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ARTICLE

Subjective resource value affects aggressive behavior independently of resource-holding-potential and color morphs in male common wall lizard

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Abstract

Game theory models predict the outcome of a dyadic contest to depend on opponents' asymmetries in three main traits: resource-holding potential (RHP), resource value (RV) and aggressiveness. Using male common wall lizards *Podarcis muralis*, a polymorphic species showing three discrete morphs (white, yellow, and red), we investigated how the aggressive behavior varies according to a change in subjective RV and color morphs, while controlling for the asymmetry in RHP (using mirrors). By comparing the aggression of the same individual towards its mirror image in two different arenas (familiar = high subjective RV; novel = low subjective RV), we showed that lizard aggressive behavior was more intense and prolonged in the familiar arena than in the new one, thus supporting the occurrence of a direct relationship between motivation and aggression in this species. We also found the overall aggressiveness to differ from individual to individual, supporting the general hypothesis that aggressiveness is a trait associated with personality. By contrast, no effect of morphs was detected, ruling out the occurrence of morph specific variation in the aggressiveness. Our results highlight that an individual's motivation and personality might be as important as RHP and RV in the resolution of animal contests.

Keywords Dyadic contests · Fighting rules · Aggressiveness · Personality · RHP · Motivation

Introduction

Agonistic encounters in animals occur when two individuals compete for a limited resource, such as food, territories or mates (Huntingford and Turner 1987; Archer 1988; Hack 1997). Contests carry costs for opponents, which may include an increased risk of injuries and mortality (Dufty 1989; Marler and Moore 1988), or predation risk (Lange and Leimar 2001; Tuttle and Ryan 1981), in addition to the costs of losing the disputed resource. Natural selection should favor the evolution of behaviors (i.e., strategies) and correlated phenotypes that minimize those costs, thus maximizing the probability of obtaining the disputed resources (Maynard-Smith and Price 1973). This in turn has favored the evolution in some species of fighting rules that normally solve intraspecific disputes without physical combat (e.g., Huntingford and Turner 1987; Jablonski and Matyjasiak 1997; López and Martín 2001), whereby interactions escalate to a physical fight only when it is not possible for the two contestants to reliably assess their respective fighting abilities (Sacchi et al. 2009).

Game theory models have shown that three main asymmetries between opponents can predict the outcome of a dyadic contest (Maynard-Smith 1982). The most common is the asymmetry in the ability to gain and hold the disputed resource (i.e., the "resource-holding potential", RHP, Parker 1974), which usually depends on body size and weapons (Caldwell and Dingle 1979; Sneddon et al. 1997). The individual with the higher RHP typically goes on to win (Parker

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1974; Maynard-Smith 1982; Elias et al. 2008; Arnott and Elwood 2009), and the more similar the opponents' RHP, the greater the probability that encounters will escalate to physical combat (Sacchi et al. 2009).

The second asymmetry affecting the contest outcome is the value for resources (RV), such as mates, territories, food or shelter (Parker 1974; Maynard-Smith and Parker 1976). In general, when the outcome of contests cannot be predicted from differences in RHPs, the individual defending a resource with higher RV is more likely to win (Parker 1974; Maynard-Smith 1982; Kokko 2013). Examples of how RV can influence fight outcome are seen in mammals (Barnard and Brown 1982), birds (Ewald 1985), amphibians (Verrell 1986), fishes (Lindström 1992), and invertebrates (Gherardi 2006; Brown et al. 2007). In some cases, a positive asymmetry in RV can compensate for negative asymmetry in RHP, as occurring in resident vs. intruder dynamics (Sacchi et al. 2009).

RV depends on both external factors, i.e., detectable properties of the resource that can be assessed by the contestants, and internal factors, i.e., the value that the individual contestants put on that type of resource (Gherardi 2006; Goubault et al. 2007; Mathiron et al. 2018). The first is often reported as the "objective RV", whereas the second one as the "subjective RV" (Gherardi 2006; Mathiron et al. 2018). The objective RV specifically relies on the fitness value intrinsic to the resource, and is dependent on its detectable properties (e.g. food, nesting sites, microclimatic conditions, refuges within a territory). By contrast, the subjective RV reflects the value that the two opponents place on that resource, and depends on the opponents having prior knowledge of the resource, as well as their own physical condition at the time of the contest. The interaction between objective and subjective RVs establishes the level of asymmetry in RV between opponents. For example, territories have their own values in term of fitness (objective RV), but residents may have a higher subjective RV than intruders due to their prior knowledge about territory properties. More generally, resource owners have higher RV than intruders (Gherardi 2006). Examples come from contests over nesting burrows in female iguanas (Rand and Rand 1976) or over females in male spiders (Austad 1983). Similarly, RV may increase following previous investment in the resource by the owner (Tobias 1997), as well as wins in previous encounters (i.e. the winner–loser effect, Mesterton-Gibbons and Dugatkin 1995; Hsu et al. 2006).

The third asymmetry concerns aggressiveness, as the individual tendency to escalate a contest independently of RHP and RV (Barlow et al. 1986; Maynard-Smith and Harper 1988). In this respect, aggressiveness differs from RHP and RV because it is an inherent property of the individual, a persistent trait of its personality, rather than a variable motivational state (Barlow et al. 1986; Santostefano et al. 2016). In comparison to RHP and RV, aggressiveness has received much less attention, despite its importance in determining an individual's fitness ability (but see Keeley and Grant 1993; Stienecker et al. 2019). For example, Barlow et al. (1986) and Keeley and Grant (1993) clearly demonstrated that cichlids become more aggressive when RV increases, therefore increasing an individual's probability of winning the contest.

Lizards have been extensively used for testing hypotheses about the effects of asymmetries in RHP (e.g., Molina-Borja et al. 1998; Sacchi et al. 2009; McLean and Stuart-Fox 2015; Quintana and Gladino 2017) and RV (Tokarz 1985; López and Martín 2001) on contest outcome. Often residency and body size predict outcomes: resource owners (i.e., residents) are more aggressive than intruders, and larger males are competitively superior to smaller ones (Molina-Borja et al. 1998; Sacchi et al. 2009; McLean and Stuart-Fox 2015; Quintana and Gladino 2017). Conversely, the roles of individual aggressiveness and motivation on contest outcome have been rarely investigated (but see Rangel-Patiño et al. 2018). This is likely due to the difficulty of controlling asymmetries in RHP, including body size and condition, between opponents. In a recent study (Scali et al. 2019), we showed that lizards consistently display an aggressive response to their own mirror image. This method can be effectively used to control asymmetries in RHP and RV between opponents when measuring contest behaviour.

In the present study, we investigated contest behavior in the common wall lizard (*Podarcis muralis*), a small (50–70 mm in adult snout–vent length, SVL) diurnal lizard of central and southeastern Europe (Sillero et al. 2014). In this species, body size and residence affect the outcome of dyadic encounters for territory ownership (Sacchi et al. 2009). Individuals of both sexes exhibit three discrete color morphs (white, yellow, and red) (Sacchi et al. 2007), which are genetically determined (Andrade et al. 2019). Correlations among morphs and aggressiveness are controversial (Sacchi et al. 2009; Abalos et al. 2016; Coladonato et al. 2020); in our previous study using a resident-intruder design (Sacchi et al. 2009), color morph did not affect the encounter outcome, but Abalos et al. (2016) were able to detect morph specific effects by analyzing dyadic encounters in a neutral arena.

We used mirrors to measure the aggressive response of a lizard in response to changes in subjective RV, accounting for potential variability in aggression between color morphs. Lizards were housed in two arenas with low and high subjective RVs, and we compared an individual's aggressive response to its mirror image. Our main prediction was that lizards would modulate their aggression according to the RV of the arena.

Methods

Lizard collection and housing

Sixty adult male common wall lizards (SVL range: 56–70 mm) were captured during spring 2018 (5th April–6th June) in and around the town of Pavia (Northern Italy, 45°11′N, 9°9′E): 36 were captured from three urban gardens in the town, and 24 were from three rural properties. Only pure morphs were collected, representing white ($n = 22$), yellow ($n = 22$), and red ($n = 16$), according to Sacchi et al. (2013). We individually housed lizards in 20 × 30 × 20 cm transparent plastic enclosures (Baeckens et al. 2016; Mangiacotti et al. 2019), with a flat brick as shelter/basking site and a small bowl of water. We provided mealworms as food (one mealworm/day). The housing room was maintained between 15 and 30 °C (the natural temperature range for the season), and large windows provided natural daylight. A minimum acclimation period of one week was given before starting trials, and we released all lizards at their capture sites following use in trials no more than 2 weeks after their capture date. All enclosures were carefully cleaned before a new individual was placed into it to remove any chemical cue of a previous subject. No lizard was injured or killed during the study, and all lizards looked healthy at release.

Experimental setting

A mirror was used to simulate the intrusion of a rival male within the enclosure and measure the male's aggressive response. We had previously shown that common wall lizards perceive their own mirror image as a rival, and behave aggressively in response, sometimes even biting (Scali et al. 2019). This method has the main advantage of allowing the experimenters to control for the effects of differences in size and motivation between opponents on the aggressive response of the focal male since the mirror image exhibits the same size and motivation of the male in this study. We measured the aggressive response of the same individual in two different contexts by the introduction of a small mirror (15 × 15 cm) into the arena. The first experimental treatment was conducted in the enclosure where the lizard had been acclimated, which was assumed to be a familiar context within its own territory (hereafter, "home" treatment). The second treatment was conducted in a new clean enclosure with the same size and setting as that of the familiar home treatment, but into which the lizard was moved only 15 min before the trial. This second treatment was assumed to be an unfamiliar context outside its own territory (hereafter, "neutral" treatment). Before starting the trial, we first put a partition dividing the arena into two halves, and placed the mirror at the far end of the half without the lizard. After a 5-min period to allow the lizard to habituate to disturbance, we removed the partition, thereby allowing the lizard to interact with the mirror. The fact that the mirror reflects the same color morph of the male is not problematic. In a parallel study involving the manipulation of throat color, we found that males deliver the highest magnitude response towards their mirror image when painted with their own color, and no significant difference occurred in the peak response among morphs (Scali et al. 2020). To avoid visual disturbance during the trials, the four sides of the arena were externally covered by opaque, white plastic panels. Before each trial, the male was heated for two minutes using a 75 W halogen infra-red lamp (Reptiles-Planet.com) positioned 40 cm above the arena. After switching off the lamp, the mean (± SD) body temperature of males just before starting the trial (measured with a handheld infra-red thermometer Lafayette TRP-39, Lafayette Instrument Co., Lafayette, Indiana, USA; sensitivity: 0.1 °C; precision: ± 2%) was 38.4 ± 1.9 °C. After removing the partition, the movements of the lizard were recorded using a webcam (Microsoft LifeCam HD 3000) mounted on an easel, 60 cm above the arena, and connected to a laptop by a 3 m cable. Recording was managed by Free2X software v1.0.0.1 (freely available at: http://www.free2x.com/webcam-recorder/), setting quality to 800 × 600 pixels and 15 frames per second (fps). Recording duration was set to 20 min (18,000 frames) after the first movement of the male. Room temperature was set to 28 °C to reduce thermal loss during the trials. Trials took place between 10:00 and 14:00. Each lizard took part in two trials (home and neutral treatments) on two subsequent days (one trial per day), and we randomized the first treatment in a way that half of the males was initially tested with the home treatment, and half with the neutral treatment. We repeated a trial the subsequent day if the lizard did not move after 10 min from the start. Overall, we performed 127 trials between 24th April and 29th June, and on average (± SD) each individual was tested 2.1 ± 0.4 times (range 2–4).

Response variables

We used BORIS (Friard and Gamba 2016) to analyse video files and extract four response variables. We used the first three variables to assess aggressive behavior as (i) the time (seconds) spent in the half of the arena containing the mirror (Time), (ii) the number of times the lizard entered the half of the arena containing the mirror (Nmirror), and (iii) the total number of bites against the mirror image (Bites). The variables can be interpreted as increasing levels in a rank of aggression from a low/moderate interest for the mirror image (Time and Nmirror) up to the open aggression against it (i.e., Bites). In detail, Nmirror measures the frequency the male approaches the "rival", irrespective of the duration of the interaction. Time was used as a proxy for the intensity of those approaches (as a sort of level of threat of the interactions): the higher the Time, the lower the mean distance of the male from the opponent. The fourth variable was the number of tongue flicks (TF) measured in the half of the arena containing the mirror. TF are used by lizards to collect chemicals from the environment and can be regarded as a proxy for the interest of an individual for an external stimulus (Cooper 1991, 1994). TF is not related to aggressive displays (Greenberg 1993), and we used it as a control for the occurrence of any effect of the experimental treatment on the lizard's behaviours other than the aggressive response. For simplicity, we hereafter refer to Bites, Time and Nmirror as forms of "aggressive behavior", and to TF as "exploratory behavior". All response variables achieved normality (Bites required a log-transformation), and all showed low intercorrelations (Pearson correlation coefficient $|r_{\text{Pearson}}| < 0.54$).

Statistical analyses

To examine if lizards responded differently to the experimental treatment, we used random intercept linear mixed models (LMM), one for each response variable. Fixed effects were the treatment (home vs neutral), the morph, and the trial (first vs second) to account for the sequence of stimulation. All the two-way interactions were added to account for possible differential effect of treatment due to the sequence of the trials and morphs. We also added, as fixed effect, SVL, temperature and date (Julian date) to control for possible confounding effect due to individual size, temperature in the arena and season. These three variables were standardized by subtracting the mean and dividing by the standard deviation. The individual entered the model as random effect. LMMs were fit in a Bayesian analytical framework available in the package JAGS 4.3.0 (http://mcmc-jags.sourceforge.net/), using flat priors for coefficients and intercept ($\mu = 0$ and $\sigma = 0.001$), and uninformative half-Cauchy priors ($x_0 = 0$, $\gamma = 25$) for both σ^2_{error} and $\sigma^2_{\text{individual}}$. For all models, Markov Chain Monte Carlo parameters were set as follows: number of independent chains = three; number of iterations = 34,000; burning = 4000; thinning = three. We checked convergence through trace plot and autocorrelation along chains and results from the posterior distribution are reported as the half sample mode (HSM, Bickel and Frühwirth 2006) with 95% and 50% highest density intervals (HDI_{95}, Kruschke 2010). In Bayesian statistics, the HSM is a commonly used estimator of the central tendency of posterior probability distribution robust to outliers, whereas the HDI_{95} defines the interval that includes the parameter with 95% probability. That is because the posterior probability distribution represents the actual parameter value, given the data, and the HDI_{95} is constructed so that it contains 95% of this distribution. Parameter values in the center of the HDI tend to have higher credibility than parameter values at the limits. Therefore, when the HDIs of two groups do not overlap, there is a credible evidence for different group means. By contrast, to the extent the two groups' HDIs overlap there is evidence of no credible difference between the means. All analyses were done in R 3.6.1 (R Core Team 2019) using the packages R2jags (Su and Yajima 2015), modest (Poncet 2012), and HDInterval (Meredith and Kruschke 2018).

Results

In all trials males crossed into the side of the enclosure with the mirror (Nmirror range: 1–24), and in 75 cases (62.5%) they actually attempted to bite the mirror image. Overall, there was substantial variation by lizards in the time spent in the half of the arena with the mirror (618 ± 25 s, range: 33–1192, Table S1 for raw data). In the neutral treatment, males spent less time in front of the mirror (Time) and bit the mirror fewer times (Bites) than they did in the home treatment. Conversely, they increased the number of times they went into the arena half with the mirror (Nmirror) (Table 1, Fig. 1), with some differences depending on morphs, and the order of treatments (Fig. 1). In contrast, the number of tongue flicks did not vary according to treatment, morphs or order of stimulation (Table 1, Fig. 1). In all cases,

Table 1 Posterior distributions of the four response variables as estimated by LMMs. HSM and HDI_{95} estimates are shown

Covariates	Behavioural response			
	Time	Nmirror	Bites	TF
SVL	1.0 (-43, 44)	-0.8 (-1.7, 0)	-0.1 (-0.4, 0.2)	3.5 (-8.6, 15.5)
Day	22 (-22, 69)	-0.2 (-1.1, 0.7)	-0.1 (-0.4, 0.2)	2.9 (-9.6, 15.4)
Temperature	-22 (-61, 18)	-0.1 (-0.8, 0.7)	0.1 (-0.1, 0.4)	-0.3 (-10.6, 10.1)

Time time in seconds spent in the half arena containing the mirror; *Nmirror* the number of times the lizard entered the half of the arena containing the mirror, *Bites* the total number of bites against the mirror image (log-transformed, see text for details), and *TF* the number of tongue flicks in the half of the arena containing the mirror

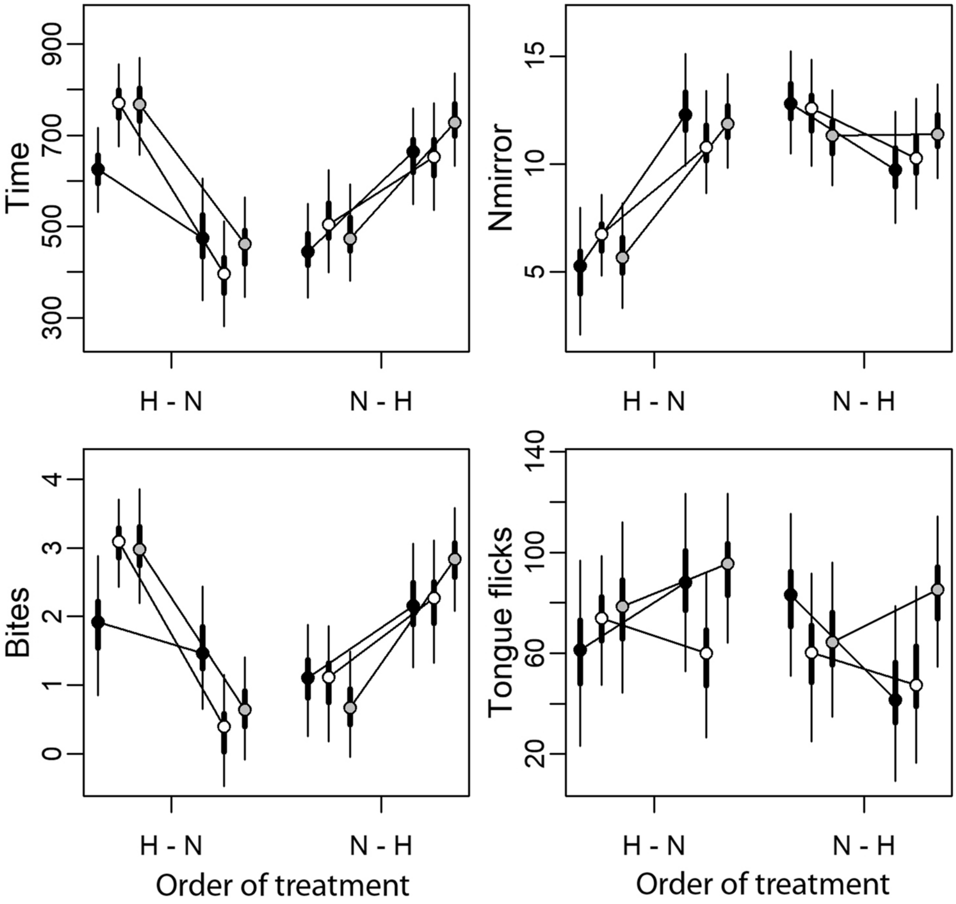

Fig. 1 Bayesian model predictions for the aggressive and exploratory responses of common wall lizards in home (H) vs neutral (N) arenas according to morph (*white*, *gray and black circles* are for white, yellow and red morphs, respectively) and experimental sequence. *Time* time in seconds spent in the half arena containing the mirror; *Nmirror* the number of times the lizard entered the half of the arena containing the mirror; *Bites* the total number of bites against the mirror image (log-transformed, see text for details); *TF* the number of tongue flicks in the half of the arena containing the mirror. *Circles* indicate HSM, and *thick and thin lines* represent HDI$_{50}$ and HDI$_{95}$, respectively

no relevant effects were detected for body size (SVL), body temperature, or date of the trial (Table 1).

With respect to Time, the response was similar among morphs, and independent of the order in which we presented the treatments to males (Fig. 1). Indeed, males of all morphs spent more time in the half with the mirror in the home than in the neutral contest in both stimulation order (Fig. 1, Table 2), whereas each morph performed similarly within treatment independently of the orders of stimulation (Fig. 1, Table 3). Nevertheless, red males in the home contest spent less time in front of the mirror than both yellow and white males, but only in the home–neutral order of stimulation (Fig. 1, Table 4).

The order in which males were tested clearly predicted the number of times they entered the half of the arena hosting the mirror. Nmirror almost doubled in all three morphs when switching from home to neutral contests (Table 2), whereas no differences were found with the reverse sequence (Table 2). Furthermore, morphs performed similarly irrespective of both contests and order of stimulation (Table 3). Consequently, in the home arena trials males exhibited a higher response if done as the second trial, whereas in the

Table 2 Posterior distributions for the difference among the response variables estimated in home and neutral contests for each male morph according to the order (in brackets beside the treatment)

Variable	Home (first)–neutral (second)			Neutral (first)–home (second)		
	Red	White	Yellow	Red	White	Yellow
Time	**-153.5** (-295, -13)	**-373.8** (-516, -222)	**-310.6** (-465, -145)	**208.3** (76, 339)	**142.9** (-27, 310)	**251.1** (102, 404)
Nmirror	**7.5** (3.3, 11.6)	**4.3** (1.2, 7.4)	**6.2** (2.8, 9.6)	-2.9 (-6.5, 0.7)	-1.9 (-5.6, 1.8)	0.3(-2.9, 3.5)
Bites	-0.3 (-1.8, 1.1)	**-2.8** (-3.8, -1.7)	**-2.4** (-3.5, -1.2)	1.1 (-0.1, 2.4)	1.2 (-0.1, 2.4)	**2.1** (1.1, 3.2)
TF	27.7 (-23.4, 79.9)	-14.9 (-56.2, 27.1)	15.4 (-31.3, 60.6)	-38.4 (-85.1, 9)	-6.9 (-58, 42.6)	18.5 (-24.4, 60.9)

HSM and HDI$_{95}$ estimates are shown. Bold values deviate from zero with $p \geq 0.95$. Variable names as in Table 1

Table 3 Posterior distributions for the difference among the response variables estimated in first and second trials (in brackets beside the treatment) in each experimental treatment for each male morph

Variable	Home (first)–home (second)			Neutral (first)–neutral (second)		
	Red	White	Yellow	Red	White	Yellow
Time	29.2 (-73, 132)	-113.5 (-235, 14)	-27.2 (-147, 99)	-19.3 (-159, 125)	52.7 (-105, 209)	58.3 (-108, 221)
Nmirror	**4.8** (1.5, 8.1)	**3.7** (0.8, 6.7)	**5.8** (2.9, 8.7)	-0.6 (-3.8, 2.7)	1.9 (-1.7, 5.4)	0.4 (-3.1, 3.9)
Bites	0.3 (-0.8, 1.5)	-0.9 (-1.9, 0.1)	-0.2 (-1.2, 0.8)	-0.9 (-2, 0.2)	0.7 (-0.5, 1.9)	0.4 (-0.8, 1.6)
TF	-16 (-57.3, 26.1)	-21.7 (-61, 17.4)	6.4 (-33.6, 46)	5.4 (-37, 48.9)	24.3 (-23.8, 72.2)	-35 (-82.6, 12.6)

HSM and HDI$_{95}$ estimates are shown. Bold values deviate from zero with $p \geq 0.95$. Variable names as in Table 1

Table 4 Posterior distributions for the difference among morphs for the response variables estimated in each trial within experimental treatment

	Red–white	Red–yellow	White–yellow	Red–white	Red–yellow	White–yellow
	Home (first)			Neutral (second)		
Time	**-140.9** (-248, -35)	**-136.8** (-251, -24)	3.8 (-119, 130)	78.3 (-78, 228)	19.3 (-126, 159)	-59.5 (-203, 87)
Nmirror	-1.6 (-4.9, 1.7)	-0.7 (-4.2, 2.9)	0.9 (-2, 3.8)	1.6 (-1.9, 5)	0.6 (-2.7, 3.8)	-1.0 (-4, 2.1)
Bites	**-1.2** (-2.3, -0.1)	**-1.2** (-2.4, 0.1)	0 (-1, 1)	**1.2** (0.1, 2.4)	0.9 (-0.2, 2)	-0.3 (-1.4, 0.7)
TF	-12.8 (-54.8, 29.2)	-18 (-64.9, 27.9)	-5.1 (-46.1, 35.4)	30 (-15.3, 75)	-5.4 (-48.9, 37)	-35.4 (-76.6, 5.9)
	Neutral (first)			Home (second)		
Time	-64.4 (-201, 72)	-37.6 (-174, 97)	26.3 (-116, 170)	2.1 (-141, 140)	-80.7 (-211, 48)	-82.1 (-226, 62)
Nmirror	0.5 (-2.7, 3.8)	1.6 (-1.5, 4.7)	1.1 (-2, 4.1)	-0.5 (-4, 2.9)	-1.7 (-4.9, 1.6)	-1.1 (-4.2, 2)
Bites	0.0 (-1.1, 1.1)	0.4 (-0.7, 1.4)	0.3 (-0.7, 1.4)	0.0 (-1.2, 1.2)	-0.7 (-1.8, 0.5)	-0.6 (-1.7, 0.4)
TF	24.2 (-19.3, 67.3)	16.9 (-25.7, 58.3)	-7.4 (-49.8, 34.5)	-7.3 (-53.9, 39.2)	-40.1 (-83.4, 2.7)	-32.8 (-76.2, 9.5)

The order of the treatment is shown in brackets. HSM and HDI$_{95}$ estimates are shown. Bold values deviate from zero with $p \geq 0.95$. Variable names as in Table 1

neutral contest no difference occurred between tests performed as first and second trials (Table 4, Fig. 1).

The number of bites to the mirror image decreased when switching from the home to the neutral contest irrespective of the order of presentation, and this effect was more/mostly evident in the yellow and white morphs (Table 2, Fig. 1). Indeed, red males assigned to the home–neutral treatment did not perform differently between first and second trials (Table 3), and performed fewer bites than both yellow and white males in the home contest, but more bites than white males in the neutral one (Table 4, Fig. 1).

Contrary to the aggressive-related variables, the posterior distributions of the number of tongue flicks largely overlapped among males, independently of the experimental contests (Table 2), the order in which the treatments were done (Table 3), and male morph (Table 4).

Finally, we found a relevant effect of the $\sigma^2_{\text{individual}}$ after controlling for the fixed effects, in all the response variables, suggesting the occurrence of an individual variability in both aggressive and exploratory behavior independent of morph and experimental treatment (Fig. 2). Such inter-individual variation accounted for at least 35% of the unexplained residual variance (HSM and HDI$_{50}$, Time: 40%, 1–47%, Nmirror: 35%, 4–48%; Bites: 38%, 6–51%; TF: 38%, 6–52%).

Discussion

The main aim of our study was to test if lizards escalate in a combat when their subjective RV is higher, after controlling for asymmetries in RHP and objective RV between the two opponents. By measuring the aggressive behavior in two opposite contexts, we clearly showed that lizards displayed a more intense aggression, and for a much longer time, when fighting for the territory of which they had a prior knowledge rather than for the territory not previously explored. Indeed, when switching from the neutral to the home arena, the interactions with the mirror image become longer and they involved a larger number of bites. A similar change in the exploratory behavior (i.e., the frequency of tongue flicks) did not occur, indicating that the shift observed for the aggressive behavior did not result from the experimental setting alone. Given that (i) the mirror removes any asymmetry in RHP between opponents, and (ii) the enclosures were identical (i.e., had the same objective RV), the only difference between the home and neutral trials was the subject's prior knowledge of the arena. So, we can conclude that the observed change in male aggressive behavior arose from a different subjective perception

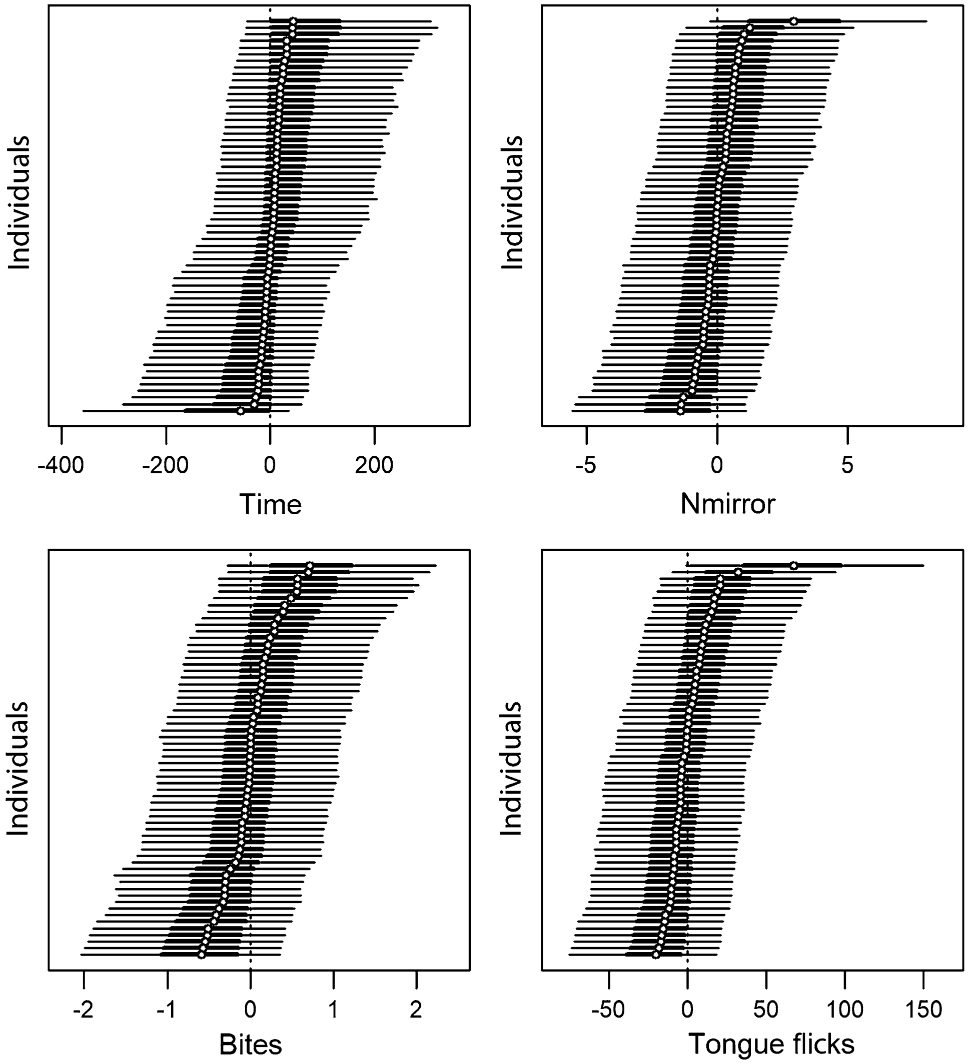

Fig. 2 Bayesian model predictions for the among-individual variation in aggressive and exploratory responses of common wall lizards. Variables as in Fig. 1. Each bar indicates each individual. *Circles* indicate HSM, and *thick and thin lines* represent HDI_{50} and HDI_{95}, respectively

that individuals have about the value of the contested resource. In other words, our data support the occurrence of a direct, positive correlation between motivation and aggression in this species. Motivation was already known to affect the contest outcome in common wall lizards (Sacchi et al. 2009), as well as in other lizard species (e.g., Stuart-Fox and Johnston 2005; Aragón et al. 2006; Carazo et al. 2008; Quintana and Gladino 2017). However, no previous studies have detected a direct correlation between subjective RV and aggression and its potential effects on the resolution of conflicts for indivisible resources. Indeed, there is general agreement that motivation in lizards can help males to overcome inferior RHP in conflicts due to residence advantage (Sacchi et al. 2009), winner–loser effect (Hsu et al. 2006) or dear–enemy effect (Carazo et al. 2008; Quintana and Gladino 2017). Unfortunately, the mechanisms which lead an individual to win over a superior opponent (in terms of RHP) have not been deeply examined yet, and the interaction between subjective RV and aggression could help us understand them.

Aggressiveness is a trait that affects the chances of winning a contest, but in a different way compared to RHP. The readiness of an individual to escalate (or to dare to escalate) during an encounter depends on an individuals' personality rather than on an individual's properties, and it is measured when the conflict is otherwise symmetrical (Barlow et al. 1986). Aggressiveness may have an even greater effect on individual fitness than RHP or RV, because willingness to escalate during an aggressive interaction may be more important in securing a territory than the ability of winning (Stamps and Krishnan 1994, 1998; Hurd 2006). In most animals, and even in common wall lizards, encounters strongly escalate when males are of similar size (Sacchi et al. 2009); in this situation, the more aggressive individual of the two opponents will increase its own possibility of winning the contest. Assuming a direct relationship between aggressive behavior and aggressiveness, the correlation between motivation and aggressiveness is likely to be the cause for the residency advantage, which was previously observed in common wall lizards. Indeed, smaller resident males are able to win when fighting with a larger intruder three times more frequently than smaller intruders fighting with a larger resident (Sacchi et al. 2009).

A second relevant result from this study was the high inter-individual variation in all variables related either to aggressive or exploratory behavior, as more than a third of the unexplained variance was associated with an individual's identity. In particular, this result suggests that aggressive behaviour varies among individual regardless of contest, supporting the idea that the inclination to attack a rival is related to aggressiveness, and ultimately the personality of each individual (Barlow et al. 1986). This result has important consequences on the general framework of assessment strategies and combat rules, as asymmetries in aggressiveness can arise independently of the opponents' motivation, as a result of differences in their personalities, and not because of a different subjective RV. On the other hand, higher motivation cannot always overcome inferior RHP if associated with a timid personality, or, at the exact opposite, an individual with lower motivation but a bold personality can still allow an individual to win if facing a shy opponent. In nearly 10% of asymmetric resident-intruder encounters of common wall lizard males, smaller intruders were able to win the contest against larger residents, when the differences in body size between contestants did not exceed 3.3% of the resident SVL (Sacchi et al. 2009). This outcome is not easily explicable only in connection to RHP and subjective RV asymmetries but becomes clearer if individuality of aggressiveness is accounted for. Indeed, the most plausible explanation is that successful intruders were individuals with a very aggressive personality, which were able to compensate for the greater motivation of the (larger) resident, given that the RHP asymmetries were not decisive for the outcome of the fight.

Game theory models suggest that aggressiveness may be more important than the ability to win fights in some species (Barlow et al. 1986; Maynard-Smith and Harper 1988), but simple strategic models of escalation have been criticized for attempts to empirically separate aggressiveness and variation in subjective RV because variation in aggressiveness may actually reflect long-term variation in subjective RV (Hurd 2006). This occurs because strategic models use the differences in payoff to predict the shift from threat display to fighting behavior, whereas aggressiveness does not affect the payoff (Hurd 2006). Consequently, the only way aggressiveness may affect the decision of escalating during a contest is when threatening and fighting have exactly the same payoff (Hurd 2006). In this paper, we were able to separate aggressiveness from subjective RV by modelling the first as a random effect and the second as a fixed effect in a linear mixed model. So, we found that if the subjective RV increases, the same occurs for the aggressive behavior and focal individuals escalate to fight as predicted by game theoretical models (Enquist et al. 1985). Simultaneously, we found that individuals significantly varied among one another for the basal level of the intensity of the aggressive display independently of the subjective RV, since the random effect actually compares the means of the response in the two contests among individuals. In other words, we separated the amount of the variability in the aggressive behavior due to the subjective RV from that due to the individuals (i.e., the aggressiveness). Nevertheless, measuring the aggressive response toward a mirror image does not allow us to measure a payoff because it is not possible to assess who is the winner, or, perhaps, the only possible outcome for the contestants is losing. This does not allow a reliable measure of benefits and costs for the contestants, and therefore the ability to model alternative strategies in terms of payoffs as in game theoretical models. Consequently, a measure of aggressive behavior using mirrors should not be able to disentangle the effects of either of RHP, RV, or aggressiveness from the others.

We did not find any evidence that throat and ventral coloration was related to male aggressive behavior despite the slight deviation of red males with respect to both white and yellow males for the time spent in front of the mirror and the number of bites to the mirror image. However, this difference appeared only in the group of males in which the sequence of stimulation was home–neutral, whereas no deviation among morphs occurred in the group stimulated with the neutral–home sequence. Thus, there was not enough difference to support the occurrence of a morph specific variation in the aggressiveness. Given the wide range of inter-individual variation in aggressiveness, it is rather more likely that the observed differences of the red morph might have been caused by a prevalence of shy individuals rather than any variability in aggressiveness on the basis of color morphs per se. Previous studies support a lack of correlation between morphs and aggressiveness. Sacchi et al. (2009) did not find any relationship between contest outcome and color morph in asymmetric resident–intruder encounters but did find a strong effect of asymmetries in RHP and motivation. Abalos et al. (2016) found that the ventral black patches emerged as a good predictor of contest outcome independently of morphs in pairwise contests in neutral arenas, even if red males lost fights against heteromorphic males more often than yellow or white males. However, this effect could be due to a correlation with the size of black patches. The plasma concentration of testosterone also did not differ among morphs (Sacchi et al. 2017), but only on the basis of the season. As a whole, these data do not support the hypothesis that aggressiveness varies among morphs.

There is increasing evidence that individuals do not use a unique assessment strategy during dyadic encounters, as has long been thought, but instead that assessment strategies can vary among individuals within populations and also within individuals during a conflict (Chapin et al. 2019). This is because the two opponents may not have the same source of information (Briffa and Elwood 2004; Arnott and Elwood 2009), may have different prior experience or knowledge (Briffa and Lane 2017; Camerlink et al. 2016), or may be differently influenced by external factors such as the distribution of resources, population demography, quality of information, ontogeny, and the expectation of future reproductive success (Chapin et al. 2019). The results of the present study show that assessment strategies for the resolution of animal contests in the common wall lizard can be very complex and combine characteristics at the species level, such as signals conveying information about RHP, with traits intrinsic to each individual, such as motivation and personality. More generally, we can say that our data show that one of three components involved in the resolution of dyadic conflict, the aggressiveness, varies from individual to individual, being a trait of individual personality. Interconnections between aggressiveness, motivation and personality have never been considered in the assessment strategies of dyadic encounters, probably because they are harder to model or because they act on a more hidden level than RHP or RV, but should attract much more attention as they represent the main source of variability in the process that leads an individual to choose to fight or retreat in a contest for an indivisible resource.

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