

Male–Male Combats in a Polymorphic Lizard: Residency and Size, but not Color, Affect Fighting Rules and Contest Outcome

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Theoretical models predict that the outcome of dyadic agonistic encounters between males is influenced by resource-holding potential, resource value, and intrinsic aggressiveness of contestants. Moreover, in territorial disputes residents enjoy a further obvious competitive advantage from the residency itself, owing to the intimate familiarity with their territory. Costs of physical combats are, however, dramatically high in many instances. Thus, signals reliably reflecting fighting ability of the opponents could easily evolve in order to reduce these costs. For example, variation in color morph in polymorphic species has been associated with dominance in several case studies. In this study, we staged asymmetric resident-intruder encounters in males of the common wall lizard *Podarcis muralis*, a species showing three discrete morphs (white, yellow, and red) to investigate the effects of asymmetries in color morph, residency, and size between contestants on the outcome of territorial contests. We collected aggression data by presenting each resident male with three intruders of different color morph, in three consecutive tests conducted in different days, and videotaping their interactions. The results showed that simple rules such as residency and body size differences could determine the outcome of agonistic interactions: residents were more aggressive than intruders, and larger males were competitively superior to smaller males. However, we did not find any effect of color on male aggression or fighting success, suggesting that color polymorphism in this species is not a signal of status or fighting ability in intermale conflicts. *Aggr. Behav.* 35:274–283, 2009. © 2009 Wiley-Liss, Inc.

Keywords: color morph; body size; contest outcome; fighting rule; residence asymmetry; RHP

INTRODUCTION

Size and previous experience are considered as the primary predictors of dominance during agonistic interactions between animals [reviewed in Alcock and Huston, 1996; Hsu et al., 2006; Huntingford and Turner, 1987]; however, there is increasing evidence that conventional signals [Guilford and Dawkins, 1995], such as colored body parts may significantly affect dominance relationships, influencing the outcome of territorial contests [e.g. Hover, 1985; Lank et al., 1995; Pryke et al., 2002; Sinervo and Lively, 1996]. In fact, an active territorial defense may be extremely costly, because of time and energy expenditure in patrolling the territory and fighting with rivals [Hack, 1997; Marler et al., 1995; Vehrencamp et al., 1989], increased the risk of injuries and mortality [Dufty, 1989; Marler and Moore, 1988], increased predation risk [Lange and Leimar, 2001; Tuttle and Ryan, 1981], and increased the risk of cuckoldry

[Sinervo and Lively, 1996]. Therefore, natural selection should favor the evolution of signals and behaviors that reduce these costs, thus maximizing the net benefits of maintaining the exclusive access to an area while minimizing the costs of excluding conspecifics [Maynard-Smith and Parker, 1973]. In some cases, animals may evolve distinct morphs that differ in fighting ability (level of aggression), which is phenotypically, honestly displayed in signals such as color badges, or is mediated via ritualized behaviors [Healey et al., 2007]. Indeed, agonistic contests frequently involve impressive visual and/or acoustic

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signals, used by competing males to intimidate and reliably inform the opponent about their fighting ability and motivation to escalate in a physical combat [e.g. Huntingford and Turner, 1987; Jablonski and Matyjasiak, 1997].

Among visual displays used in agonistic encounters, the exhibition of brightly colored body parts or patches has been shown to peacefully resolve contests among rivals in a number of species of different taxa [insects: Ahnesjö and Forsman, 2003; fishes: Hooper et al., 2006; Hutchings and Myers, 1994; Pryke and Griffith, 2006; Pryke et al., 2002; reptiles: Hover, 1985; Sinervo and Lively, 1996; Thompson and Moore, 1991a, b; birds: Lank et al., 1995; Tuttle, 2003]. In fact, such visual signals may correlate with individual physical attributes or status, and, being often condition-dependent traits, they may reveal the general health of rivals, thus determining the outcome of the agonistic interaction irrespective of other asymmetries between opponents [Baube, 1997; Maynard-Smith and Harper, 2003; Olsson, 1994; Pryke and Griffith, 2006; Pryke et al., 2002; Thompson and Moore, 1991a].

Most asymmetries influencing the outcome of a contest originate from: (a) the subjective evaluation of resources by each contestant [the resource value, RV; Parker, 1974; Maynard-Smith and Parker, 1976], (b) the competitive ability of an individual in retaining or acquiring resources [the resource-holding potential, RHP; Hammerstein, 1981; Maynard-Smith and Parker, 1976; Parker, 1974], which mainly depends on body size and weapons [reviewed in Alcock and Huston, 1996; Huntingford and Turner, 1987], and (c) the individual aggressiveness, which is the intrinsic tendency to escalate a contest independently of RHP and RV [Barlow et al., 1986; Hurd, 2006; Maynard-Smith and Harper, 1988]. In addition, residency status often confers an advantage in contests over intruders of similar RHP, because the territory owner (the resident male) has an accurate knowledge of the territory value, whereas the intruding male has no information on the RV. Thus, in territorial contests, resident individuals may win because, having a great familiarity with the physical and social environment, they are more motivated to escalate the combat than intruders [Holberton et al., 1990; Kemp and Wiklund, 2004; Moretz, 2003; Stamps and Krishnan, 1994; Stuart-Fox and Johnston, 2005; Temeles, 1994]. Finally, prior fighting experience could influence the outcome of subsequent agonistic interactions by altering the estimated fighting ability of an individual, i.e. males that succeed in their first contest are more likely to win subsequent contests

irrespective of opponent's RHP because winning experiences would raise (and losing experiences would lower) an individual's perceived fighting ability [the so-called "winner-loser effect," Hsu et al., 2006; Mesterton-Gibbons and Dugatkin, 1995].

In some territorial species of lizards color polymorphisms is associated with alternative reproductive/territorial strategies, and the color morph of the opponents may predict the contest outcome, irrespective of other asymmetries in size, residency or prior experience [Hover, 1985; Sinervo and Lively, 1996; Thompson and Moore, 1991a, b]. For example, green tree lizard males (*Urosaurus ornatus*) are more likely to dominate orange ones, despite the orange morphs being generally larger [Hover, 1985]; orange-throated males of side-blotched lizards (*Uta stansburiana*) are highly aggressive and dominant over the other morphs [Sinervo and Lively, 1996], and red males of the Australian painted dragon (*Ctenophorus pictus*) are more likely to win dyadic contests with yellow males [Healey et al., 2007]. However, in other lizard species the role of color signals in intra-sexual contests is controversial, and coloration appears to influence only the fight outcome between unfamiliar opponents [Stuart-Fox and Johnston, 2005].

This study experimentally investigated the effects of asymmetries in color morph, residency, and body size on the agonistic behavior and the outcome of male-male territorial combats in a polymorphic lacertid lizard, the common wall lizard (*Podarcis muralis*), a small (50–70 mm adult snout-vent length, SVL) diurnal lizard of central and southeastern Europe. In this species, body size affects territorial behavior, large males being highly aggressive and defending long-term territories, whereas small males are subordinate and may be both nonterritorial and territorial [Edsman, 1990]. In this latter case, small individuals defend small territories settled in the space left open by larger males [Edsman, 1990; Sacchi and Scali, unpublished data]. Individuals of both sexes exhibit three discrete color morphs (white, yellow, and red) differing in throat and belly coloration [Cheylan, 1988; Sacchi et al., 2007a]. This coloration develops after the second year of life, is permanent throughout life, and does not show any seasonal variation [Cheylan, 1988; Scali and Sacchi, unpublished data]. Morph relative frequency is highly variable among populations, the white morph being generally more frequent, although populations where red and yellow morphs prevail are not uncommon [Sacchi et al., 2007b]. To date, the adaptive function of color polymorphism is unknown in this species, but it may likely involve status signaling or fighting ability and intrinsic aggressiveness of the bearer.

In this paper, we staged dyadic encounters between wall lizard males in order to assess: (1) whether color morph and body size affect the outcome of agonistic interactions; (2) whether the residence condition confers an advantage in combats to individuals irrespective of other physical attributes, and (3) what fighting rules were adopted by contestants during the agonistic encounters.

METHODS

Subjects and Housing Conditions

We captured 33 adult male lizards by noosing [SVL, > 50 mm, Barbault and Mou, 1986] at several locations in the surroundings of Pavia (Northern Italy), during May–June 2006. The SVL of each individual was measured to the nearest 0.5 mm; males were weighed (to the nearest 0.1 g) and classified as white, yellow, or red according to their throat coloration [see Sacchi et al. 2007a for a picture of the three morphs]. Males were housed individually in outdoor plastic cages (60 × 50 × 50 cm) containing soil mixed with small stones as substrate and a single brick as shelter. We provided mealworms dusted with a multivitamin powder as food and water *ad libitum*; two crickets were also supplied to each individual every 2 weeks. All lizards were maintained and fed for at least 3 weeks before staged encounters, and released in their capture sites at the end of the experiment. Before release, we again weighed a subsample of individuals, and found that all of them maintained their original body mass (paired-samples *t*-test: $t_{14} = 6.8 \times 10^{-15}$, $P = 1.0$, $n = 15$).

Experimental Setting

We formed 11 groups of three males (“triads” hereafter), by randomly choosing one male of each color morph among individuals from the same collection site. Mean SVL was 67.1 mm (range: 61.2–71.5 mm) and mean body mass was 7.5 g (range 6.4–9.1 g) in white-throated males, 66.6 mm (range = 60.7–73.2 mm) and 7.0 g (range = 5.4–8.8 g) in yellow-throated males, and 66.9 mm (range = 60.6–72.9 mm) and 7.2 g (5.8–8.9 g) in red-throated males, with no significant differences among morphs in either SVL or body mass ($F_{2,33} = 0.46$, $P = .95$ and $F_{2,33} = 0.21$, $P = .81$, respectively). As body mass and SVL were strongly related in all morphs ($r > .78$, $P < .005$ in all three groups), and body mass could vary according to the amount of food eaten before capture, we used SVL as a measure of body size. Mean size difference between males within a given triad was 5.8% of SVL (range = 0.2–15.2%), and between pairs of contestants

was on average $3.8 \text{ mm} \pm 0.29$ standard error (SE) (range = 0.1–10.8 mm).

We staged asymmetric encounters between pairs of triads, where each male of the first triad (the intruding triad) was introduced into the cage of each male of the second triad (the resident triad). Trials were conducted during three consecutive days, where each male of the resident triad was subjected to an intrusion by one male of the intruding triad every day. Males belonging to different triads within each pair originated from different sites, thus excluding any confounding effect of previous territorial encounters between them. By this design, we tried to mimic the natural field situation where one resident male detects an unknown conspecific intruder within his own home range, and we tested all possible combinations of color morphs in a balanced design. In short, the males of each triad acted first as residents (three days) and then as intruders (the following three days), with the only exception of the males of the first triad, which acted only as intruders, and those of the final triad, which acted only as residents. Importantly, this experimental design assured that no males encountered the same rival more than once.

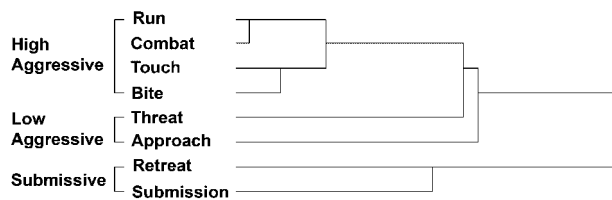
All experiments were conducted outdoor from 5 June to 2 July on sunny days between 10.00 and 14.30 hr, when the animals are naturally active and with air temperature ranging from 20.5 to 31.5°C. Briefly, we gently took the male lizard acting as intruder from his cage and placed it in a 15 cm pipe (diameter 1.5 cm) provided with a removable gate at one end. The pipe was cautiously inserted into the cage of the resident male through a small hole, and the gate was then opened, allowing the intruder to freely enter the cage, thus mimicking a natural intrusion. The trial started when the intruder and the resident were visually in contact with each other. All trials lasted 15 min and all behaviors displayed by the two contestants were videotaped with a Sony DCR-TRV25E digital camera. To reduce the risk of injuries during encounters, animals were separated and the trial stopped if one opponent suffered persistent attacks or was clasped and blocked for long time by the rival. This occurred only in a single trial, which was discarded, but in fact, most trials involved only quick chases with brief combats that did not cause visible injuries to individuals. Overall, we collected data for 85 trials out of 90 performed, because one trial was discarded and four trials failed (i.e. the opponents did not interact).

Measure of Male Aggression

During contests, males adopted a number of behavioral displays (see Table I). We analyzed video

TABLE I. Description of behaviors exhibited by common wall lizard males during staged dyadic encounters

Behaviors	Description
Approach	Male simply approaches his opponent
Threat	Male approaches his opponent with threatening postures
Touch	Male approaches his opponent and touch him without biting
Run after	Male approaches his opponent and runs after him
Bite	Male approaches his opponent and bites him
Physical combat	Males simultaneously seize each other by jaws, reciprocally biting and claspings
Retreat	Male approached by his opponent runs away without facing him
Submission	The approached males swings the tail or scratches the ground with the fore- or hind limbs, without facing the opponent

**Fig. 1.** Dendrogram showing relationships among behavioral displays exhibited by male common wall lizards during dyadic encounters.

recordings of lizard interactions to calculate the frequency of each behavioral display over the total displays exhibited by resident males during each contest, and performed a cluster analysis (between-group linkage method with Pearson correlation matrix) on these frequencies in order to highlight their relationships and classify behaviors accordingly. Based on this analysis, we separated submissive behaviors (retreat and submission) from aggressive behaviors, and split the latter into low-aggressive displays not involving physical contact between opponents (i.e. approach and threat), and high-aggressive displays (Fig. 1). We counted the number of aggressive and submissive displays used by each contestant [see also Lopez and Martin, 2001], and we calculated a synthetic index of response intensity by the resident and the intruder (*aggression score* hereafter) by subtracting the total of submissive displays from the total of aggressive displays adopted by each contestant during a contest.

We used the difference between the aggression scores of the resident and the intruder as a measure of the contest outcome (*contest score* hereafter). Increasingly positive values of contest score denote the success of the resident, whereas negative values denote the victory of the intruder [see also Lopez and Martin, 2001; Martin and Salvador, 1993].

Statistical Analyses

The way resident males used low-aggressive, high-aggressive, and submissive displays in relation to intruder's size was analyzed by means of logistic regression models. In order to account for repeated measures of the same individuals, we selected only the resident males that interacted in all trials ($n = 23$), and performed three separate analyses, one for each trial, with SVL difference between the resident and the intruder as the only predictor, and the frequencies of each kind of display (relative to the total number of displays exhibited during combats) as the dependent variables. Both linear and quadratic models were run, to test for nonlinear variation of behavioral displays in relation to body size.

The aggression scores of both residents and intruders and the contest score were ranked with respect to 0 in order to reduce the influence of a few outlying extreme data points having either very low or very large values. Briefly, the first smallest negative value was assigned a score of -1 , whereas the first smallest positive value was assigned a value of $+1$, and so on. Equal values were assigned the same rank. Ranks were calculated for overall aggression score (including both residents and intruders, $n = 170$), resident aggression score ($n = 85$), intruder aggression score ($n = 85$), and contest outcome separately ($n = 85$). The ranked aggression and contest scores were normally distributed (Kolmogorov-Smirnov tests, all P -values $> .22$).

To investigate the within-subject effect of color morph, residency, and SVL on individual behavior, the aggression scores of the same individuals were analyzed in a mixed model where male identity was the random factor (to account for the repeated testing of the same individuals), and color morph, role in the contest (resident vs. intruder) and trial order were the fixed factors, while SVL and air temperature were included as covariates. The role \times morph and role \times SVL interactions were also included in the initial model. This model was run on a subset of 57 trials involving 19 males for which we obtained aggression scores from all six combats they were involved ($n = 114$ cases). We also run the same model while including date of testing (with day 1 = 1 June) instead of air temperature, which was highly correlated with date ($r = .82$, $n = 57$, $P < .001$), but the results were qualitatively similar and were not reported for brevity.

The between-subjects effects were investigated by analyzing the contest score from all trials ($n = 85$) in a similar mixed model, where resident and intruder male identity were the random factors (to account for the repeated testing of both residents and intruders),

while resident and intruder color morph, and trial order were the fixed factors, and relative SVL difference (resident minus intruder) and air temperature were the covariates. The interaction between resident and intruder color morph was also included in the initial model. This model was run also while including date of testing instead of air temperature (see above), but results were qualitatively unchanged (detail not shown). All models were subjected to a stepdown simplification procedure, where nonsignificant ($P > .05$) terms were removed at each step, starting from the least significant interaction terms, until a minimal adequate model, containing only significant ($P < .05$) terms, was obtained [Crawley, 1993].

Mixed models (REML method) were performed by means of the SPSS software (vers. 15.0.1), whereas logistic models were run by R statistical software [vers. 2.6.1, R Development Core Team, 2007]. Unless otherwise stated, means and parameter estimates are reported through the text together with their associated SEs.

RESULTS

Fighting Rules

The frequency resident males used high-aggressive displays was best predicted by the quadratic term of SVL difference in all trials (Table II). On the other

TABLE II. Logistic regression models on frequencies of low-aggressive, high-aggressive and submissive displays used by common wall lizard males during each trial

Models	β (SE)	Z (P)	LR- χ^2	df	P
FIRST TRIAL					
Low aggressive displays					
(SVL difference)	0.212 (0.032)	6.55 (<.001)	53.61	1	<.001
(SVL difference)+(SVL difference) ²	0.189 (0.036)	5.22 (<.001)			
	0.008 (0.006)	1.07 (.28)	1.050	1	.31
High aggressive displays					
(SVL difference)	0.062 (0.021)	2.97 (.003)	9.100	1	.003
(SVL difference)+(SVL difference) ²	0.071 (0.022)	3.17 (.001)			
	-0.009 (0.004)	2.88 (.028)	5.269	1	.022
Submissive displays					
(SVL difference)	-0.272 (0.034)	7.94 (<.001)	98.05	1	<.001
(SVL difference)+(SVL difference) ²	-0.317 (0.044)	7.12 (<.001)			
	-0.015 (0.006)	2.60 (.009)	6.93	1	.008
SECOND TRIAL					
Low aggressive displays					
(SVL difference)	0.147 (0.044)	3.33 (<.001)	12.201	1	<.001
(SVL difference)+(SVL difference) ²	0.152 (0.037)	4.05 (<.001)			
	0.015 (0.005)	2.87 (.004)	7.212	1	.007
High aggressive displays					
(SVL difference)	0.226 (0.037)	6.05 (<.001)	49.63	1	<.001
(SVL difference)+(SVL difference) ²	0.320 (0.056)	5.72 (<.001)			
	-0.057 (0.011)	5.04 (<.001)	36.49	1	<.001
Submissive displays					
(SVL difference)	-0.454 (0.061)	7.98 (<.001)	114.40	1	<.001
(SVL difference)+(SVL difference) ²	-0.611 (0.100)	6.11 (<.001)			
	-0.027 (0.012)	2.43 (.015)	5.89	1	.015
THIRD TRIAL					
Low aggressive displays					
(SVL difference)	0.212 (0.048)	4.40 (<.001)	25.97	1	<.001
(SVL difference)+(SVL difference) ²	0.217 (0.048)	4.53 (<.001)			
	0.009 (0.008)	1.10 (.27)	1.292	1	.26
High aggressive displays					
(SVL difference)	0.211 (0.035)	5.99 (<.001)	45.21	1	<.001
(SVL difference)+(SVL difference) ²	0.126 (0.051)	2.46 (.014)			
	-0.044 (0.010)	4.33 (<.001)	35.59	1	<.001
Submissive displays					
(SVL difference)	-0.398 (0.044)	8.89 (<.001)	123.82	1	<.001
(SVL difference)+(SVL difference) ²	-0.306 (0.050)	6.05 (<.001)			
	-0.022 (0.009)	2.46 (.014)	4.192	1	.041

The likelihood-ratio test (LR- χ^2) compares model fit with respect to the simpler model (intercept only model for those including only SVL difference, and model including SVL difference for those including the squared term of SVL difference).

hand, the frequency of low-aggressive and submissive displays increased linearly with SVL difference in the first and third trial, whereas in the second trial the increase was nonlinear (Table II). Finally, the frequency of submissive displays decreased nonlinearly with SVL difference in all trials. Therefore, resident males preferentially used low-aggressive displays (i.e. they approached or threatened without any physical contact) more frequently when facing intruders much smaller than them (Fig. 2 top), while high-aggressive displays were mainly performed against size-matched rivals (Fig. 2 middle). On the other hand, residents used only avoidance or submissive displays when facing intruders much larger than them (Fig. 2 bottom); thus, asymmetry in body size determined the fighting rules adopted by resident against intruders: fight strongly against rivals of similar size, display ritually against smaller rivals, submit to or avoid larger rivals. In particular, when analyzing high- and low-aggressive displays separately for both residents and intruders, it emerged that resident lizards, particularly smaller ones, used significantly more high- than low-aggressive displays (all trials pooled, larger residents: $Z = 2.42$, $P = .016$, $n = 36$; smaller residents: $Z = 2.80$, $P = .005$, $n = 20$, Wilcoxon matched-samples test, Fig. 3a), whereas intruder lizards, particularly larger intruders, used low- and

high-aggressive displays with similar frequencies (both $P > .10$, Fig. 3b).

Aggression Score

The mean rank of the aggression score was significantly higher than 0 for resident males (mean rank: 4.32 ± 1.38 , $n = 85$, one sample t -test, $t = 3.13$, $P = .002$), suggesting that resident lizards displayed more aggressive than submissive behaviors against intruders. Similarly, the mean rank of the aggression score by intruders significantly differed from 0 (mean rank: -3.19 ± 1.29 , $n = 85$, one sample t -test, $t = 2.48$, $P = .015$), thus indicating that intruding lizards used more submissive than aggressive displays. The aggression score by a given lizard showed a significant consistency across trials performed as resident as well as across the trials performed as intruder (resident trials, repeatability = .50, $F_{29,55} = 3.85$, $P < .001$; intruder trials, repeatability = .34, $F_{29,55} = 2.52$, $P < .01$).

The mixed model run on the aggression scores of the same males acting first as residents and then as intruders showed, as expected, that residency greatly influenced individual behavior during contests ($F_{1,94} = 17.22$, $P < .0001$, Fig. 4), whereas body size had a minor role, though statistically significant, in determining individual agonistic response ($\beta \pm \text{SE}$: 1.19 ± 0.55 , $F_{1,17} = 4.71$, $P = .044$). Conversely, color

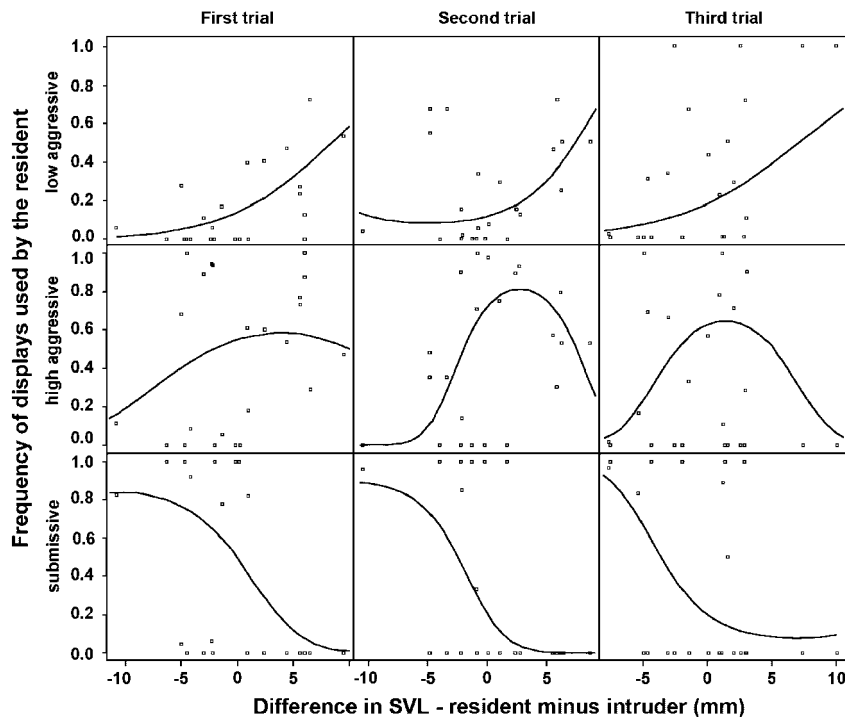


Fig. 2. Relationships between frequency of low-aggressive display (top), high-aggressive displays (middle), submissive display (bottom), and relative SVL difference between contestants in each of three fight trials.

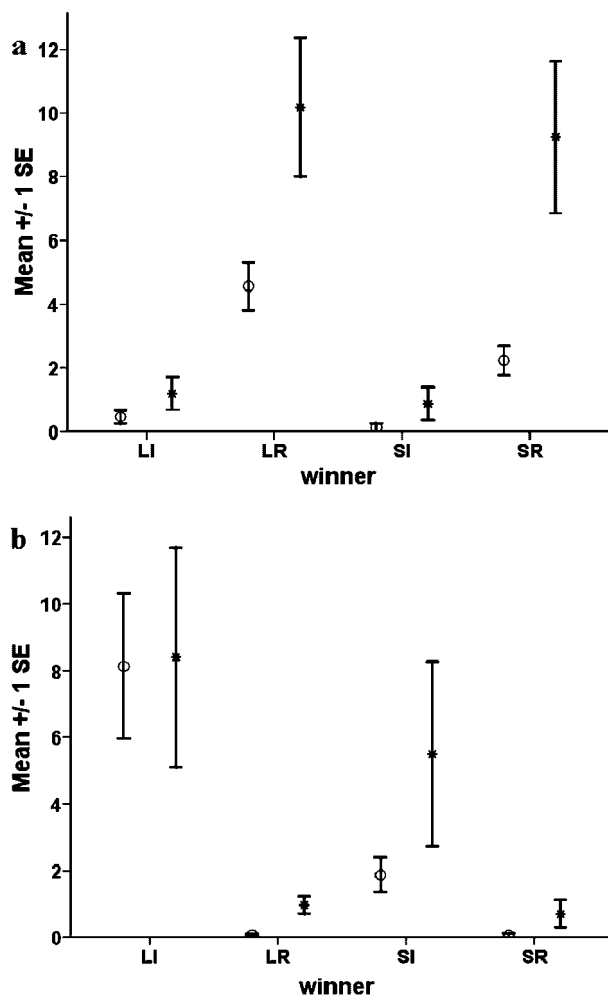


Fig. 3. Mean number of high-aggressive displays (\circ) and low-aggressive displays ($*$) exhibited by resident (a) and intruder lizards (b) in contests won by larger intruders (LI, $n = 19$), larger residents (LR, $n = 36$), smaller intruders (SI, $n = 9$), and smaller residents (SR, $n = 20$) (data from all trials pooled).

morph did not have any effect on the aggression score of males (P at removal $> .65$, Fig. 4), and the interactions were not significant (details not shown). Thus, males exhibited much more aggression when playing the resident role and showed lower aggression when playing the intruder role, but larger males used anyway more aggressive displays than smaller males irrespective of role. The absence of any effect of trial order on aggression score (P -value at removal $> .57$) rules out the possibility that exhaustion may have interfered with the agonistic behavior of the experimental lizards.

Contest Score

The mean difference in aggression scores between residents and intruders, i.e. the mean contest score

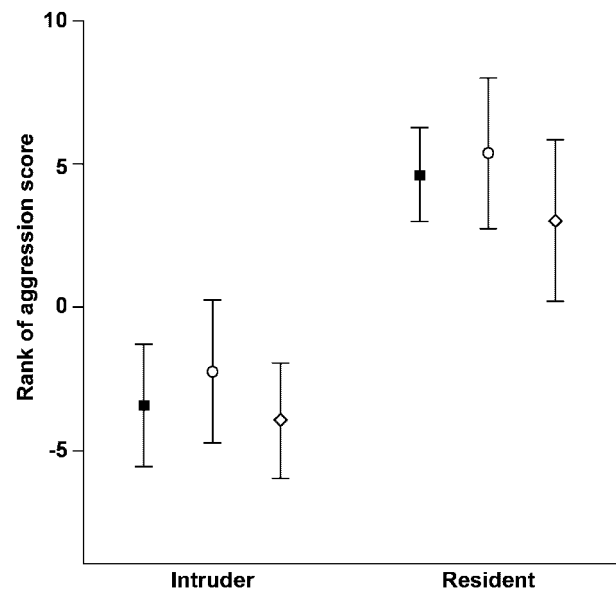


Fig. 4. Effect of residency on aggression score of the same common wall lizard male according to its role in the contest (intruder or resident). Marks on the bars indicate color morph (\blacksquare : red morph, \circ : white morph, \diamond : yellow morph). Means and SE are reported.

across all trials, was significantly greater than 0 (mean ranks: 6.65 ± 1.36 , $n = 85$, one sample t -test, $t = 4.88$, $P < .001$), confirming that resident males won most contests. Across the three trials in which males acted as residents, the contest score was significantly consistent for a given resident (repeatability = .46, $F_{29,55} = 3.49$, $P < .001$).

We could safely establish the contest winning in 84 trials, as in one trial the contest score was 0. In contests where the larger lizards were also the residents, the larger lizards were the winners in 80% (36/45) of the fights, compared with 48.7% (19/39) of successful fights in contests where the larger lizards were the intruders (two-tailed binomial test, $P < .0001$), whereas the smaller lizards won 51.3% (20/39) of the fights when they were the residents, and only 20% (9/45) of fights when they were the intruders (two-tailed binomial test, $P < .0001$). Thus, although a larger body size conferred always an advantage to the bearer irrespective of role, the residence asymmetry favored more the smaller individuals, which nearly tripled their success rate when they were the residents (+156%), than the larger ones, whose success rate increased only by 64% when they were the residents. However, when the smaller resident lizards won the fight, the mean difference in body size between opponents was smaller (2.71 ± 0.36 mm on average) than when the larger resident lizards won (4.53 ± 0.45 mm), and this difference in body size

between opponents further decreased in contests won by the smaller intruder lizards (2.24 ± 0.52 mm). In any case, the residents, either larger or smaller than the opponents, won always with significantly higher scores compared with intruders, either larger or smaller than the opponent (mean contest scores 14.2 and 8.1 for larger residents and larger intruders, respectively; $t = 2.94$, $P = .005$, $n_1 = 36$, $n_2 = 19$; mean contest score of smaller residents and smaller intruders: 12.3 vs. 5.56; $t = 2.77$, $P = .011$, $n_1 = 20$, $n_2 = 9$), indicating that, in the case of an intruder winning, the differences in aggression between contestants were smaller, i.e. residents and intruders behaved in a similar way.

The mixed model including all trials confirmed these results, showing that the contest score increased with increasing relative SVL difference ($\beta \pm \text{SE}$: 0.66 ± 0.30 , $F_{1,80.32} = 4.90$, $P = .030$), i.e. when the difference in body size between contestants was maximal (> 5 mm SVL in favor of either resident or intruder) the contest outcome was clear-cut: the relatively larger individual, either resident or intruder, won the contest outclassing the opponent (Fig. 5). When body difference between contestants decreased (from 5 to 0 mm), the contest score had lower values, indicating that the differences in response intensity between contestants were smaller. Resident male identity accounted for 41% of the variance in the contest score (LR test, $\chi^2 = 11.07$, $\text{df} = 1$, $P < .001$), whereas the intruder male identity variance component could not be reliably estimated and was removed from the final model (details not shown). The effects of color morph of resident or intruder, their interaction, and the other covariates were not significant (all P -values at removal $> .18$). Similarly to previous analyses, trial order did not affect contest score (P -value at removal $> .34$).

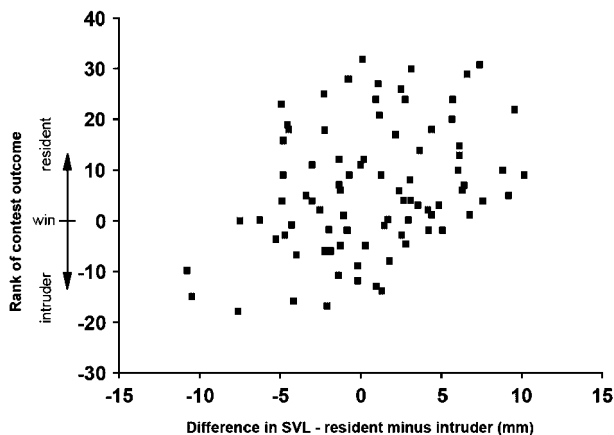


Fig. 5. Effect of relative difference in body size (snout-vent length, SVL) on contest outcome between males of common wall lizards.

DISCUSSION

The results of this experiment showed that the outcome of intermale territorial combats in wall lizards was predicted by the asymmetry in residency and body size between contestants, but not by throat and ventral coloration. In addition, according to the sequential assessment model [Enquist and Leimar, 1983], when body differences between contestants were large, aggression by larger males were mostly ritualized and avoidance or submission behaviors by smaller males frequently occurred, while encounters strongly escalated when males were of similar size.

As expected, residency gave a great advantage to male lizards, as they won most fights when they were acting as residents, although larger males were generally more aggressive than smaller males irrespective of role (resident/intruder). Thus, beside residency, body size appears to play an important role in determining the contest outcome in common wall lizard males, as observed in other lizard species [e.g. Hsu et al., 2006; Huntingford and Turner, 1987]. In fact, the larger the asymmetry in size between opponents, the larger the score obtained by the winner, with larger males dominating over smaller males in most contests irrespective of roles. Under this scenario, submissive displays by smaller males may help reducing the costs of agonistic encounters for these generally subordinate individuals [Aragon et al., 2006]. However, although a larger body size confers always an advantage to the bearer irrespective of role, the residence asymmetry appeared to greatly favor the smaller individuals, which nearly triplicated their success rate in combats when they were acting as residents. Thus, smaller lizards appeared to offset their lower fighting ability, resulting from a smaller body size, when they were residents. However, the greater success rate of small lizards when acting as residents could have been confounded by winner-loser effects [Mesterton-Gibbons and Dugatkin, 1995; Hsu et al., 2006] generated by our experimental setup, implying repeated testing of the same lizards first as residents and then as intruders. In fact, small lizards were more likely to loose contests when acting as residents compared with large lizards, and could have thus been more likely to loose contests when acting as intruders simply because they were negatively affected by their previous loosing experience (i.e. when acting as residents).

Surprisingly, some smaller intruders were also able to win the contest against larger residents, but this happened only when the difference in body size between contestants was very small (2.21 mm, i.e.

3.3% of resident SVL). Body size is by far the most important physical attribute affecting RHP in lizards and other species [Carpenter, 1995; Hsu et al., 2006; Lopez and Martin, 2001; McMann, 1993; Stamps and Krishna, 1994, 1998; Summers and Greenberg, 1994; Tokarz, 1985; Zucker and Murray, 1996], as large individuals have a greater capacity to physically displace smaller opponents or to dominate them, and accordingly, size asymmetry between opponents was a critical factor affecting contest outcome in the common wall lizard too. In fact, combats in this species consist mainly of biting and grasping by jaws, whose strength is strictly correlated with the muscle mass [Lappin et al., 2006]. Hence, body size reliably reflects actual fighting ability of male lizards (i.e. their RHP).

The intensity of interactions between male *P. muralis* could partly be explained by the “sequential assessment model” [Enquist and Leimar, 1983], which would suggest that this species acquires information about fighting ability gradually during the progress of a fight. In our experiment, interactions were more intense when size differences were smaller and, therefore, asymmetries were presumably more difficult to assess by contestants. However, contrary to predictions of the model, contests in wall lizards were not stronger when intruders were larger than residents, and contests were not more intense if won by the intruder than by the owner [Leimar and Enquist, 1984]. This result therefore suggests that the predominant behavioral tactic of resident males would be to escalate the contest irrespective of rival's body size (Fig. 5a), whereas intruders would be more willing to ritualize the fight.

Surprisingly, we did not find any evidence that throat and ventral coloration was related to male aggressive behavior during agonistic interactions, or to the outcome of contests, thus apparently ruling out the hypothesis that throat color signals RHP in common wall lizards. Therefore, color polymorphism in this species does not appear to be maintained by alternative territorial/mating strategies as occurs in other vertebrates, including some lizard species [Lank et al., 1995; Pryke and Griffith, 2006; Sinervo and Lively, 1996; Sinervo and Zamudio, 2001]. For example, in the side-blotched lizard, orange-throated males are dominant and defend larger territories, whereas white-throated males are sneakers and do not defend territories, and morphs differ in size and aggression accordingly [Sinervo and Clobert, 2003; Sinervo and Lively, 1996; Zamudio and Sinervo, 2000]. In the common wall lizard, color morphs do not differ in size [Sacchi et al., 2007b], but only in immune competence, yellow-throated males being immune depressed compared with the other morphs

[Sacchi et al., 2007a]. Therefore, color polymorphism in our species might be maintained by physiological/immunological factors not directly affecting the individual fighting ability.

In conclusion, this study showed that the outcome of male–male contests in the common wall lizard is mainly determined by asymmetries in residency and body size, whereas apparently ventral colorations does not play any role. Our results also provide some support to the sequential assessment model [Enquist and Leimar, 1983], in that male common wall lizards used high-aggressive displays when fighting with a rival of similar size while adopting low-aggressive displays when the difference in body size was large.

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