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Cooperate or compete? Influence of sex and body size on sheltering behaviour in the wall lizard, *Podarcis muralis*

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Abstract

Reptile sheltering behaviour, despite profound life history ramifications, remains poorly investigated. Whether or not individuals share a suitable shelter or, conversely, exclude conspecifics may depend on associated costs (resource partitioning, sexual harassment, disease or parasite contamination) and benefits (predation risk dilution, thermal resilience, information sharing). We performed two experiments on field caught wall lizards (*Podarcis muralis*), a highly territorial species, to investigate the relative roles of sex and body size in night sheltering. In the first experiment, random pairs of lizards were offered two identical shelters. Lizards either shared a shelter, or sheltered separately. In the second experiment, different random pairs of lizards were offered only one shelter so as to elicit a share or compete response. Body size and sex both appeared as significant drivers for sheltering patterns. Unexpectedly, wall lizards often chose to share shelters. When only one shelter (too small to accommodate two adult lizards) was available, many lizards rejected the sheltering option in preference for aggregation. Such aggregative behaviour was not sex dependant, and may reflect thermoregulatory or anti-predatory benefits. Our results nevertheless suggest that cooperative behaviour may exist in wall lizards.

Keywords

competition, cooperation, lacertid, night shelter, body size, sex.

1. Introduction

Research on reptile behavioural ecology has recently bloomed and widened our understanding of their previously overlooked sociality (Chapple, 2003;

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Fox et al., 2003; Wilkinson et al., 2010; Leal & Powell, 2012; Doody et al., 2013; Ballen et al., 2014). A large body of both empirical and theoretical work has notably been devoted to lizard behaviour, and particularly to lizard social interactions (Mouton et al., 1999; Bull, 2000; Stow & Sunnucks, 2004; Chapple & Keogh, 2006; While et al., 2009; Leu et al., 2010). These studies have revealed the extent to which such interactions may reach high levels of complexity, comparable to those seen in mammals or birds; from 'rock-paper-scissors' social system strategies (Sinervo & Lively, 1996; Sinervo et al., 2007), to family-type social structures and kin discrimination (Gardner et al., 2001; Masters & Shine, 2003; O'Connor & Shine, 2003, 2006; Davis et al., 2011), through to parental care and male mate guarding (Lanham & Bull, 2000; Huang, 2006; Sinn et al., 2008, Ancona et al., 2010). Yet, sheltering behaviour has attracted much less attention, and few studies have looked at the factors influencing the selection of suitable shelters (e.g., Downes & Shine, 1998; Beck & Jennings, 2003; Langkilde et al., 2003; Carazo et al., 2011), or the overall use of shelters within and across lizard species (Shah et al., 2003; Langkilde et al., 2003; Langkilde & Shine, 2004, 2005; Leu et al., 2011; Mouton, 2011; Qi et al., 2012). More specifically, they have studied (1) whether individual lizards may share shelters with conspecifics or not, (2) whether individuals may share with some conspecifics but defend shelters from others and (3) which individual criteria (e.g., body size, sex, hierarchical status, prior experience) might drive the above behaviour, remain poorly understood.

Why lizards shelter is obvious. Shelters are used primarily as a daily retreat from unsuitable external conditions (heat, cold), as overwintering refuges, and to escape predation. Sheltering at night is a necessity under a temperate climate, as ambient temperature is often too low to allow for normal activity. Given a suitable retreat site (i.e., large enough to accommodate at least two individuals), sharing this resource with conspecifics may confer advantages. Most obviously, shelter sharing (1) dilutes predation risk, which is roughly divided by the number of individuals within the shelter (Downes & Hoefer, 2004; Lanham & Bull, 2004), (2) conveys thermal benefits via aggregation, where cooling is slowed by aggregative behaviour (Aleksiuk, 1977; Shah et al., 2003; Aubret & Shine, 2009) and (3) offers direct mating opportunities, notably for males (Carazo et al., 2011). On the other hand, shelter sharing may increase intra- and inter-specific competition for territory and associated resources (food, mating opportunities, shelters; Stamps, 1977; Connell, 1983). In particular, females sharing shelters with males have an increased risk of sexual harassment (Kokko & Rankin, 2006). Shelter sharing also increases the risk of transmission of potential parasites and diseases (Lubin et al., 2001; Milner-Gulland, 2001; Rifkin et al., 2012).

A number of factors have been identified that may influence the cost versus benefit trade-off of shelter sharing, of which sex and body size are paramount. In territorial lizard species, males tend to exclude other males from their territories, including shelters (Pianka & Vitt, 2003). Females of several territorial lacertid species are capable of using male scent marks left in shelters to indirectly assess subtle aspects of male phenotypic quality (e.g., body condition, fluctuating asymmetry, parasite load, social dominance) as well as genetic compatibility (Carazo et al., 2011). Torr & Shine (1996) showed that both body size and sex influenced position within the social structure, where larger, more dominant males displaying agonistic behaviour resulted in the displacement of smaller males from shelter sites (see also Whitaker, 1968a for a similar result on *Leiolopisma moco* skinks). In the same study, large males were found sheltered with females more often than smaller males. In the skink *Leiolopisma suteri*, although burrows may house two or three individuals, adult males were never found to share home sites with other males (Towns, 1975). In situations where animals occur in high density, such that basking or shelter sites are scarce, shelter defence may be costly in terms of time and energy and thus may not be favoured. The same may be true if shelter and basking sites are abundant and thus not worth defending (Whitaker, 1968a; Wilson & Knowles, 1988; Greer, 1989), as is usually the case in small species (Torr & Shine, 1996).

The wall lizard (*Podarcis muralis*) is a widespread European species, which occurs at high densities (>500 individuals/ha; Barbault & Mou, 1988). Such high densities are known to promote the establishment of hierarchical rather than territorial social structures in lizards (e.g., Barwick, 1959; Whitaker, 1968b, 1973; Henle, 1989). Fights and chases between individuals of all sizes and sexes are indeed frequently observed in the wild (Edsman, 1990), presumably driven by competition for resources, such as mating partners, food and shelter (Edsman, 1990). On the other hand, a shelter (usually a rock crevice) is often used as a refuge by several lizards (of the same or different sex; pers. obs.). Wall lizards thus appear as a suitable model to investigate trade-offs in sheltering behaviour. In this context, we wished to experimentally investigate the following questions. Do wall lizards share or compete for shelters? Is this behaviour dependent on sex and/or body size characteristics? We randomly allocated pairs of lizards of varying sex and size in test enclosures under two distinct scenarios. First, pairs of lizards were offered two identical shelters, where they were able to either share one of the two shelters, or shelter separately. In a second experiment, different pairs of lizards were offered only one potential shelter to generate competition between the two lizards of each pair. This study therefore focused on understanding how the relative contributions and interactions of associated (and potentially confounding) factors such sex, body mass and body length influence access to a limited resource.

2. Methods

2.1. Study species

A total of 1003 lizards (466 females and 537 males) were captured in the Ariège region (southern France) during the years 2009, 2010 and 2011. Lizards were captured within a 40 km stretch of pasture land and small villages from Mercenac (43°02′29″N; 1°04′41″E) to the Col de la Core (42°51′31″N; 1°06′18″E). Lizards were caught using a noose and fishing rod apparatus and were kept in buckets for the duration of sampling. In order to minimise stress, the bottom of the bucket was filled with a 10 cm layer made of grass and dead leaves. The buckets and lizards were brought back (short car drive, usually less than 10 min) to the laboratory for overnight experiments (see below). The following morning they were sexed by eversion of the hemipenes, and their body mass (BM) was weighed using a digital scale to the nearest 0.1 g. Snout-vent length (SVL) was measured with a digital calliper to the nearest 0.1 mm. Approximately 40% of lizards are found in the wild with one or more fingers and toes missing (as many as 13 missing toes on a single individual, pers. obs.), presumably lost during intra-specific fights, mating bouts, predation related injuries, or other occasional injuries (Edsman, 1990). Such markings were recorded as a code for future identification. Intact lizards were marked by toe-clipping and care was taken to minimise injuries (Ferner, 2007). After measurements were completed, all lizards were released at their capture site.

2.2. Experimental design

2.2.1. Two shelters available to two lizards

A total of 318 lizards were tested in pairs in a dual shelter choice design. Between 10 and 20 lizards were caught and tested daily. All tests were performed in a controlled temperature room (25°C from 8:00 h to 19:00 h; following outside variations during the night). Testing enclosures were 20 plastic tubs (60 × 50 × 50 cm) featuring two shelters placed symmetrically at opposite ends of each tub (Durand et al., 2012). Shelters were kitchen tiles (10 × 10 × 0.6 cm) placed on four supports (small pieces of broken tiles) to provide an 8 mm clearance. Immediately after all pairs were introduced into their testing environment, the room was left undisturbed from 17:00 h to 22:00 h. One large window allowed some natural light into the room, allowing several hours for lizards to assess each other's traits. Darkness occurred naturally during the experiment. At 22:00 h, full darkness was reached in the experimental room. The data were then collected by lifting both tiles in each enclosure. Results were that either both lizards were found under the same shelter, or lizards were found under different shelters. On three occasions, one lizard was found under a shelter while the other was not sheltered. These three results were discarded from data analysis.

2.2.2. *One shelter available to two lizards*

In total 382 lizards were caught for the purpose of this test. Scenario 2 followed the same protocol as scenario 1, but used a single shelter placed in the centre of each enclosure. The shelter was a 1.4 cm wide (internal diameter) and 8 cm long PVC pipe (i.e., approximately the same length as the body length of an adult lizard). This size ensured that two adult lizards (male or female) could not fit both their bodies in the shelter at the same time. Inevitably though, pairs that included at least one juvenile lizard had more sheltering options (see below). At 22:00 h we recorded the outcome as (1) one lizard in the shelter and one outside (hereafter 'exclusion'), (2) two lizards outside the shelter ('both out'; either aggregated or separated) or (3) two lizards inside the shelter ('both in').

2.3. *Statistical analyses*

The analyses were performed using R 3.0.2 (R statistical Core Team, Vienna, Austria) and Statistica® (Statsoft, Tulsa, OK, USA).

Body size analyses were performed on adult lizards only (age category estimation was based on SVL thresholds in adults: >59 mm for males and >57 mm for females; Barbault & Mou, 1988). We then wished to test for the effect of sex and body size (BM and SVL) and their interactions. To do so, we first performed analyses at the 'pair of individuals' level where we looked at the effects of trait differences between the two individuals involved in each trial (i.e., sex combinations (MM, MF or FF), absolute difference in BM and absolute difference in SVL). Then we analysed the data at the 'individual level' where we tested the effects of individual traits (sex, BM and SVL) on the outcome of the test. At this level, because the results of the two individuals involved in a pair are not independent from each other, we only included the results for one lizard of each pair (randomly chosen) in the analysis. All tests were performed using generalised linear models with a binomial error and complementary log–log link. We proceeded to a stepwise model selection procedure, starting with the most complex model including all main effects and pairwise interactions (chi-squared tests ANOVA).

In the first experiment the outcome (binary response variable) was either both lizards found under the same shelter or under different shelters. The results of the second experiment (one shelter available) were analysed in two-steps. First, the response variable was two of the possible outcomes of the experiment: (1) both lizards found inside the shelter (i.e., share) versus (2) one lizard found in the shelter and the other outside (exclusion). Cases where both lizards were found outside (shelter was left empty) were discarded from this analysis as it was unclear whether this result reflected lizard behaviours (i.e., both lizards chose to remain outside, no winner) or the fact that lizards failed to locate the shelter. Second, we separately analysed exclusion cases to test for the effect of sex and body size, as well as their interaction, on the outcome (i.e., lizards were either excluders or excluded).

3. Results

3.1. Morphology

Males were larger than females in BM (pregnant females excluded; 5.88 ± 1.95 versus 4.42 ± 0.95 g; $F_{1,446} = 217.35$; $p < 0.0001$) and SVL (64.50 ± 2.97 versus 62.18 ± 3.35 mm; $F_{1,598} = 80.64$; $p < 0.0001$).

3.2. Two shelters available to two lizards

Out of 159 pairs of lizards tested, 73 were found under the same shelter (hereafter 'together'), while 86 sheltered apart (hereafter 'apart'; Chi-square test $\chi^2_1 = 1.06$; $p = 0.30$).

3.2.1. Analyses at the pair level

The final statistical model included two variables: sex pairs, SVL difference, and their interaction (Table 1). In the case of same-sex pairs, the difference

Table 1.
Results of the two shelters experiment analysed at the pair level.

	Estimate	SE	p
Intercept	0.26	0.50	0.61
Sex pair MF	−1.02	0.59	0.09
Sex pair MM	−0.43	0.63	0.50
SVL difference	−0.15	0.1	0.14
MF × SVL difference	0.19	0.10	0.07
MM × SVL difference	0.07	0.11	0.50

Statistical model selection procedure retained two variables: sex pairs (MM, FF or FM), the difference in SVL between the two lizards, and their interaction.

in SVL of the lizards found in different shelters was slightly but significantly larger than that of the lizards found under the same shelter (Figure 1). In the case of male–female pairs, the opposite result was found: lizards of greater difference in SVL were more frequently found sharing a shelter.

3.2.2. Analyses at the individual level

The factors included in the final statistical model were sex, body mass, and their interaction (Table 2, Figure 2). Individual males that shared a shelter were heavier on average than those that used different shelters. The reverse was true in females however.

3.3. One shelter available to two lizards

From 191 trials we obtained the following results: 63 exclusions, 38 both in and 90 both out ($\chi_2^2 = 21.17$, $p = 0.0001$). In the latter case, 17 pairs of lizards were found separated, while 20 pairs were found aggregated side by side (in the remaining tests the data was not recorded). Status (aggregated versus separated) did not depend on the sex of the individuals in the pair ($\chi_2^2 = 2.28$, $p = 0.31$).

3.3.1. Analyses at the pair level

The final statistical model included only sex pairs (Table 3). MM pairs resulted in more frequent exclusions than MF pairs, which themselves resulted in more exclusions than FF pairs (Figure 3).

3.3.2. Analyses at the individual level

BM and sex factored into the test outcome (i.e., sharing or exclusion; Table 4). Unsurprisingly, the average BM of individuals was significantly

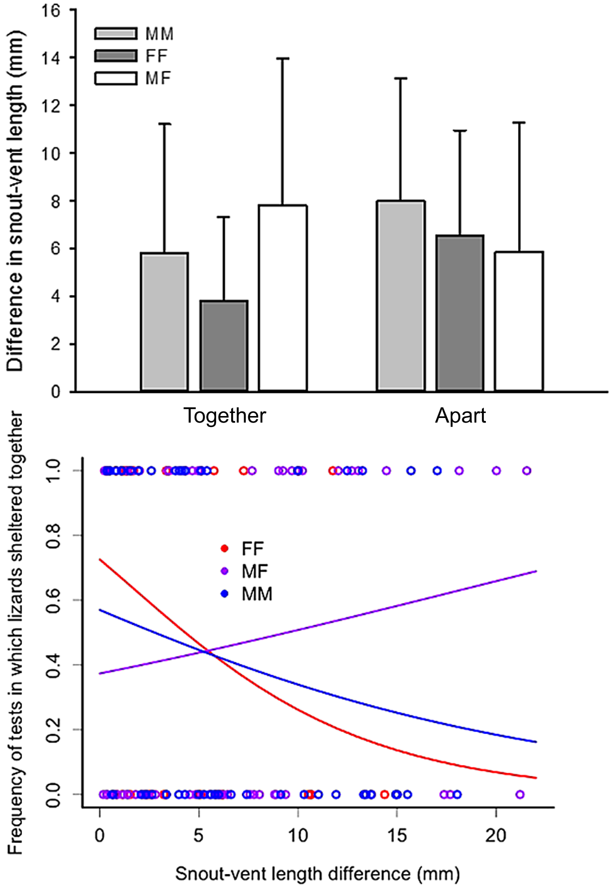

Figure 1. Results of the two shelters experiment analysed at the pair level. (Top) Means ± SD of the difference in snout-vent length for male–male ('MM'), female–female ('FF') and male–female ('MF') pairs and the different experiment outcomes (the two individuals were found under the same shelter, 'together', or under different shelters, 'apart'). (Bottom) GLM predictions (lines) of the test outcome as a function of SVL difference, for the three types of sex combinations; dots represent observed values (0 = apart, 1 = together). This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x.

higher in exclusion rather than both in outcomes (5.18 ± 1.37 versus 3.56 ± 1.15 g; Figure 4, top panel). Tests that involved at least one male resulted more frequently in exclusion than tests involving at least one female (males: 37 exclusions and 8 both in versus females: 26 exclusions and 30 both in; Figure 4, bottom panel).

Table 2.
Results of the two shelters experiment analysed at the individual level.

	Estimate	SE	*p*
Intercept	0.94	0.71	0.19
Sex	−2.54	1.02	0.01
BM	−0.30	0.16	0.06
Sex:BM	0.49	0.21	0.02

Statistical model selection procedure retained two variables: sex, body mass, and their interaction.

3.3.3. Position of the individuals in exclusion cases

BM and sex were retained in the final statistical model (Table 5). The interaction term was close to the conventional level of significance ($p = 0.06$). In both sexes, shelter occupying lizards were heavier than lizards found outside the shelter (5.20 ± 1.27 versus 4.71 ± 1.35 g; Figure 5, top panel). Males were more frequently found outside rather than inside the shelter (24 versus 13 cases) whereas the opposite was true for females (10 outside versus 16 inside; Figure 5, bottom panel).

4. Discussion

In this study we investigated the potential occurrence of competition for shelters in pairs of lizards of varying sex and size under two scenarios (availability of two shelters or only one shelter to a pair of lizards). In the first scenario (two shelters available), similar sized males preferentially shared shelters. Males with significant size difference however selected different shelters. In the second experiment (one shelter available) males, regardless of size, preferentially avoided each other, while females tended to share the unique shelter. The former result is supported by field observations (Edsman, 1990) where body size affects territorial behaviour: large males being highly aggressive and defending long-term territories, while small males are subordinate (Edsman, 1990; Sacchi et al., 2009). On the other hand, it is plausible that large males forced smaller conspecifics out of the shelter, while this did not occur with similar-sized animals: costs, without a clear anticipated winner, may have outweighed the benefits of fighting (Clutton-Brock et al., 1979; Sacchi et al., 2009). However, the opposite result, for which we have no clear explanation (inter-sexual competition?), was found in female–male

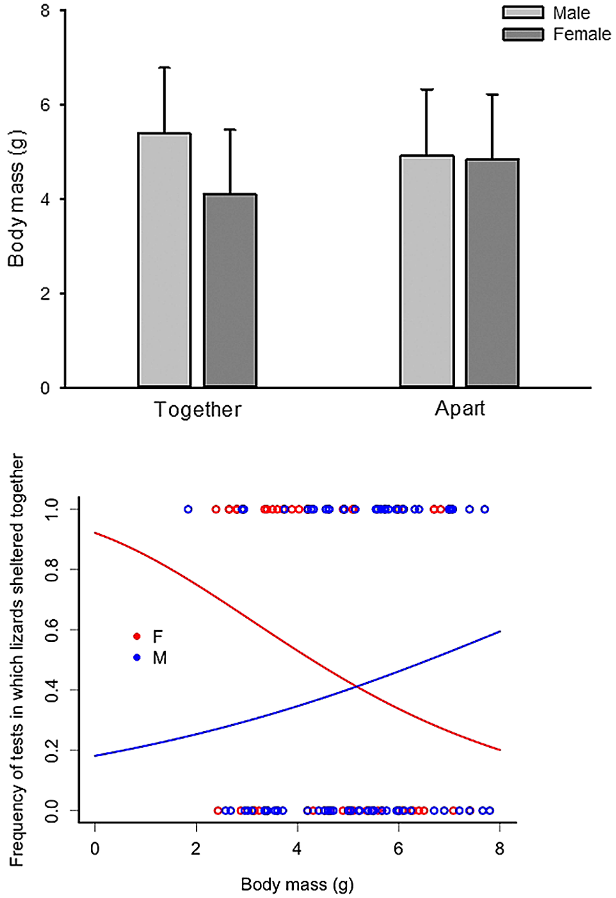

Figure 2. Results of the two shelters experiment analysed at the individual level. (Top) Means ± SD of body mass for males and females and the different experiment outcomes (the two individuals were found under the same shelter, 'together', or under different shelters, 'apart'). (Bottom) GLM predictions (lines) of the test outcome as a function of body mass and sex; dots represent observed values (0 = apart, 1 = together). This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x.

tests of the first scenario experiment: individuals that selected different shelters were similar in body size.

Large males (both in body mass and length) tended to share shelter with other individuals, while smaller males tended to shelter alone. It is however unclear whether large males actively selected communal sheltering or if large males attracted conspecifics by providing information about habitat quality

Table 3.
Results of the one shelter experiment analysed at the pair level.

	Estimate	SE	*p*
Intercept	−0.83	0.29	0.004
Sex pair FM	0.88	0.36	0.02
Sex pair MM	1.67	0.38	<0.001

Statistical model selection procedure retained one factor: the category of sex pair.

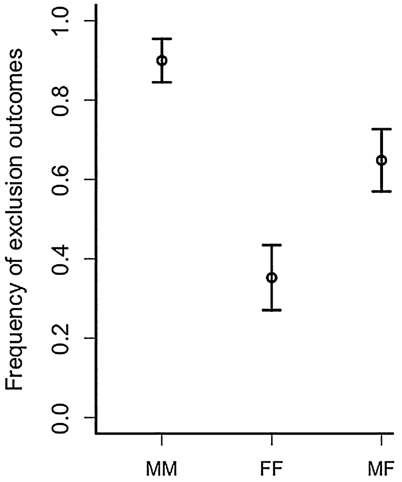

Figure 3. Results of the one shelter experiment analysed at the pair level: frequency of tests that resulted in one individual sheltered and one not sheltered (‘exclusion’) for the three types of combinations of sexes (male–male (MM), female–female (FF) and male–female (MF)). Bars represent the standard errors of the predictions of the corresponding GLM.

Table 4.
Results of the one shelter experiment analysed at the individual level.

	Estimate	SE	*p*
Intercept	−2.26	0.55	<0.001
Sex	0.66	0.30	0.029
BM	0.45	0.12	<0.001

Statistical model selection procedure retained two variables: sex and body mass.

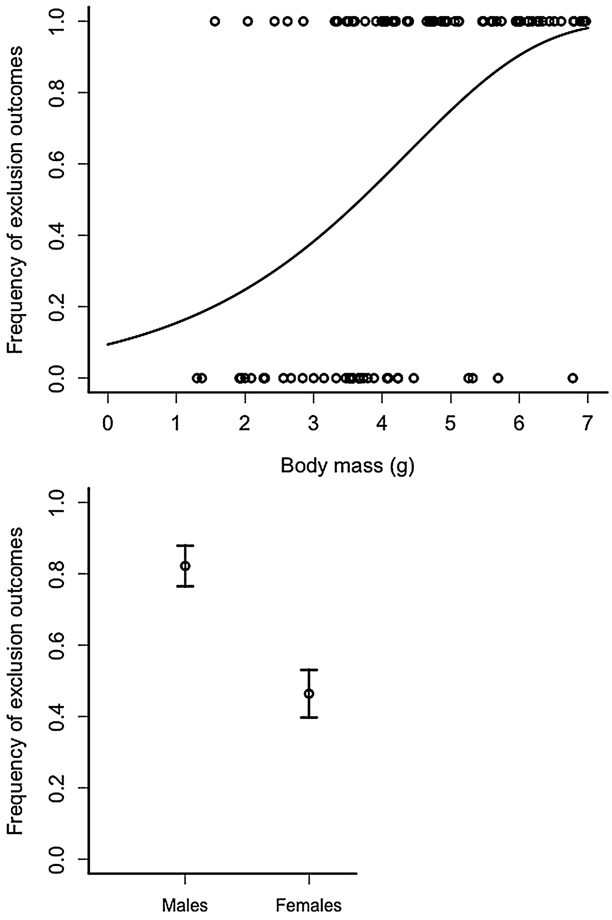

Figure 4. Results of the one shelter experiment analysed at the individual level. (Top) GLM predictions (lines) of the test outcome as a function of body mass; dots represent observed values (0 = both inside, 1 = exclusion). (Bottom) Frequency of tests that resulted in one individual sheltered and one not sheltered ('exclusion') for males and females; bars represent the standard errors of the predictions of the corresponding GLM.

and potential mating prospects (Carazo et al., 2011). When offered only one potential retreat site, the effects of body size on test outcomes were also predominant. Where exclusion occurred, the heaviest lizards, regardless of sex, were significantly more often found occupying the shelter. This result was previously found in other studies (Edsman, 1990; Sacchi et al., 2009). Body size may have been the deciding factor in the exclusion outcome, as

Table 5.
Results of the one shelter experiment in the case of exclusion outcomes (one lizard sheltered, one not sheltered): analysis of the factors affecting the location of the individuals at the end of the experiment (in or out).

	Estimate	SE	*p*
Intercept	−1.66	0.88	0.06
Sex	−1.15	0.43	0.007
BM	0.36	0.18	0.04

Statistical model selection procedure retained two variables: sex and body mass.

fighting was observed during the experiments, toes occasionally bitten off and tails broken as a result of the interactions between lizards.

The main and somehow surprising result of this study is that wall lizards often chose to share shelters, potentially demonstrating a form of sociality in this species (as observed in several other lizard species: Bull et al., 2000; Shah et al., 2003; Chapple & Keogh, 2006). Even in the case of competition for a single shelter, lizards often rejected the sheltering option in preference for aggregation: in 20% of the tests both lizards managed to fit into the shelter, in 47% of the tests the shelter was left empty and both lizards remained in the open, aggregated side by side in 54% of those cases. This result is very counter-intuitive. However, a similar observation was previously made: in the lizard *Cordylus cataphractus*, grouping in the wild was not the result of limited refuge sites as sheltering sites are often left empty but a preference for aggregation under communal shelters (Visagie et al., 2005). In the wall lizard, such aggregative behaviour was not sex dependant, and may reflect thermoregulatory benefits (Aubret & Shine, 2009), stress relief (i.e., sociality; Galeotti et al., 2010) or some sort of cryptic cooperative behaviour (Lanham & Bull, 2004). We suggest that many pairs of lizards also aggregated in the first scenario (two shelters), although they did so under a shared shelter, because the shelter was large enough to accommodate them both. In support of this idea, we noted that no pair of juvenile lizards was found ‘both out’ when only one shelter was available, most likely because both were able to fit within the tube. This result may reflect some cryptic hierarchy in the sheltering behaviours of individual wall lizards, from preferred to least preferred configuration: (1) sheltering in close contact with a conspecific, (2) being in close contact with a conspecific even in a vulnerable situation (i.e., not sheltered) and (3) being sheltered alone. This pattern was

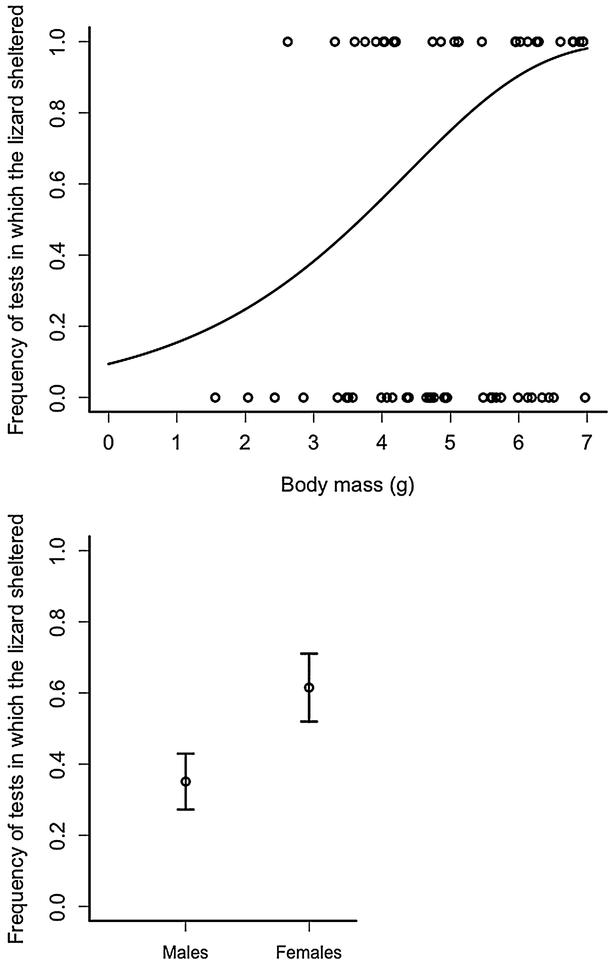

Figure 5. Results of the one shelter experiment in the case of exclusion outcomes (one lizard sheltered one not sheltered). (Top) GLM predictions (lines) of the test outcome as a function of body mass; dots represent observed values (0 = individual outside, 1 = individual sheltered). (Bottom) Frequency of tests in which an individual sheltered, depending on its sex; bars represent the standard errors of the predictions of the corresponding GLM.

not observed in all tested individuals as competition and fighting were observed, suggesting that it may only occur in the absence of direct competition between lizards (for instance between two large males). This observation nevertheless suggests that cooperative behaviour may exist in wall lizards, perhaps driven by thermal or anti-predatory benefits. Further experiments may also investigate the potential role of information copying as observed in birds (Seppänen et al., 2007): lizards sharing shelters resulting from one lizard mimicking a 'safe' behaviour displayed by one of his conspecifics.

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