

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

ANNA KAWAMOTO<sup>1,\*,\*</sup>, JEAN-FRANÇOIS LE GALLIARD<sup>1,2,\*</sup> and ARNAUD BADIANE<sup>1,\*,\*</sup>

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

<sup>2</sup>*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*

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According to animal signalling theory, social costs incurred by aggressive conspecifics are one mechanism maintaining signal honesty. Although 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-reflecting signals displayed on male throats is under social control. To do so, we staged agonistic interactions between non-manipulated focal males and opponents of either larger or smaller body size. We manipulated the UV component of the male throat colour patch 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 confirm that male UV reflectance 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.

**ADDITIONAL KEYWORDS:** animal communication – deception – male competition – ultraviolet – *Zootoca vivipara*.

## 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 fitness benefits to both senders and receivers and this condition can be achieved only if signals are honest to some degree (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 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 *et al.*, 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 *et al.*, 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 social costs during agonistic interactions (Higham, 2014; Weaver *et al.*, 2017). Tibbetts (2014) and Webster *et al.* (2018) further

\*Corresponding author. E-mail: [annakaw423@gmail.com](mailto:annakaw423@gmail.com)

\*Both authors contributed equally to this work

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 a similar signalling level to their own (Tibbetts, 2014), 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 that are potentially costly to produce (Martín & Forsman, 1997).

The costs of 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 *et al.*, 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 (*Cyanistes caeruleus*), three important studies suggested that the

UV coloration displayed on male crowns may function as a conventional signal during male contests (Alonso-Alvarez *et al.*, 2004; Poesel *et al.*, 2007; Rémy *et al.*, 2010). These studies, 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-of-equilibrium 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-reflecting signals. Male common lizards display UV-reflecting signals on their throat (Martin *et al.*, 2013) that play a role during male-male competition and female mate choice. Previous studies indeed showed that an experimental reduction of UV reflectance on male throats influenced male contest outcome (Martin *et al.*, 2016), increased female aggressiveness during pre-copulatory interactions, and lowered male fertilization success (Badiane *et al.*, 2020). In addition, UV chroma on male throats 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*, although correlations between signal features and male quality traits are yet to be uncovered (Martin *et al.*, 2016). 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 dominance status because it correlates with age or individual 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-reflecting signals in this species, and then investigated the relative importance of male UV features, 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 and quality, we used lizards of different body size. Our rationale was that precise quality traits advertised by UV-reflecting signals are not completely known yet in this species; however, body size is a well-known cue of male quality that correlates with UV-reflecting signals in this and other lizard 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 a 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 a socially enforced conventional signal, 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). At our study site, adult males usually emerge from hibernation in March. The emergence of females starts approximately 3–4 weeks later at the beginning of April, depending on weather conditions, and marks the beginning of the mating season (Massot *et al.*, 1992). During the mating season, there is an endurance competition among males over access to females (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 few black spots, and extends on to 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 on the male's throat (Martin *et al.*, 2013).

### SAMPLING AND MEASUREMENTS

On March 19<sup>th</sup> 2019, we captured 61 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-m<sup>2</sup> enclosures under natural, outdoor environmental conditions. We brought the lizards to the laboratory, measured their snout-vent length (SVL) with a ruler ( $\pm 1$  mm), and their body mass using a digital scale ( $\pm 1$  mg). Most males (53/61) were 2 years old, five males were 3 years old, and the three remaining males were 4, 5 and 7 years old. Age significantly explained 13% of male body size variation ( $F_{1,58} = 0.79$ ,  $P = 0.003$ ,

$R^2 = 0.13$ ), meaning that 87% of male body size variation was explained by other factors. These factors may include genetic quality, pre-natal environmental conditions and post-natal environmental conditions. 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 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) using a USB-2000 spectrophotometer following Badiane *et al.* (2017) recommendations (Supporting Information, Data S1). We then 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. We extracted two UV-related colorimetric variables from the throat spectra, namely spectral intensity (i.e.  $R_{300-700}$ ), and UV chroma (i.e.  $R_{300-400}/R_{300-700}$ ) because they are biologically relevant in this and other lacertid lizards (Martin *et al.*, 2013; Bonnaffé *et al.*, 2018; Names *et al.*, 2019). Males from this study had a belly coloration ranging from yellow to orange (Supporting Information, Fig. S2).

Following measurement, we housed the lizards in our husbandry (Supporting Information, Fig. S3) for a total of 18 days, including 10 days of acclimation to laboratory conditions [during which we waited for the lizard's first moult to occur as it marks the onset of sexual activity (Laloi *et al.*, 2011)], and 8 days of experimentation.

### 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 (75 × 50 × 40 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

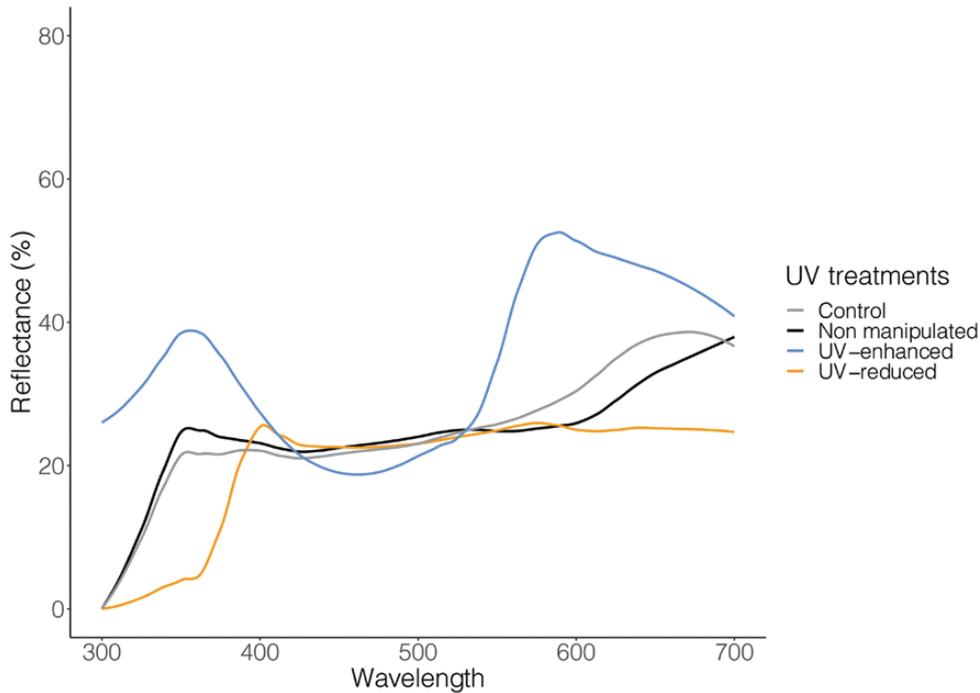
heat bulb placed 15 cm above a shelter (Exoterra Inc.) that also acted as basking spot. In the central compartment, we placed another 30-W heat bulb 15 cm above a wooden basking spot (12 × 8 × 1.5 cm). We illuminated the arenas with a light-emitting plasma fixture (Gavita Pro 270<sup>e</sup> GROW LEP) 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 (a Nikon D500 and a 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-reflecting signals in common lizards, we staged dyadic encounters using 61 adult male common lizards (SVL, range = 50–63 mm, mean = 57 ± 0.39 mm; body mass, range = 2.4–5.3 g, mean = 3.8 ± 0.08 g). Each dyadic interaction was unique and involved medium-sized (56–60 mm SVL), non-manipulated focal males ( $N = 29$ ), which faced opponents of either larger ( $N = 15$ ) or smaller size ( $N = 17$ ) with control or manipulated throat UV reflectance. Small opponents (50–55 mm SVL) were either UV-control or UV-enhanced. Large opponents (60–63 mm 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 body size is a primary predictor of fighting ability and male contest outcome in lizards (Carpenter, 1995; Karsten *et al.*, 2009; Baird, 2013; Names *et al.*, 2019). Focal males were 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:  $\beta = 0.37 \pm 0.22$ ,  $P = 0.465$ ). The yellow-orange belly coloration (hue, yellow-orange chroma, intensity) did not differ either between small controls and small cheaters (hue:  $\beta = 0.39 \pm 0.50$ ,  $P = 0.930$ ; chroma:  $\beta = -0.04 \pm 0.48$ ,  $P = 0.999$ ; intensity:  $\beta = -1.05 \pm 0.41$ ,  $P = 0.224$ ), nor between large control and large cheaters (hue:  $\beta = -0.44 \pm 0.52$ ,  $P = 0.908$ ; chroma:  $\beta = -0.04 \pm 0.48$ ,  $P = 0.999$ ; intensity:  $\beta = 0.50 \pm 0.45$ ,  $P = 0.798$ ).

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 (6:4:50:40, respectively, for 100 g). Large males of the control group were treated with the fat combination (petroleum jelly and liquid paraffin, 56.6:44.4) and large males of the UV-reduced treatment were treated with the fat combination mixed with the inorganic agents (Fig. 1). We applied both mixtures using a thin paintbrush on the lizard's 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 marker application on the lizard's 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 lizard's 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 whereas small lizards from the UV-control group were not treated at all (Fig. 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. We used visual modelling using the common lizard visual system to quantify the differences between our colour treatments (Supporting Information, Fig. S4).

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 (Supporting Information, Fig. S5). 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 vice versa. We designed the experiment such that focal males participated in encounters only once every 2 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 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 interactions (12%) for which both males came from the same 100-m<sup>2</sup> enclosure. However, in 12 out of these



**Figure 1.** 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.

14 encounters, both males were entering their first reproductive season (2 years old) and had therefore not competed in the past. The two remaining contests both involved a sexually mature male (3 years old) against a newly sexually mature male (2 years old), and had therefore never competed against each other. It is therefore 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 for a first 10-min acclimation period. 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 was the wooden plate at the centre of the arena

(Supporting Information, Fig. S6). 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 interacted with each other and competed for the basking spot. Next, a single observer, blind to the experimental treatments, used Jwatcher (Blumstein & Daniel, 2007) to analyse the lizard's behaviours from all the video recordings.

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 *et al.*, 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

**Table 1.** List and descriptions of the different behaviours displayed by male *Z. vivipara* and their associated coefficients 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 affects our results

Scores	Behaviours	Descriptions	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
	Bury	Number of times a lizard buries 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	-	-	-

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 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 *et al.*, 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 experimentation.

#### STATISTICAL ANALYSES

We used R v.3.3.2 (R Development Core Team, 2017) to perform all statistical analyses.

#### SOCIAL COSTS ON DISHONEST UV-REFLECTING SIGNALS

First, to test whether or not social costs are imposed on dishonest male UV-reflecting signals, we calculated two categorical variables named ‘opponent size’ with two levels (‘large’ and ‘small’) and ‘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 linear mixed-effects models (LMMs) for Gaussian variables and generalized linear mixed-effects models (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 a 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 two-way 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. 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 LMMs and 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 (Baroń, 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 (Supporting Information, Tables S1 and S2).

### RESULTS

#### SOCIAL COSTS ON DISHONEST UV-REFLECTING SIGNALS

We found that the two-way interaction between opponent size and opponent honesty significantly influenced the aggression score of focal males. In conflicts with smaller males, opponent honesty did not significantly explain the aggression score of focal males, though the tendency was towards a smaller aggression score for 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

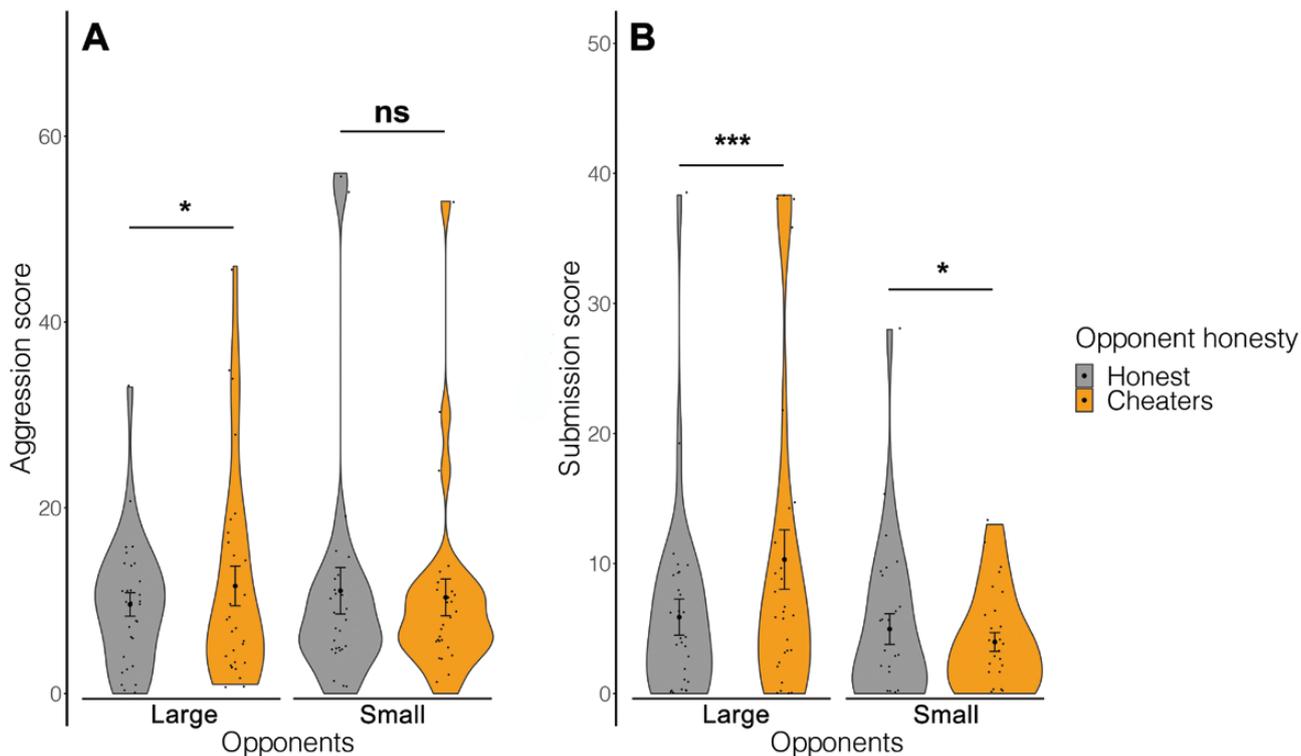
( $\beta = 0.18 \pm 0.08$ ,  $P = 0.021$ , Fig. 2A). When the two alternative versions of the aggression score were used, the results were qualitatively similar.

Furthermore, our analyses revealed that the two-way interaction between opponent size and opponent honesty best explained the submission score of focal males. 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 ( $\beta = -0.33 \pm 0.13$ ,  $P = 0.012$ ), but more submissive (by 1.7 units on average) against large cheaters (UV-reduced) than against large honest males ( $\beta = 0.50 \pm 0.11$ ,  $P < 0.001$ ; Fig. 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 not significantly explain the time focal males spent at the basking spot, nor the time spent performing wall-scratching behaviours. Statistics are fully reported in Table 2. When we included trial order as a fixed instead of a 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 ( $\beta = -0.26 \pm 0.09$ ,  $P = 0.013$ ).

#### 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 Supporting Information (Data S7). When we included trial order as a fixed instead of a 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 ( $\beta = -1.19 \pm 0.27$ ,  $P < 0.001$ ).



**Figure 2.** Violin plots including the mean and standard errors of the aggression score (A) and the submission score (B) of focal males according to the opponent body size and UV treatment. Aggression and submission scores were calculated by adding the aggressive and submissive behaviours, respectively, weighted by their coefficient (coef.1 from Table 1). UV signals were reduced in large cheaters but enhanced in small cheaters. Levels of significance are indicated ( $P < 0.05$  \*,  $P < 0.001$  \*\*\*), ns, not significant.

**Table 2.** 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 (\*  $< 0.05$ , \*\*  $< 0.01$ , \*\*\*  $< 0.001$ )

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

## 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-REFLECTING SIGNALS

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. First, large males with UV-reduced throats received more aggressive behaviours but also triggered more submissive behaviours in focal males. This result suggests that, for large males, downplaying UV-reflecting 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, our findings support the idea that social costs are associated with UV-reflecting signals in this species. 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). Second, small UV-enhanced cheaters did not receive more aggressive behaviours 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 on 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 in, depending on whether the signal is very labile and can change rapidly or not (Akçay *et al.*, 2013; Wilson & Angilletta, 2015; Ligon & McGraw, 2016). In common lizards, the UV-reflecting coloration on the male's 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 social costs. Our aggression score is the most meaningful factor because it can 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 one of the two males biting the other one. Thus, the risk of injury due to physical aggression cannot be neglected in this species (Le Galliard *et al.*, 2005). On top of this, other behaviours, in the form of non-physical aggression or spatial dominance, not necessarily measured, may enhance social costs. Our submission score may therefore capture the effects of 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 signalling component than for a large male that downplays it. However, we would expect social costs to prevent low-quality males from signalling high quality, and gain advantage in terms of resources and/or access to females over males 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 close contact with larger opponents. 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 signalling above a given threshold intensity, and that small control males are already signalling at that threshold, we would not see any difference in terms of aggression score between small, UV-enhanced cheaters and their honest counterparts. If so, we would not expect to find differences in the submission score as we did here. Finally, we could speculate that we did not find social costs in smaller males because other honesty-guaranteeing mechanisms are preponderant (e.g. physiological costs) in those males.

It is also equally likely that our results were obscured by our UV manipulation protocol. Although the experimental reduction of 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 experimentally 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* (Johnsen *et al.*, 2005; Poesel *et al.*, 2007; Rémy *et al.*, 2010)] and one study in the common wall lizard (*Podarcis muralis*) (Names *et al.*, 2019). In these studies 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 (the same was found to a lesser extent with the UV reduction treatment) and we do not know how this may have influenced 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 the female’s throats (Martin *et al.*, 2013) or the male’s ventral coloration, and confuse the receivers. In addition, we cannot exclude that the artificial light orange colour faded to some extent during the experiment. 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, focal males were more submissive when they faced opponents with high throat spectral intensity. However, when focal males had a high throat spectral intensity, they performed more wall-scratching behaviours. It seems contradictory if we interpret wall-scratching behaviour as a submissive behaviour, which is a possibility, 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 sets 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 the UV component of male throat coloration plays a role during male contests, both from the point of view of the signaller, as it correlates with the signaller’s behaviour, and from the receiver’s perspective since receivers adjust their behaviour based on these signals. Therefore, our study confirms the importance of UV reflectance as predictor of male contest outcomes in the common lizard (Martin *et al.*, 2016). We provide partial evidence that social costs maintain the honesty of UV-reflecting signals. We indeed observed different patterns of physical and non-physical aggression towards cheaters depending on opponent’s body size. Although not entirely conclusive, this suggests that UV-reflecting 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-reflecting signals to improve our understanding of animal communication in a wider context.

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### SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Data S1.** Collection of spectral data.

**Figure S2.** Belly coloration.

**Figure S3.** Housing conditions.

**Figure S4.** Visual modelling.

**Figure S5.** Experimental design.

**Figure S6.** Experimental arena.

**Data S7.** Contest outcome in control interactions.

**Table S1.** Best models for each response variable.

**Table S2.** Conditional model-averaged coefficient ( $\beta \pm se$ ), *P*-value, and sum of weights (sw) for each predictor and response variable.

### SHARED DATA

All data used in this study are freely available on the public repository Zenodo (doi: 10.5281/zenodo.4430455).