Why can’t we all just get along? Interspecific aggression in resident and non-resident *Podarcis melisellensis* lizards

S. P. Lailvaux¹, K. Huyghe² & R. Van Damme²

1 Department of Biological Sciences, University of New Orleans, New Orleans, LA, USA
2 Functional Morphology Laboratory, Department of Biology, University of Antwerp, Antwerp, Belgium

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Correspondence
Simon P. Lailvaux, Department of Biological Sciences, University of New Orleans, 2000 Lakeshore Drive, New Orleans, LA 70148, USA. Tel: +1 504 280 6740; Fax: +1 504 280 6121
Email: slailvaux@gmail.com

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Abstract

Interspecific aggression is thought to be driven by competition over either shared resources or mates, with the latter facilitated by mistaken or poor species recognition. However, such aggression may potentially also be modulated by other factors, including residency in territorial species. We tested the relative strengths of intra- and interspecific aggression in the lacertid lizard *Podarcis melisellensis* by introducing males to both the territories of conspecific males and the territories of a sympatric lizard, *Dalmatolacerta oxycephala*. We also conducted reciprocal introductions to test the effect of residency on interspecific aggression in *P. melisellensis*. Our results show that *P. melisellensis* exhibit significantly more aggression towards *D. oxycephala* than towards conspecifics, even though these two species do not closely resemble one another and do not exhibit extensive overlap in diet preferences. We also found an overall effect of residency on behavioural measures of aggression, as well as a clear increase in interspecific aggression towards *D. oxycephala* in resident relative to non-resident *P. melisellensis*. These results show that interspecific aggression between sympatric species can exist in the absence of breeding competition and with little resource overlap.

Introduction

Intraspecific aggression arises as a result of competition over resources or mates, and may be affected by a variety of factors including residency (e.g. Jennions & Backwell, 1996; Kemp, 2000), size (Langkilde & Shine, 2004), degree of sociality (Peiman & Robinson, 2010) and population density (Knell, 2009). By contrast, interspecific aggression is thought to be based either on interference competition over resources (Nishikawa, 1987; Brawn, 1990) or on mistaken or poor species recognition (i.e. aggression directed towards phenotypically similar heterospecifics; Nishikawa, 1987; Korner, Whiting & Ferguson, 2000). This aggression among species can result in ecological outcomes such as territoriality and/or niche partitioning (Peiman & Robinson, 2010) and ecological character displacement (Schluter, 2000, Tynkkynen, Rantal & Su honen, 2004). Thus, depending on the nature of the dominance relationships that are established, aggression between two or more species may play an important proximate role in shaping ecological communities and could also ultimately incur important fitness-related costs (Tynkkynen et al., 2005).

Although aggression does not necessarily translate into dominance, studies of interspecific competition suggest that aggressive behavioural interactions are often asymmetric such that one species consistently dominates the other (Robinson & Terborgh, 1995). For example, *Anolis cristatellus* lizards tend to dominate the syntopic *Anolis carolinensis* during staged encoun-
several insects (Resende, 2010; e.g. Becerril-Morales & Macias-Ordonez, 2009), but has seldom been tested explicitly in vertebrates (but see Smith & Pough, 1994 for an example). Understanding the role of residency in affecting interspecific aggression is important for understanding interspecific interactions because it may potentially explain why some species consistently dominate heterospecifics in aggressive and competitive interactions.

We staged field introductions to induce aggressive, interspecific interactions between males from two unrelated lacertid lizard species occurring sympatrically on the Croatian island of Lastovo: the Dalmatian wall lizard Podarcis melisellensis and the sharp-snouted rock lizard Dalmatolacerta oxycephala (previously Lacerta oxycephala; see Arnold, Arribas & Carranza, 2007). Although ecologically similar in terms of body plan and foraging characteristics, these two species do not resemble one another, possessing strikingly different colour patterns (Fig. 1). In addition, while both prey on small arthropods, the proportions of prey taken in terms of size and ‘hardness’ may differ among males of each species (Verwaijen, Van Damme & Herrel, 2002). The two species are also clearly ‘hardness’ may differ among males of each species (Verwaijen, Van Damme & Herrel, 2002). The two species are also clearly segregated along ecological axes of habitat use (Nevo; see Arnold, Arribas & Carranza, 2007). Although ecologically similar in terms of body plan and foraging characteristics, these two species do not resemble one another, possessing strikingly different colour patterns (Fig. 1). In addition, while both prey on small arthropods, the proportions of prey taken in terms of size and ‘hardness’ may differ among males of each species (Verwaijen, Van Damme & Herrel, 2002). The two species are also clearly segregated along ecological axes of habitat use (Nevo et al., 1972) and temperature (Scheers & Van Damme, 2002), with P. melisellensis inhabiting lower vegetative habitats and selecting warmer body temperatures (T’s) than D. oxycephala. Given these differences in appearance and potential resource use, we predicted that males of these two species would exhibit little aggression towards each other during experimentally induced interactions. Specifically, we tested the following hypotheses: (1) P. melisellensis would be more aggressive towards ‘invasive’ heterospecifics when resident than when they are non-residents invading D. oxycephala territories; (2) P. melisellensis males would exhibit overall significantly more aggressive behaviours towards conspecific males than towards heterospecific D. oxycephala males.

**Materials and methods**

We conducted behavioural trials in the field using animals noosed from the roadside leading from Pasadur to Malo Lago on the north-western tip of the main island of Lastovo (42°45N, 16°52E) in August/September 2006. Podarcis melisellensis males exhibit a striking but little-understood polymorphism in ventral coloration; orange, yellow and white-bellied males occur sympatriically (Huyghe et al., 2007). Although Huyghe et al. (2009) showed that these three morphs are similar in morphology and behaviour, they differ significantly in bite force, with the orange-bellied males biting significantly harder than yellow or white ones. Given this variation, we used only white-bellied males in behavioural trials as these were the most common on Lastovo. Furthermore, we studied only males of both species to avoid potentially confounding effects of sex (Brecko et al., 2008). Prior to conducting trials, we surveyed the study area for several days to determine the locations of individual animals. All behavioural trials were carried out between 2 and 6 pm and when the substrate temperature was between 30 and 40°C (cf. Husak & Fox, 2003), a range that encompasses the optimal temperatures for both species (Scheers & Van Damme, 2002).

**Behavioural trials**

All trials were conducted by the same investigator (S. P. L.). Captured animals were introduced into the natural territories of lizards along the roadside. We conducted three types of introductions: novel D. oxycephala males introduced to resident P. melisellensis males (Pm-Do); novel P. melisellensis males introduced to resident P. melisellensis males (Pm-Pm); and novel P. melisellensis males introduced to resident D. oxycephala males (Do-Pm). Adult males were introduced at least 1.5 m away from resident males by tethering them around the waist with 10 cm of light thread tied to the end of a 4.5-m lizard noosing pole (following Husak & Fox, 2003). Previous studies have shown that both intra- and interspecific aggressive interactions can be influenced by body size in a variety of animal species. We therefore measured the size of each lizard involved in an interaction wherever possible. We measured the snout-vent length (SVL) for all lizards upon capture using Mitutoyo digital callipers (Mitutoyo America Corporation, Aurora, IL, USA) (±0.01 mm). Because we did not know the size of resident males prior to each introduction, we captured the resident at the end of each trial and measured his SVL. Thus, we were able to compare SVLs of each lizard within a dyad, but in several cases (11 out of 49 trials), the resident lizard evaded capture and could not be identified with confidence at

**Figure 1** Podarcis melisellensis (top) and Dalmatolacerta oxycephala (bottom) on Lastovo.
a later time for recapture. Thus, we treat comparisons of resident/intruder SVLs with caution (although note that our results are qualitatively similar if trials with unmeasured lizards are excluded). To control for potentially confounding effects of familiarity, we only introduced lizards that were captured at least 700 m away from the site of the resident.

Following introductions, we conducted focal observations for 10 min to measure the behaviour of each focal lizard (always *P. melisellensis*). In the case of Pm-Pm trials, the focal male was always the resident. We only recorded the behaviour of focal lizards due to the difficulty of keeping track of behaviours of multiple lizards at the same time without the aid of a video camera. Agonistic behaviours were measured by quantifying the frequency of submissive and aggressive displays during these encounters. We scored the aggressive behaviours of individual *P. melisellensis* exhibited during staged intrusions using a system similar to those used to quantify aggression in other lizard taxa (e.g. Husak & Fox, 2003; Lailvaux et al., 2004; Lailvaux & Irschick, 2007). Aggressive postures (head raised, forearms straightened) were given a score of 1, chasing was given a score of 2, and biting a score of 3, whereas fleeing was assigned a score of −1. These scores were summed for each individual. Finally, we also measured the latency to attack (the time in seconds from the beginning of a trial until the onset of any aggressive response) with a stopwatch, and the distance to attack (the centimeter distance between the intruder and resident lizard at the onset of an aggressive response) with a tape measure. We only recorded behaviours of *P. melisellensis* males in this manner, as we were primarily interested in the aggressive responses of *P. melisellensis* to the appearance of novel males. For this same reason, we did not conduct reciprocal introductions for *D. oxycephala*, that is, *D. oxycephala* male intruders introduced to *D. oxycephala* resident males.

**Analysis**

We analysed behavioural data in two different ways. We first tested for differences among interaction types for each variable by using separate one-way ANOVAs with behavioural interaction type [Do-Pm (*n* = 16 trials), Pm-Pm (*n* = 17 trials) or Pm-Do (*n* = 16 trials), with the resident species always shown as the first of each pair] as a factor and latency to attack, distance to attack and aggressive score as dependent variables. Second, we used multivariate analyses of variance (MANOVAs) to explicitly test the effects of residency on interspecific aggression (using only Pm-Do and Do-Pm data) and type of behavioural interaction (conspecific vs. heterospecific, using only Pm-Pm and Pm-Do data) on the variables latency to attack, attack distance and aggression score. Due to the nature of our dataset, we did not have sufficient power to perform a global MANOVA testing for an interaction between type of aggression and residency. Size comparisons of resident and intruder lizards were made using two-tailed *t*-tests. All analyses were performed using SPSS v. 16 (SPSS Inc., Chicago, IL, USA).

**Results**

The three interaction types differed significantly in latency to attack (*F*<sub>2,46</sub> = 5.925, *P* < 0.005; Fig. 2a), with the quickest attacks exhibited by resident *P. melisellensis* presented with...
novel *D. oxycephala*. Resident *P. melisellensis* were significantly faster to attack *D. oxycephala* than they were to attack conspecifics [Tukey’s honestly significant difference (HSD) post-hoc test, *P* < 0.004], with the difference in attack times between Pm-Do and Do-Pm being marginally non-significant (Tukey’s HSD post-hoc test, *P* < 0.093). In addition to differences in attack latency, the distance over which attacks occurred differed significantly between interaction types (*F*<sub>2,45</sub> = 5.467, *P* < 0.007). Specifically, resident *P. melisellensis* allowed conspecific intruders to approach closer than heterospecifics before initiating attacks, although differences were marginally non-significant (Tukey’s HSD post-hoc test *P* < 0.058). Intruding *P. melisellensis*, however, attacked *D. oxycephala* over a shorter distance compared to interspecific interactions when *P. melisellensis* were residents (Tukey’s post-hoc test *P* < 0.007) (Fig. 2b). Finally, there was a significant effect of interaction type on aggressive score (*F*<sub>2,46</sub> = 5.533, *P* < 0.007) driven by a marked reduction in aggressive behaviours during Do-Pm interactions (Tukey’s post-hoc test *P* < 0.005) as compared with the other two interaction types (Fig. 2c). Measured resident and intruder individuals did not differ in SVL in any interaction type (Table 1).

The overall MANOVA test for residency showed a significant effect of residency status on interspecific aggression in *P. melisellensis* towards *D. oxycephala* (Pillai’s trace = 0.480, *F*<sub>3,28</sub> = 8.632, *P* < 0.001). Here, resident *P. melisellensis* exhibited significantly shorter latency to attack (*F*<sub>1,32</sub> = 9.442, *P* = 0.04; Fig. 3a) and attack distance (*F*<sub>1,32</sub> = 9.781, *P* < 0.04; Fig. 3b) as well as higher aggression scores (*F*<sub>1,32</sub> = 14.023, *P* < 0.001; Fig. 3c) than intruders. The MANOVA also showed a significant effect of conspecific versus heterospecific aggression on all aggression measures (Pillai’s trace = 0.404, *F*<sub>3,29</sub> = 6.555, *P* = 0.002), with *P. melisellensis* exhibiting shorter latency to attack (*F*<sub>1,33</sub> = 10.779, *P* = 0.003; Fig. 4a) and longer attack distances (*F*<sub>1,33</sub> = 4.588, *P* = 0.04; Fig. 4b) but similar aggressive scores (*F*<sub>1,33</sub> = 2.541, *P* = 0.121; Fig. 4c) in interspecific as opposed to intraspecific interactions.

**Discussion**

Interspecific aggression may be triggered either by mistaken identity or by common resource overlap in sympatric species. Here, we show that male *P. melisellensis* lizards exhibit elevated aggression towards sympatric *D. oxycephala* males despite these two species not closely resembling each other and exhibiting differences in proportions (but not types) of prey taken by males. We found that resident *P. melisellensis* males attacked invasive *D. oxycephala* males with less delay (Figs 2a and 3a) and over longer distance (Figs 2b and 3b) compared to when they were invaders entering *D. oxycephala* territories. Resident *P. melisellensis* were also more aggressive towards invasive *D. oxycephala* than the reciprocal case (Figs 2c and 3c). These findings support the hypothesis that residency enhanced aggression in *P. melisellensis* towards ‘invasive’...
heterospecíficos. Sin embargo, rechazamos nuestra segunda hipótesis de que los machos de *P. melisellensis* serían más agresivos en interacciones conspecíficas que interacciones heterospecíficas debido a las interacciones entre los especímenes que provocan ataques (Fig. 4a) a mayor distancia de aproximación (Fig. 4b) de *P. melisellensis* que las interacciones entre conspecíficos. Así, *P. melisellensis* en general serían más agresivos que *D. oxycephala* que otros *P. melisellensis*. Pero no pudiendo realizar interacciones específicas con los machos de estudio para un efecto específico de la residencia dentro de *P. melisellensis*, no podemos explicitamente evaluar la relación entre la efectividad de residencia sobre interacciones intraspecíficas e interspecíficas. Una posible explicación para nuestros resultados generales es que la interacción conspecífica entre *P. melisellensis* y *D. oxycephala* (Fig. 3) no difiere significativamente entre las interacciones conspecíficas y heterospecíficas. Sin embargo, consideramos que esto es poco probable dado que los resultados MANOVA fueron exclusivamente entre las interacciones entre conspecíficos y heterospecíficos. Además, las diferencias entre las interacciones Pm-Pm y Pm-Do son significativas (Fig. 2) y sugieren que *P. melisellensis* modula su comportamiento agresivo dependiendo de si el agonista es conspecífico o heterospecífico.

En el caso de la extensión de la superposición de recursos, que puede influir en la existencia simple de la agresión en *P. melisellensis* y *D. oxycephala* (ver Fig. 3). Finalmente, consideramos que no se explicita el efecto residencia sobre la agresión en *P. melisellensis* ( overall MANOVA test for residency; Fig. 3). No obstante, consideramos que el efecto residencia puede ser la razón por la que las interacciones Pm-Pm y Pm-Do son significativas (Figs 2 and 4) que *P. melisellensis* modula su comportamiento agresivo dependiendo de si el agonista es conspecífico o heterospecífico.

En términos de la existencia simple de la agresión en *P. melisellensis* y *D. oxycephala*, las interacciones conspecíficas de *P. melisellensis* y *D. oxycephala* son curiosas. Esta agresión también parece ser altamente simétrica dado que *D. oxycephala* exhiben menos, si hay, agresividad conspecífica y aparecen a ser los especímenes más agresivos de *P. melisellensis* en situaciones de interacciones (Lailvaux, pers. obs.). Estos resultados son consistentes con las predicciones sobre la hipótesis de la incertidumbre, que sugiere que interacciones heterospecíficas serían menos intensas en términos de agresión que las interacciones conspecíficas. Los resultados de interacciones que elevan los encuentros entre machos con fuerzas de mordedura más débiles sugieren que la fuerza de mordedura no afecta las interacciones conspecíficas en *P. melisellensis* (Lailvaux et al., 2004; Huyghe et al., 2005; Husak et al., 2006; Lailvaux & Irschick, 2007). 

Aunque la interacción conspecífica de agresión es común y se distribuye ampliamente entre especies simpatricas y syntipicas (Peiman & Robinson, 2010), especímenes con extensión territorial
tend to exhibit reduced aggression towards each other, or not to interact aggressively at all (Robinson & Terborgh, 1995). One alternative possible explanation for our results is therefore that these sympatric lizards seldom hold overlapping territories. Consequently, natural rates of aggression between *P. melisellensis* and *D. oxycephala* might be extremely low if these two species never venture into each other’s territories, and the experimental incursions that we staged could occur only rarely in nature. This explanation seems likely given that these lizards appear to segregate along several microhabitat axes, with *D. oxycephala* favouring elevated rocky refuges and *P. melisellensis* tending to occupy low herbaceous vegetation (Verwaijen et al., 2002). Indeed, Nevo et al. (1972) specifically noted that *D. oxycephala* and *P. melisellensis* exhibit very distinct habitat preferences (although exclusion between *D. oxycephala* and *P. sicula* was considered to be a likely possibility, with *P. sicula* likely having a distinct negative effect on *D. oxycephala* density). In addition to habitat, these two species also exhibit clear differences in thermoregulation, with *D. oxycephala* selecting significantly lower field *T*₂₀’s than those favoured by *P. melisellensis* (Scheers & Van Damme, 2002). If these two species have been separated in terms of microhabitat and resource use for some time, then a current low rate of interspecific interaction in nature may be the result of past competitive interactions.

In conclusion, we present evidence for high rates (relative to intraspecific aggression) of interspecific aggression in *P. melisellensis* during staged introductions with the sympatric *D. oxycephala*. We also show that residency is likely to be an important factor regulating levels of interspecific aggression in these two species, with resident *P. melisellensis* tending to be more aggressive to intruding *D. oxycephala* compared with non-residents intruding on a heterospecific. The source of this aggression is unclear given the separation in terms of both morphology and, likely, resource use between the males of these species, but may stem from significant asymmetries in fighting ability or from a complete separation of territories and life histories. Further work on the ecology and behaviour of these lizards in the field, as well as in other comparable systems where residency is likely to affect the outcome of interspecific interactions, is required to make sense of these counter-intuitive results.

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