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

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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 lacertid, *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 & Fergusen, 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 & Suhonen, 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 cooki* during staged encounters (Ortiz & Jenssen, 1982) and in the field (Jenssen *et al.*, 1984). Similarly, the presence of *Anolis sagrei* lizards forces the related *Anolis carolinensis* to select higher perches than they would in the presence of a conspecific competitor (Losos & Spiller, 1999; Edwards & Lailvaux, 2012). A second general characteristic of interspecific aggression is that the different costs of aggression cause individuals to respond more strongly to conspecific aggressive signals than to those of heterospecifics (Peiman & Robinson, 2010; but see Ord and Stamps 2009). Indeed, the increased uncertainty with regard to intent of escalation in heterospecific–conspecific aggressive interactions (i.e. the 'uncertainty hypothesis') suggests that signalling should be more common between heterospecifics. Individuals should therefore be more wary approaching a heterospecific than a conspecific (Peiman & Robinson, 2010). Ultimately, this should translate into less actual aggression between heterospecifics in areas where two or more species coexist.

A large body of literature shows that residency is an important factor affecting the outcome of aggressive intraspecific interactions, with residents often having an advantage over non-residents in territorial disputes (for some recent examples, see Aragon, Lopez and Martin, 2006; Fuxjager *et al.* 2009; Sacchi *et al.* 2009; Booksmythe, Jennions & Backwell 2010). However, the effect of residency on the interspecific aggressive interactions has received less attention. A residency advantage to interspecific territorial disputes has been demonstrated in

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 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_b's) than *D. oxycephala*. Given these differences in appearance and potential resource use, we predicted that males of these two species

Figure 1 *Podarcis melisellensis* (top) and *Dalmatolacerta oxycephala* (bottom) on Lastovo.

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 sympatrically (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

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 difficultly 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 ($F_{2,46} = 5.925$, $P < 0.005$; Fig. 2a), with the quickest attacks exhibited by resident *P. melisellensis* presented with
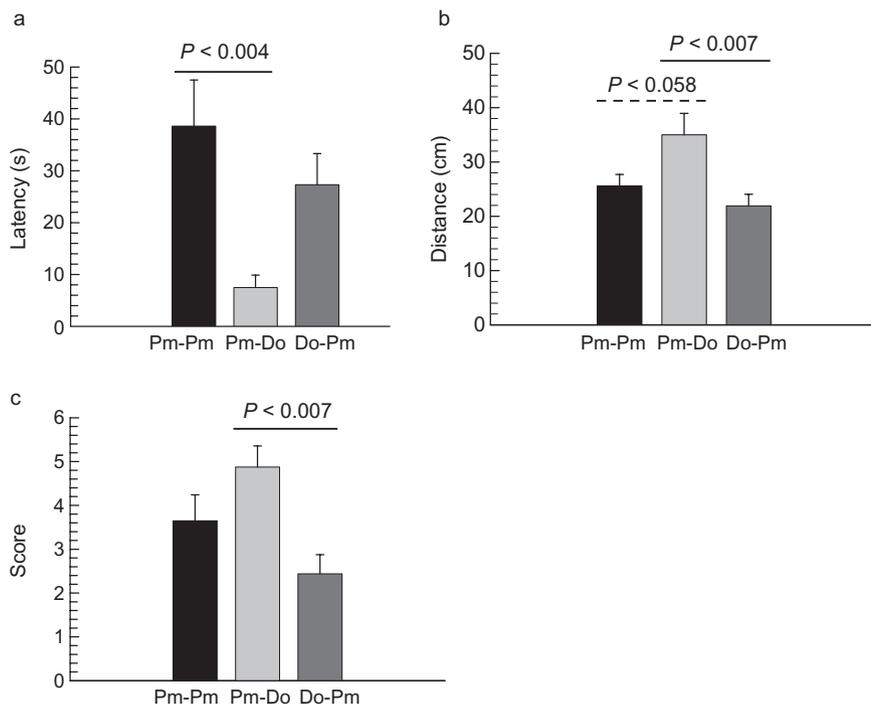
Figure 2 Mean values (+1 se) for (a) latency to attack; (b) attack distance; and (c) aggression score for each of the three interaction types. Horizontal lines represent significant (or marginally non-significant) differences between treatments. Indicated *P*-values are derived from Tukey honestly significant difference post-hoc tests. Note that species pairs are always listed with the resident species first.

Table 1 Results of two-way *t*-tests comparing mean SVLs of intruder and resident individuals for each interaction measured

Interaction	N	Resident SVL (mm)	n	Intruder SVL (mm)	d.f.	t	P
Pm-Pm	13	64.194	16	64.351	27	0.149	0.883
Pm-Do	15	64.348	17	62.837	30	1.751	0.09
Do-Pm	10	63.071	16	65.035	24	1.674	0.107

d.f., degrees of freedom; SVL, snout-vent length.
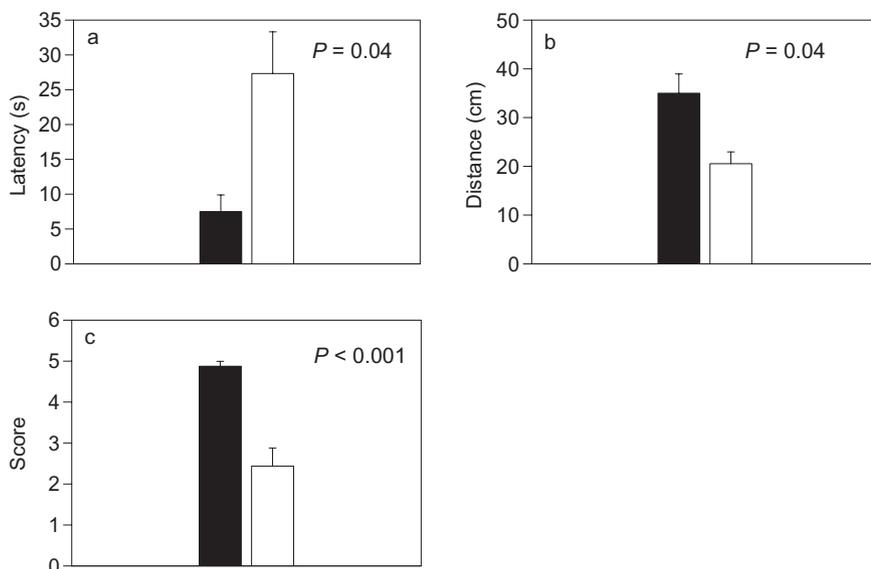
Figure 3 Mean values (+1 se) for (a) latency to attack; (b) attack distance; and (c) aggression score for resident (black) and intruder (white) *Podarcis melisellensis*.

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 ($F_{2,45} = 5.467$, $P < 0.007$). 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 ($F_{2,46} = 5.533$, $P < 0.007$) 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, $F_{3,28} = 8.632$, $P < 0.001$). Here, resident *P. melisellensis* exhibited significantly shorter latency to attack ($F_{1,32} = 9.442$, $P =$

0.04; Fig. 3a) and attack distance ($F_{1,32} = 9.781$, $P < 0.04$; Fig. 3b) as well as higher aggression scores ($F_{1,32} = 14.023$, $P < 0.001$; 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, $F_{3,29} = 6.555$, $P = 0.002$), with *P. melisellensis* exhibiting shorter latency to attack ($F_{1,33} = 10.779$, $P = 0.003$; Fig. 4a) and longer attack distances ($F_{1,33} = 4.588$, $P = 0.04$; Fig. 4b) but similar aggressive scores ($F_{1,33} = 2.541$, $P = 0.121$; 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'
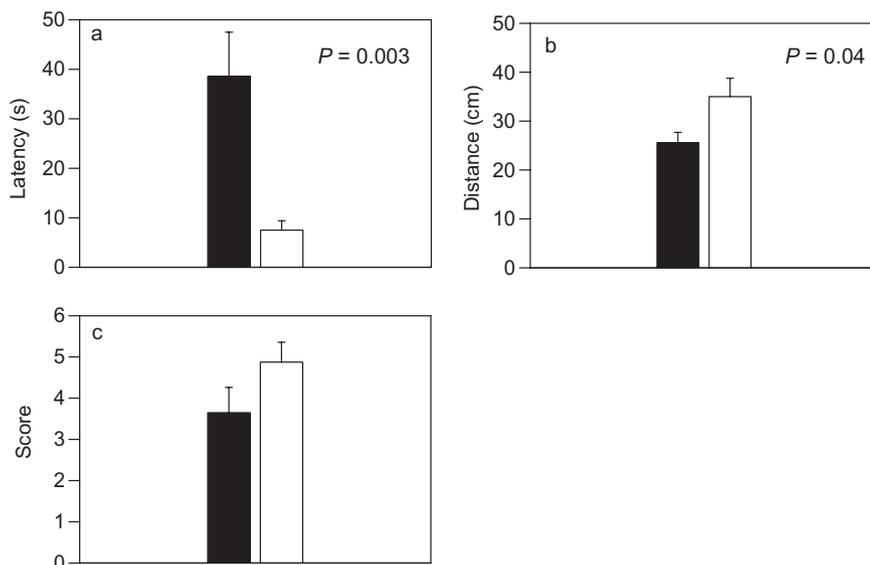
Figure 4 Mean values (+1 SE) for (a) latency to attack; (b) attack distance; and (c) aggression score for *Podarcis melisellensis* in conspecific (black) and heterospecific (white) interactions.

heterospecifics. However, we rejected our second hypothesis that *P. melisellensis* males would be more aggressive towards conspecifics than towards heterospecifics because interactions between heterospecifics elicited quicker attacks (Fig. 4a) over longer approach distances (Fig. 4b) from *P. melisellensis* males than interactions between conspecifics. Thus, *P. melisellensis* males were generally more aggressive towards *D. oxycephala* than towards other *P. melisellensis*. Because we did not conduct reciprocal intraspecific interactions to test for an intraspecific effect of residency within *P. melisellensis*, we cannot explicitly evaluate the relative effects of residency on intra- and interspecific aggression. One possible explanation for our observed results is therefore that the increased aggression towards *D. oxycephala* stems from a general residency effect on aggression in *P. melisellensis* (overall MANOVA test for residency; Fig. 3). Nonetheless, we consider this to be unlikely given that the MANOVA results were driven entirely by interspecific differences (Fig. 3). Furthermore, the observed differences between the Pm-Pm and Pm-Do interactions (Figs 2 and 4) show that *P. melisellensis* modulates its aggressive behaviour depending on whether the agonist is conspecific or heterospecific.

Regardless of the extent of resource overlap, which might by itself explain the simple existence of aggression in *P. melisellensis* towards heterospecifics, the *elevated* aggression of *P. melisellensis* towards *D. oxycephala* is curious. This aggression also appears to be highly asymmetric given that *D. oxycephala* exhibit little, if any, interspecific aggression and appear to be routinely dominated by *P. melisellensis* in staged interactions (Lailvaux, pers. obs.). These results are at odds with the predictions of the uncertainty hypothesis, which suggests that heterospecific interactions should be less intense in terms of aggression than intraspecific interactions. The outcomes of escalated male–male interactions are strongly influenced by relative bite force in many lizard species where harder-biting individuals tend to win fights against males with weaker bite forces (Lailvaux *et al.*, 2004; Huyghe *et al.*, 2005; Husak *et al.*, 2006; Lailvaux & Irschick, 2007). High bite forces can inflict serious injury during combat in other lizard species (e.g. Lappin & Husak, 2005), including the closely related *Podarcis sicula* (Vervust *et al.*, 2009), and the risk of such injury represents a significant cost to aggression and combat. This asymmetry in aggressive behaviour may therefore be influenced by differing performance capacities and hence likely different resource-holding potential of these two species (Lailvaux & Irschick, 2006; Irschick *et al.*, 2007). Although the utility of bite force for resolving intraspecific conflicts in these two species is unknown, adult male *P. melisellensis* bite significantly harder than adult male *D. oxycephala* (Verwaijen *et al.*, 2002) and were also observed to bite frequently in interspecific interactions in the current study. Thus, rather than uncertainty over the outcome of interactions (cf. Peiman & Robinson, 2010), it may be that the elevated aggression of *P. melisellensis* towards *D. oxycephala* represents a learned response arising from the greater relative fighting ability or resource-holding potential of *P. melisellensis* – in effect, an inverse of the intraspecific 'dear enemy' phenomenon (Fisher, 1954) whereby individuals are more aggressive towards others that are known to pose little threat and/or can be easily dominated. Thus far, the only study to our knowledge that has evaluated the role of bite force in determining the outcomes of interspecific interactions in lizards is that of Langkilde & Shine (2007), who showed that bite force does not affect interspecific dominance in sympatric montane skinks. Future studies of this type considering measures of fighting ability grounded in measurable, functional traits such as bite force might prove useful for understanding the costs and benefits of interspecific aggression in these and other species.

Although interspecific aggression is common and widespread among sympatric and syntopic species (Peiman & Robinson, 2010), species with extensive territorial overlap

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 syntopic 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_b'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.

Acknowledgements

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