validated in the common lizard (Martin et al., 2016; Badiane et al., 2020) and other lizard species (Martin et al., 2015; Names et al., 2019), it is much more difficult to enhance UV reflectance. To the best of our knowledge, only a handful of studies have experimentally augmented the UV coloration of animals, mostly in the blue tit Cyanistes caeruleus (Poesel et al., 2007; Rémy et al., 2010) and one study in the common wall lizard Podarcis muralis (Names et al., 2019). In these and our study, whether or not these UV-enhanced patches can be considered to be within the natural range of variation remains debatable, since spectral shape can look artificial. In addition, our marker pen did not only increase reflectance in the UV range but also in the orange part of the spectrum (idem, to a lesser extent, with the UV reduction treatment) and this may set a limit to results' interpretations since we do not know how this may have influenced the outcome of our behavioural experiments. It is therefore possible that the focal males did not consider the UV-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

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

behaviour, and from the perspective of the receiver since receivers adjust their behaviour based on these signals. Therefore, our study confirms the importance of UV coloration as predictors of male contest outcomes in the common lizard (Martin et al., 2016). However, we can only provide partial evidence that social costs maintain the honesty of UV-reflecting signals. This is because we observed different patterns of physical and non-physical aggression in the face of deception in situations where focal males faced small opponents than with large opponents. Although not entirely conclusive, this suggests that UV signals can be honest thanks to context-dependent social costs imposed by rival males during male-male competition. Future work should keep investigating these avenues of signal honesty with UV signals to improve our understanding of animal communication at large.

498 Research data

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

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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, Decencière 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.

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UU	

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

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563 multiple-partner mating between males and females of the polygynandrous common lizards.

564 *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.

567 **Fitzpatrick S**. **1998**. Colour schemes for birds: Structural coloration and signals of quality in

568 feathers. *Annales Zoologici Fennici* **35**: 67–77.

569 de Fraipont M, Colbert J, John-Alder H & Meylan S. 2000. Increased pre-natal maternal

570 corticosterone promotes in common of offspring philopatry lizards Lacerta vivipara. Journal

571 of Animal Ecology **69**: 404–413.

572 Le Galliard JF, Fitze PS, Ferrière R & Clobert J. 2005. Sex ratio bias, male aggression,

573 and population collapse in lizards. *Proceedings of the National Academy of Sciences* **102**:

574 18231–18236.

575 Grafen A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology* 144: 517–
576 546.

577 Guilford T & Dawkins MS. 1995. What are conventional signals? *Animal Behaviour* 49:
578 1689–1695.

579 Heulin B. 1988. Observations sur l'organisation de la reproduction et sur les comportements
580 sexuels et agonistiques chez *Lacerta vivipara*. *Vie et milieu* 38: 177–187.

581 Higham JP. 2014. How does honest costly signaling work? *Behavioral Ecology* 25: 8–11.

582 **Hurd PL**. **1997**. Is signalling of fighting ability costlier for weaker individuals? *Journal of*

583 *Theoretical Biology* **184**: 83–88.

584 Hurd PL & Enquist M. 2005. A strategic taxonomy of biological communication. *Animal*585 *Behaviour* 70: 1155–1170.

586 Husak JF, Lappin KA, Fox SF & Lemos-Espinal JA. 2006. Bite-Force Performance

587 Predicts Dominance in Male Venerable Collared Lizards (Crotaphytus antiquus). Copeia

589

2006: 301–306.

1

Huvghe K, Vanhoovdonck B, Scheers H, Molina-Borja M & Van Damme R. 2005.

2	
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4	
5	
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9 10	
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Morphology, performance and fighting capacity in male lizards, Gallotia galloti. Functional 590 *Ecology* **19**: 800–807. 591 Johnstone RA & Norris K. 1993. Badges of status and the cost of aggression. Behavioral 592 Ecology and Sociobiology 32: 127:134. 593 Karsten KB, Andriamandimbiarisoa LN, Fox SF & Raxworthy CJ. 2009. Sexual 594 selection on body size and secondary sexual characters in 2 closely related, sympatric 595 chameleons in Madagascar. *Behavioral Ecology* **20**: 1079–1088. 596 597 Kemp DJ & Grether GF. 2015. Integrating functional and evolutionary approaches to the study of color-based animal signals. In: Animal Signaling and Function: An Integrative 598 *Approach.*, 111–140. 599 Kemp DJ, Herberstein ME & Grether GF. 2012. Unraveling the true complexity of costly 600 color signaling. *Behavioral Ecology* **23**: 233–236. 601 Kemp DJ & Rutowski RL. 2007. Condition dependence, quantitative genetics, and the 602 potential signal content of iridescent ultraviolet butterfly coloration. *Evolution* **61**: 168–183. 603 Kurvers RHJM, Delhey K, Roberts ML & Peters A. 2010. No consistent female 604 605 preference for higher crown UV reflectance in Blue Tits Cyanistes caeruleus: A mate choice experiment. Ibis 152: 393-396. 606 Laloi D, Richard M, Lecomte J, Massot M & Clobert J. 2004. Multiple paternity in 607 608 clutches of common lizard Lacerta vivipara: Data from microsatellite markers. Molecular *Ecology* **13**: 719–723. 609 Laloi D, Eizaguirre C, Fédérici P & Massot M. 2011. Female choice for heterozygous 610 mates changes along successive matings in a lizard. Behavioural Processes 88: 149-154. 611 Lappin AK & Husak JF. 2005. Weapon performance, not size, determines mating success 612

613 and potential reproductive output in the collared lizard (Crotaphytus collaris). American

Naturalist **166**: 426–436.

615 Lappin AK & Jones MEH. 2014. Reliable quantification of bite-force performance requires

616 use of appropriate biting substrate and standardization of bite out-lever. *The Journal of*

- *Experimental Biology* **217**: 4303–4312.
- 618 Ligon RA & McGraw KJ. 2016. Social costs enforce honesty of a dynamic signal of
- 619 motivation. *Proceedings of the Royal Society B: Biological Sciences* 283.
- 620 Lüdecke D, Makowski D, Waggoner P & Patil I. 2020. Performance: Assessment of
- 621 regression models performance, CRAN, R package.
- 622 Maia R, Gruson H, Endler JA & White TE. 2019. pavo 2: new tools for the spectral and
- 623 spatial analysis of colour in R. *Methods in Ecology and Evolution* **10**: 1097-1107.

624 Martin M, Meylan S, Gomez D & Le Galliard JF. 2013. Ultraviolet and carotenoid-based

- 625 coloration in the viviparous lizard Zootoca vivipara (Squamata: Lacertidae) in relation to age,
- 626 sex, and morphology. *Biological Journal of the Linnean Society* **110**: 128–141.
- 627 Martin M, Meylan S, Perret S & Le Galliard JF. 2015. UV coloration influences spatial
- 628 dominance but not agonistic behaviors in male wall lizards. *Behavioral Ecology and*
- 629 Sociobiology **69**: 1483–1491.
- 630 Martin M, Meylan S, Haussy C, Decencière B, Perret S & Le Galliard JF. 2016. UV
 - 631 color determines the issue of conflicts but does not covary with individual quality in a lizard.
 - *Behavioral Ecology* **27**: 262–270.
 - Martín 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.

1

Maynard Smith J & Harper D. 2003. Animal signals. New York: Orford University Press.

2	
3	
4	
5	
6	
7	
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55	
56	
57	
58	
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Møller AP. 1987. Variation in badge size in male house sparrows *Passer domesticus*: 639 evidence for status signalling. Animal Behaviour 35: 1637–1644. 640 Molles LE & Vehrencamp SL. 2001. Songbird cheaters pay a retaliation cost: Evidence for 641 auditory conventional signals. Proceedings of the Royal Society B: Biological Sciences 268: 642 2013-2019. 643 Names G, Martin M, Badiane A & Le Galliard JF. 2019. The relative importance of body 644 size and UV coloration in influencing male-male competition in a lacertid lizard. Behavioral 645 Ecology and Sociobiology 73: 98. 646 Pinheiro J, Bates D, DebRoy S, Sarkar D & RCoreTeam. 2019. nlme: Linear and 647 nonlinear mixed effects models. 648 Poesel A, Peters A, Dabelsteen T, Darden SK & Delhey K. 2007. Territorial responses of 649 male blue tits, Cyanistes caeruleus, to UV-manipulated neighbours. Journal of Ornithology 650 **148**: 179–187. 651 Qvarnstrom A. 1997. Experimentally increased badge size increases male competition and 652 reduces male parental care in the collared flycatcher. *Proceedings of the Royal Society B:* 653 Biological Sciences 264: 1225–1231. 654 655 R Development Core Team. 2017. R: A language and environment for statistical computing. Rémy A, Grégoire A, Perret P & Doutrelant C. 2010. Mediating male-male interactions: 656 The role of the UV blue crest coloration in blue tits. *Behavioral Ecology and Sociobiology* 64: 657 1839–1847. 658 Rohwer S & Rohwer FC. 1978. Status signalling in Harris Sparrows. Animal Behaviour 26: 659 1012-1022. 660 Roulin A. 2016. Condition-dependence, pleiotropy and the handicap principle of sexual 661 selection in melanin-based colouration. *Biological Reviews* 91: 328-348. 662 Biological Journal of the Linnean Society

663 Rozen-Rechels D, Badiane A, Agostini S, Meylan S & Le Galliard J. 2020. Water

restriction induces behavioral fight but impairs thermoregulation in a dry-skinned ectotherm.

Oikos **129**: 572–584.

666 Rozen-Rechels D, Dupoué A, Meylan S, Decencière B, Guingand S & Le Galliard JF.

2018. Water restriction in viviparous lizards causes transgenerational effects on behavioral

anxiety and immediate effects on exploration behavior. Behavioral Ecology and Sociobiology

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*

Naturalist **192**: 111–130.

676 Schielzeth H. 2010. Simple means to improve the interpretability of regression coefficients.

Methods in Ecology and Evolution **1**: 103–113.

678 Searcy W & Nowicki S. 2005. The evolution of animal communication: reliability and

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.

Tibbetts EA. **2014**. The evolution of honest communication: Integrating social and

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51
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53
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54 57
55
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58
59

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

Biological Journal of the Linnean Society

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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 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*

2 and their associated coefficient used to calculate scores. Coef.1 corresponds to the first set of

3 coefficients that we assigned to the behaviours and consider as the most realistic ranking.

4 Coef.2 and Coef.3 are two additional sets of coefficients that vary slightly from Coef.1 to

5 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	-	-	-

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Biological Journal of the Linnean Society

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* ~ *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).

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

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

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,

Biological Journal of the Linnean Society

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

the ΔAICc, and the weight of each one of the best models. Table S3 summarises the
conditional model averaging and indicates the estimates ± 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* ~ *predictors* + *random intercept factors*. Random factors were always ID of the focal male and
trial order.

26 Table S2. Best models for each response variable.

Response	Predictors	AICc	ΔAICc	Weight
	Bite Force	374.07	0.00	0.16
Aggression	Bite Force + UV_{chroma}	375.30	1.23	0.09
score	Bite Force + Opponent UV _{intensity}	375.61	1.44	0.08
	Bite Force + UV _{intensity}	375.71	1.64	0.07
	Null	377.81	3.74	0.02
Submission	Opponent UV _{intensity}	348.57	0.00	0.23
score	Opponent UV _{intensity} + UV _{intensity}	350.36	1.78	0.09
	Null	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
	Null	157.20	2.32	0.03
Wall-	UV _{intensity}	136.69	0.00	0.18
	Opponent Body Size + UV _{intensity}	138.05	1.36	0.09
duration	$UV_{chroma} + UV_{intensity}$	138.27	1.58	0.08
uuration	Null	140.44	3.75	0.03

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

29 for each predictor and response variable.

Page 35 of 35

Biological Journal of the Linnean Society

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

0.15 ± 0.12 P = 0.249	-0.11 ± 0.23	0.10 + 0.17		
P = 0.249		0.12 ± 0.17	-0.21 ± 0.17	
	P = 0.626	P = 0.503	P = 0.218	
sw = 0.36	sw = 0.23	sw = 0.26	sw = 0.30	
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	
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	
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	
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	
0.29 ± 0.11	-0.06 ± 0.24	0.31 ± 0.16	$0;04 \pm 017$	
P = 0.010*	P = 0.812	P = 0.059	P = 0.838	
sw = 0.84	sw = 0.23	sw = 0.66	sw = 0.22	
	P = 0.452 sw = 0.27 0.04 ± 0.14 P = 0.771 sw = 0.23 0.13 ± 0.14 P = 0.357 sw = 0.30 0.11 ± 0.28 P = 0.703 sw = 0.23 0.29 ± 0.11 P = 0.010* sw = 0.84	$P = 0.452$ $P = 0.297$ $sw = 0.27$ $sw = 0.29$ 0.04 ± 0.14 -0.04 ± 0.15 $P = 0.771$ $P = 0.818$ $sw = 0.23$ $sw = 0.23$ 0.13 ± 0.14 0.26 ± 0.12 $P = 0.357$ $P = 0.038^*$ $sw = 0.30$ $sw = 0.94$ 0.11 ± 0.28 -0.24 ± 0.20 $P = 0.703$ $P = 0.239$ $sw = 0.23$ $sw = 0.23$ $sw = 0.23$ $sw = 0.23$ $sw = 0.11$ -0.06 ± 0.24 $P = 0.010^*$ $P = 0.812$ $sw = 0.84$ $sw = 0.23$	$P = 0.452$ $P = 0.297$ $P = 0.183$ $sw = 0.27$ $sw = 0.29$ $sw = 0.43$ 0.04 ± 0.14 -0.04 ± 0.15 -0.19 ± 0.14 $P = 0.771$ $P = 0.818$ $P = 0.186$ $sw = 0.23$ $sw = 0.23$ $sw = 0.47$ 0.13 ± 0.14 0.26 ± 0.12 -0.06 ± 0.14 $P = 0.357$ $P = 0.038*$ $P = 0.652$ $sw = 0.30$ $sw = 0.94$ $sw = 0.23$ 0.11 ± 0.28 -0.24 ± 0.20 -0.19 ± 0.31 $P = 0.703$ $P = 0.239$ $P = 0.554$ $sw = 0.23$ $sw = 0.25$ $sw = 0.33$ 0.29 ± 0.11 -0.06 ± 0.24 0.31 ± 0.16 $P = 0.010*$ $P = 0.812$ $P = 0.059$ $sw = 0.84$ $sw = 0.23$ $sw = 0.666$	

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