

Better to be resident, larger or coloured? Experimental analysis on intraspecific aggression in the ruin lizard

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Abstract

Territoriality evolves when the benefits gained from exclusive access to limited resources exceed the costs of defence. Sometimes animals evolve distinct morphs, that may reflect different capability, and in some territorial species of lizards the polymorphism is associated to alternative strategies, both for reproductive efficiency and territorial dominance. It is known that normally larger males are more aggressive and are able to defend a larger area and for longer than small males; in fact this dynamic is widespread in many animal species including the genus *Podarcis*. The aim of our study was to test which factors determine the outcome of fighting in the strongly territorial Italian ruin lizard, *Podarcis siculus*, using two types of contests: (1) resident versus intruder and (2) in a neutral arena. Furthermore, because these lizards are characterized by strong ventral colour variability, usually restricted to jaws and throat, we wanted to investigate if coloured lizards have higher chances at winning than white lizards. The results showed that the fight's result was significantly influenced by the state of residence, while the colour had no effect; instead, the snout to vent length difference between opponents had significant influence on the outcome in the neutral arena. Our results suggest that, in this lizard, both the size and the state of residency, no matter of colour, play an important role to determine the outcome of a fight, however, highly depending on the contest. We think that *P. siculus* should be object of future studies, focusing on behavioural and ecological aspects, even considering the occurrence of different colours within and among populations.

Introduction

Territoriality evolves when the benefits gained from exclusive access to limited resources exceed the costs of defence (Brown, 1964). Territorialism and correlated behaviours are widespread among animals, in invertebrates (Jacobs, 1955; Alcock & Bailey, 1997; Hoefler, 2002) as well as in vertebrates (Beacham, 1988; Fox & Baird, 1992; Forester, Cover & Wisniewski, 1993; Beaugrand, Payette & Goulet, 1996). In aggressive interactions, natural selection should promote the evolution of those signals, behaviours and characteristics that express the right balance between costs and benefits, minimizing the formers and maximizing the latter (Krebs & Davies, 1998). The major underlying assumption of decision-making process is that animals use information conveyed by different signals to weigh the costs and benefits of an action, and maximize the net benefits (Dukas, 1998; Krebs & Davies, 1998; Shettleworth, 1998). Applied to the case of male–male aggressive interactions, the above paradigm predicts that males are able to process information and make decisions during the 'pre-confrontation' stage assuming the relative fighting abilities of opponents (Labra, 2006).

Lizards offer an optimal model for studying the determinants of the outcome of male–male combats as they are strongly territorial, show high aggressive displays during intrasexual interactions and are quite easy to keep in captivity and observe under highly standardized conditions. Several previous studies have addressed aggressive interactions in male lizards. They generally agree in pointing size as the first determinant of combat outcomes (e.g. Tokarz, 1985; Carpenter, 1995), as larger males are usually dominant over smaller ones (Cooper & Vitt, 1987; Olson, 1992; Molina-Borja, Andron-Fumer & Alfonso-Martin, 1998; Sacchi *et al.*, 2009). By avoiding fights with a larger male that presumably is the owner of a territory, an intruding small male may reduce the costs of aggressive interactions (Marler & Moore, 1988, 1989; Marler *et al.*, 1995). By contrast, when the contenders have similar body sizes, the probability that an intruding male wins a fight with a territory owner would be actually low, with the resident male having the highest motivation to the territory defence (Sacchi *et al.*, 2009).

Braddock (1949) coined the term 'prior residence effect' to define this latter phenomenon where territorial residents generally win conflicts with intruders, describing the tendency of resident males to respond more aggressively than intruders.

After its definition, the resident effect has been confirmed in a diverse assemblage of animals ranging from lepidopterans (Davies, 1978) to cichlid fish (Figler & Einhorn, 1983), lungless salamanders (Cupp, 1980; Nunes & Jaeger, 1989) and it frequently occurs also in lizards (e.g. Carpenter, 1995; Aragón, López & Martín, 2006; Sacchi *et al.*, 2009). For example, territorial males react more likely than intruders in escalating aggression to defend their territory (Krebs, 1982; López & Martín, 2001; Aragón *et al.*, 2006). This is because a specific area has a greater value to residents than to intruders because of residents' familiarity with the physical and social environment (Stamps & Krishnan, 1994; Stamps, 1995). In this way, size and residency (or site familiarity) may strictly interact in determining the outcomes of social contests, for example, in lizards (Cooper & Vitt, 1987; Stamps & Krishnan, 1994; López & Martín, 2001; Sacchi *et al.*, 2009).

Colour in lizards is an important pattern in sexual recognition and both intra- and intersexual competition (Bohórquez-Alonso & Molina-Borja, 2014; Klomp *et al.*, 2016). Notably, brilliant colours of the back, throat and vent may determine the fighting outcome (Klomp *et al.*, 2016) by revealing male's quality and fighting ability to the opponent. Furthermore, it has been demonstrated that blue–green colours visible in the UV spectrum still signal healthy, reproductive status (Bajer *et al.*, 2010) and dominance status of the animal (Anderholm *et al.*, 2004; Whiting *et al.*, 2006; Bohórquez-Alonso & Molina-Borja, 2014). This may arise important as determinant during intraspecific aggressions, especially in species keeping condition-dependent colourations.

We analysed the effect of size, residence and colouration in the Italian ruin lizard *Podarcis siculus*, which is widely distributed in most Mediterranean areas of peninsular and insular Italy, coastal Slovenia and northern Croatia. It is a small lacertid lizard, with an average size (snout to vent length, SVL) of 65 mm and 6 g in adult males, smaller in females. Considered aggressive and invasive (Downes & Bauwens, 2002; Mangiacotti *et al.*, 2013), allochthonous in several European and non-European countries (Corti, Biaggini & Capula, 2011), this species is an excellent model for aggressive experiments. In addition, *P. siculus* is quite variable in the dorsal patterns as well as in the throat and ventral colouration (not only white, green, blue, but also orange to red in southern populations; Corti *et al.*, 2011), albeit not showing a true colour polymorphism, as in other *Podarcis* species (e. g., *P. muralis*, Sacchi *et al.*, 2007). The functions of throat and ventral colour variability in this species are totally unknown, so we investigated the possible role of colour in intrasexual aggressive behaviours. Our study aimed to determine the effect of size, residency and throat colour during combats by using two types of contests: (1) resident versus intruder to monitor displays and behaviours in a territoriality scenario and (2) in a neutral arena to monitor displays and behaviours in a scenario without the residence advantage. Our predictions were that larger and resident individuals will win the combats more frequently than smaller and non-resident ones. The only *a priori* hypothesis concerning colour was that green-throated individuals should win combats more frequently if greenness honestly signals male quality (Leal, 1999; Vanhooydonk *et al.*, 2006).

Materials and Methods

Study animals

We captured sexually mature male lizards (SVL > 50 mm, Zuffi, Casu & Marino, 2012) by noosing and pitfall traps in five sites in the surroundings of Pisa, from February–March to July 2015. Overall, we caught 86 individuals; for each lizard, we took snout to vent length (SVL, to the nearest 0.5 mm), body mass (to the nearest 0.5 g) and maxilla–jaw colour coded as green or white. We considered 'green' all those lizards being avowedly not white, ranging from completely green or green–orange, yellow–green, even to green–blue.

Lizard housing and experimental setup

Each male was maintained in terrarium (46 × 29 × 20 cm), setup with shelters, a raised area, water *ad libitum* and food (*Tenebrio molitor* larvae). The heating was ensured using 15 W heating wires, placed under the terraria and with 40 W incandescent lamps with day–night cycle controlled by timer (14:10, May–June photoperiod). Lizards were housed individually for 1 week to let them acclimate and to establish residency and scent mark their cages (Aragón, López & Martín, 2003). Before the test, lizards were placed under lamps for 20 min to reach a proper activity temperature, ranging between 28.5 and 37°C, with an average temperature between 29°C. Temperature was measured with a laser gun thermometer (Lafayette, mod. TRP39, range –50 to 1000°C) with a precision ratio of 50:1 (i.e. from 50 cm distance, the scanned area equals to a 1 cm diameter spot), selecting a spot on the right flank. Encounters with opponents did not result in injuries and all lizards were healthy during trials. At the end of the experiment, they were released at their capture points.

We performed the test in two different experimental contests: (1) resident versus intruder where the intruder was removed from its own terrarium and inserted in the resident's one, covered with a removable glass sheet to allow top view and camera recording; (2) neutral arena, a plexiglass enclosure of 100 × 60 × 60 cm. Each test, recorded with a Nikon P90 camera, lasted 15 min for contest 1 and 20 min for contest 2 (5 min for relax + 15 min for interactions test). Relax time was realized inserting lizards initially into a paper tube (40–50 cm apart from each other), inside the arena (Fig. 1), then removing the tubes allowing animals see each other and the test started. In order to avoid the effect given by the 'dear enemy' and 'nasty neighbours' phenomena (Carazo, Font & Desfilis, 2008), we tested individuals belonging to different and distant populations. Each individual was randomly assigned to pairs, according to colours in order to create a balanced number of heteromorphic and homomorphic dyads for each experimental contest (Table 1).

An individual was submitted to a maximum of three tests, without role's repetition (i.e. one as resident, one as intruder and one in the neutral arena). No lizard was tested more than once a day, nor did any lizard face the same opponent more than once in territorialism contest. We also randomly

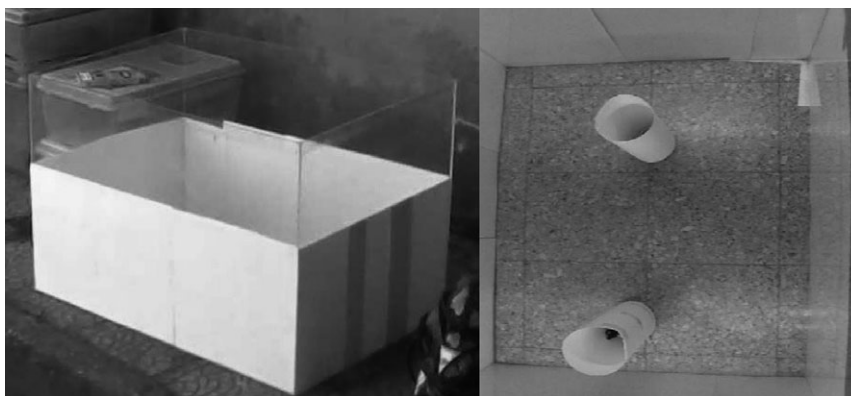


Figure 1 Neutral arena setup.

Table 1 Distribution of heteromorphic and homomorphic dyads for each experimental contest

Colour dyads	Contest 1	Contest 2
WW	12	4
WG	13	8
GW	13	
GG	11	4
Total	49	16

selected the contenders to make size variable as it does in natural populations, with the resident smaller, larger or of similar size than the intruder. The average size of opponents did not vary depending on the role (two samples *t*-test, resident vs. intruder body mass: $t = -0.121$, d.f. = 96, $P = 0.904$, mean difference = -0.1 mm, range -0.7 to 0.6 ; SVL: $t = -0.182$, d.f. = 96, $P = 0.856$, mean difference = 0.2 mm, range -2.2 to 1.8). The arena ground was uncovered (transparent plexiglass), and the vertical walls were lined with sheets of white paper (Fig. 1), thereby preventing the external view in the horizontal plane and thus any possible disturbance; the room lighting was of artificial source, perpendicular to the arena to avoid any directional reference for the experimental animals. In the arena, we placed two reptile star lamps symmetrically on the top of the two shorter sides of the arena. At the end of each trial, the enclosure was carefully washed and cleaned to remove any possible chemical scent. In total we performed 65 tests, 49 resident versus intruder (experimental contest 1) and 16 in neutral arena (experimental contest 2).

Aggressiveness scoring

For the videotape dataset, we used BORIS (Behavioural Observation Research Interactive Software, available at: <http://www.boris.unito.it/>; Friard & Gamba, 2016), setting up the ethogram detailed in Table 2. According to previous literature (Torr & Shine, 1994; Langkilde, Schwarzkopf & Alford, 2003; Huyghe *et al.*, 2005; Sánchez-Hernández, Ramírez-Pinilla & Molina-Borja, 2012), we considered (1) aggressive behaviours,

those as raised posture on all fours legs, buckle back, flank exposure, mouth opening, bites; and (2) subordination behaviours those as tail swing, posture, attempts to escape or seek shelter and the relative time spent in those attempts (Aragón *et al.*, 2003; Carazo *et al.*, 2008; Sacchi *et al.*, 2009). The different amount of time spent in each recorded pattern was coded to assess different levels of aggressiveness, thus defining dominance (D) or subordination (S) patterns for the individuals involved in the tests, for both residence and arena contests (Table 2). We thus obtained a D and S values for each individual. The difference between those values (D-S, dominance-subordination), normalized on the time length of the test (900 s), was used as a score to estimate the differential time spent to show aggression or subordination of an individual towards the opponent. D-S ranges between -1 and 1 : negative scores mean that a lizard spent more time showing subordination than dominance or aggression behaviours; on the contrary, positive scores mean that a lizard spent more time showing dominance or aggression than subordination behaviours. For the couples of lizards tested, the individual that obtained a positive or higher value of D-S was declared the winner (more aggressive), the individual that obtained a negative or lower value of D-S was declared the loser (less aggressive). In addition we used the total number of bites as a proxy for the intensity of the aggressive behaviour irrespective of the combat outcome.

Statistical analyses

Data obtained from territorialism tests were analysed with a linear mixed model (LMM) on IBM® SPSS® version 20.0. We considered D-S difference and number of bites as dependent variables, status (two levels factor, resident or intruder), maxilla-throat colour and their interaction, svl difference (size of resident minus size of intruder, svl_diff) of opponents as predictors, while the individual entered the model as random factor. Data from the neutral arena were analysed using a linear model (LM) considering D-S score as dependent variable, maxilla-throat colour as factor and svl_diff (size of the winner minus the size of the loser) as covariate. All data are expressed as mean \pm 1 SE.

Table 2 Ethogram of *Podarcis siculus* used to code the agonistic interactions

Behaviour	Description	Category
Approaching	One lizard walks directly towards the other.	Dominance/Aggression
Arch neck	The apex of snout is pointed towards the ground, displaying also Gular expansion.	Dominance/Aggression
Bite	One lizard bites the other one.	Dominance/Aggression
Chase	One lizard rapidly follows another FLEEING lizard.	Dominance/Aggression
Eat	Lizard eats.	Neutral
Flee	One lizard moves away from another CHASING lizard.	Submission
Gular expansion	Expansion of the throat region.	Dominance/Aggression
Hide	Finding or looking for refuge.	Avoidance/Submission
Immobility	A lizard holds the same position.	Submission
Lateral orientation	Body raised up on the four legs, dorsolateral compression, flanks exposure, lateral back distortion.	Dominance/Aggression
Lunge	Rapid jumping movement by one lizard towards another.	Dominance/Aggression
Nip	One lizard grasps another with its jaws and then releases immediately (<1 second later).	Dominance/Aggression
Open mouth	Lizard maintains the mouth open facing the opponent.	Dominance/Aggression
Patrol	Running, climbing along the perimeter/scratching the cage's walls.	Avoidance
Tail undulation	Movement of the tail in a waving motion.	Submission
Strobe motion	Lizard displays movement in short, rapid jerks, to get closer the other lizard, displaying also the behaviour Gular expansion, Ark neck and Lateral orientation.	Dominance/Aggression
Walking	Walk around the cage.	Neutral

Results

In the experimental contest 1, D-S score was significantly higher than 0 in resident (0.15 ± 0.06 , $t = 2.330$, d.f. = 48, $P = 0.024$), suggesting that resident males display more aggressive than submissive behaviours against intruders. Similarly, D-S score was significantly lower than 0 in intruders (-0.21 ± 0.05 , $t = 3.951$, d.f. = 48, $P < 0.0001$), also indicating that intruder males used submissive behaviours more frequently than aggressive behaviours. In accordance, we obtained 35 victories for the resident, 14 victories for the intruder, while in the experimental contest 2, we obtained 15 victories for the larger individuals and only one for the smaller one. The LMM showed that D-S score increased with residency ($\beta_{\text{residency}} = 0.338 \pm 0.115$, $F = 19.696$, d.f. = 1, 88.2, $P < 0.0001$) (Fig. 2), irrespective of colour ($F = 0.731$, d.f. = 1, 64.8, $P = 0.40$), their interaction ($F = 0.104$, d.f. = 1, 88.9, $P = 0.75$) or of *svl_diff* ($F = 0.429$, d.f. = 1, 91.1, $P = 0.51$). Additionally, the random effect of individual identity was also not significant (Wald $Z = 0.982$, $P = 0.33$). The number of bites also increased as a function of the residence status ($\beta_{\text{residency}} = 7.28 \pm 2.52$, $F = 8.610$, d.f. = 1, 92.4, $P = 0.004$), independent of colour ($F = 0.392$, d.f. = 1, 67.3, $P = 0.53$), their interaction ($F = 1.245$, d.f. = 1, 92.6, $P = 0.27$) or *svl_diff* ($F = 0.518$, d.f. = 1, 90.8, $P = 0.47$). Furthermore, the random effect of ID was also not significant (Wald $Z = 0.490$, $P = 0.62$).

With regards to the experimental arena contest, we unexpectedly obtained that both winners as well as losers achieved D-S scores significantly lower than 0 (winner: -0.11 ± 0.06 , $t = 6.518$, d.f. = 15, $P < 0.0001$; loser: -0.45 ± 0.18 , $t = 9.755$, d.f. = 15, $P < 0.0001$). These results suggest that all

lizards displayed on average more submissive than aggressive behaviours in a neutral contest. The LM showed that D-S score significantly increased with male body size ($F = 22.397$, d.f. = 1, 29, $P < 0.0001$) (Fig. 3), and was independently of colour ($F = 0.317$, d.f. = 1, 29, $P = 0.58$).

Discussion

Our results showed that the fight outcome in Italian ruin lizards was primarily influenced by the state of residence. The results from the neutral arena experiment were significant for body size, and not at all by the throat colour. Often, the result of a combat is defined from the asymmetries of a lizard status. In fact, current state of residence may constitute an advantage for lizards, since the resident has an accurate knowledge of territory's value, which is rather unknown to the intruder, thus conferring greater motivation to the fighting (Holberton, Hanano & Able, 1990; Stamps & Krishnan, 1994; Temeles, 1994; Moretz, 2003; Keemp & Wiklund, 2004; Stuart-Fox & Johnston, 2005). Asymmetries can be represented also by a subjective evaluation of the contention resource (Parker, 1974; Maynard-Smith & Parker, 1976), by different competitive abilities in order to maintain or acquire a resource (Parker, 1974; Maynard-Smith & Parker, 1976; Hammerstein, 1981), which may depend on body size or on any possible 'weapon' (Huntingford & Turner, 1987; Alcock & Huston, 1996), or by the individual aggressiveness (Barlow, Rogers & Fraley, 1986; Maynard-Smith & Harper, 1988; Hurd, 2006).

The best strategy for intruders is to avoid conflicts, as they have a higher probability of losing even when they are larger than the residents. In our tests, this residence advantage is made evident by the numerous smaller resident individuals that

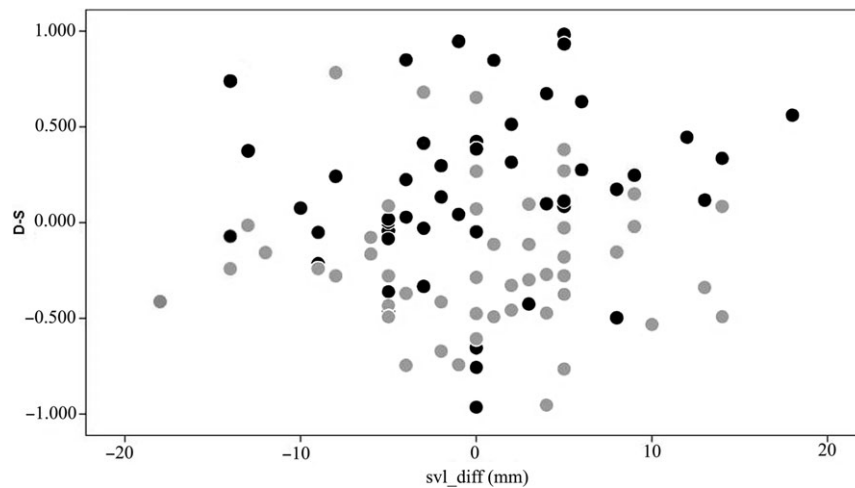


Figure 2 Relationship of D-S (dominance–subordination) with *svl_diff* (size of resident minus size of intruder) in contest 1 between residents (black circles) versus intruders (grey circles).

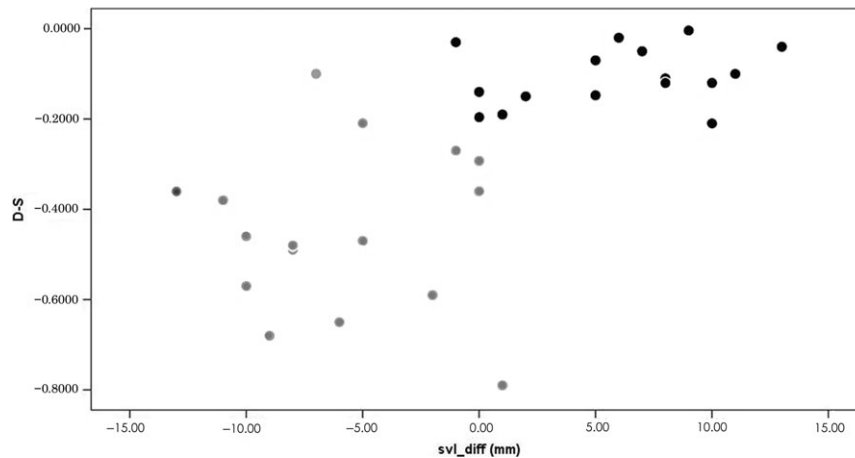


Figure 3 Relationship of D-S (dominance–subordination) with *svl_diff* (size of the winner minus the size of the loser) in contest 2 between winners (black circles) and losers (grey circles).

show more aggressive behaviours than expected and display the ‘Napoleon strategy’, fighting and winning against larger intruders (Just & Morris, 2003; Moretz, 2003). We actually demonstrated that resident lizards spent less time than intruders in the avoidance activity, as the state of residency was the most important factor that predicted the outcome of a fight, while there was not any size effect, in this contest, and for both the roles (average value: $\text{Large}_{\text{resident}} = 2.54\%$; $\text{Small}_{\text{resident}} = 3.87\%$; $\text{Large}_{\text{intruder}} = 9.34\%$; $\text{Small}_{\text{intruder}} = 13.09\%$). In fact, the difference between larger and smaller residents or intruders were not significant even if, just from a quantitative point of view, larger lizards spent less time fleeing than small ones, no matter the roles they play. The importance of the residence status in this *Podarcis* lizard could be the one of the most important factors that, together with other unique physiological and behavioural features of this species (Vervust *et al.*, 2010; Kapsalas *et al.*, 2016), enable *P. siculus* to rapidly colonize

new areas (Downes & Bauwens, 2002; Mangiacotti *et al.*, 2013), a pattern that would deserve forthcoming analyses and experimental research.

Second relevant result of this study is the opposite effect of body size in the neutral arena. While in the experimental contest 1, body size did not apparently affect the outcome of the combat, in the experimental contest 2, size was the main factor that could reveal the outcome. Furthermore, the avoidance activity was markedly evident in both roles (winner, loser) where, unexpectedly, the winners displayed on average more submissive than aggressive behaviours. When both contenders do not have any previous knowledge of the territory’s value (neutral arena), being bigger confers an advantage.

In lizards, SVL is in general the primary predictor of dominance during combats (e.g. *Lacerta agilis*, Olsson, 1992; *Anolis aeneus*, Stamps & Krishnan, 1994; *L. monticola*, Aragón *et al.*, 2006; *P. muralis*, Sacchi *et al.*, 2009; *P. gaigeae*, Cooper,

Dimopoulos & Pafilis, 2015). In this scenario, the ruin lizard could be the exception. Indeed, the relative importance of size and residency seem to be reversed compared to the other species. If the power of the residency effect could be considered a proxy for the 'territoriality' of a species, we can say that *P. siculus* is actually a much territorial species, as recently demonstrated when it directly competes with other species (Downes & Bauwens, 2002; Mangiacotti *et al.*, 2013).

Finally, throat colour does not seem to play a role in the dominance versus subordination ranking establishment, not supporting the hypothesis that greenness conveys information about male quality. The ventral colour variability of *P. siculus* still remains unexplained and does not seem to be comparable to the colour polymorphism expressed by other lacertid lizards (e.g. *P. muralis* and *P. melisellensis*). No evidence of similar patterns are still available for the ruin lizard, thus further studies are needed to investigate the real role of the species polymorphism (Corti *et al.*, 2011). Interestingly, in other territorial not polymorphic species, it has been found that, for instance, chromatic patches may function as status signalling badges of aggressiveness, fighting ability or dominance in males (Bohórquez-Alonso & Molina-Borja, 2014). In addition, it has been suggested a possible role of testosterone as modulating factor (i.e. enhancing or inhibiting) of the UV throat (Whiting *et al.*, 2006), a complex system that should actually be investigated also in *P. siculus*. In gliding lizards, characterized by dewlaps used in social communication, it has been found that the dewlap is solely used for communicating in territory defence and mate attraction (Vanhooydonk *et al.*, 2006), where the strong colouration and contrast seem play such relevant role (Klomp *et al.*, 2016).

Considering our results, it should be worth studying, under controlled conditions, the extent of aggressive behaviour of *P. siculus* (1) versus the sympatric and often syntopic *P. muralis*, the species that very often share many (micro) habitats in Mediterranean central western Italy; and also (2) versus some of the other Italian *Podarcis* lizards, that seem actually mostly constrained by *P. siculus* in its distribution (*P. tiliguerta*; Mangiacotti *et al.*, 2013) or that, in contact zones, suffer of the *P. siculus* aggressiveness (*P. melisellensis*; Downes & Bauwens, 2002).

In conclusion, our results show that (1) male size gives higher advantage in defend each territory, but more importantly when in combination with a specific contest and a strong motivation (Downes & Bauwens, 2002), and that (2) maxillary and throat colouration does not seem to supply a straightforward contribution in dominance versus subordination behavioural contests.

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