# An experimental demonstration of direct behavioural interference in two Mediterranean lacertid lizard species

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*Podarcis sicula* of Italian origin has expanded its range along the Adriatic coast of Croatia, apparently replacing the autochthonous species *P. melisellensis* by competitive exclusion. We used an experimental approach on newborn lizards to test the hypothesis that direct behavioural interference occurs between *P. sicula* and *P. melisellensis*, whereby the former obtains an advantage over the latter. Brief encounters between *P. sicula* and *P. melisellensis* were more aggressive and more likely to result in clear dominant–subordinate relationships than were brief encounters between pairs of conspecific *P. melisellensis*. When they cohabited for 3 weeks, individuals in heterospecific pairs were less likely to occupy a thermal microhabitat simultaneously than individuals from homospecific pairs. Contrasts of individuals in heterospecific pairs showed that behavioural interference was asymmetric in favour of *P. sicula*. During brief encounters *P. sicula* were more aggressive and dominant than *P. melisellensis* opponents. When the two species cohabited for longer periods *P. sicula* used better, and *P. melisellensis* poorer, thermal microhabitats than when reared in isolation. In addition, *P. sicula* grew faster, and *P. melisellensis* slower, than in isolation. These within-species shifts in microhabitat use and growth were not evident for homospecific pairs living together. Thus, our observations indicate that asymmetric aggressive interactions between hatchlings of our study species reduce an important fitness component (i.e. growth rate) of *P. melisellensis*. These findings are consistent with the hypothesis that direct behavioural interference by *P. sicula* is the mechanistic basis of the competitive exclusion of *P. melisellensis*.

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The essence of interspecific competition is that individuals of one species suffer a reduction in some components of fitness (e.g. growth, fecundity, survivorship) as a result of interactions with individuals of another species (reviewed in Tanner 1997; Bardsley & Beebee 1998; Caruso 1999). Competitive interactions may be manifested as exploitation of resources or direct behavioural interference (Schoener 1986). Interactions with heterospecifics will restrict the behavioural options available to a species and can have important consequences for its use of resources, and ultimately its distribution (e.g. Pizzimenti & DeSalle 1981; Keen 1982; Parmenter & MacMahon 1983; Adolph 1990; Bourski & Forstmeier 2000). For example, among ectotherms microhabitat use often correlates with, and appears to be limited by, the microhabitat use of heterospecifics (e.g. Stamps & Tanaka 1981; Tokarz & Beck 1987; Hertz et al. 1994; Leal et al. 1998). Thus, competitively inferior species may be forced

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to use suboptimal microhabitats to minimize interactions with sympatric species ('competitive exclusion' sensu Connell 1961; Toft 1985; Schoener 1986). In extreme cases, this process can result in the allopatric distribution of the species involved (e.g. Spellerberg 1972; Banks & Beebee 1987; Neet & Hausser 1990; Hess & Losos 1991).

Lizards have proved to be good organisms for studies of competition between species. Several investigations of members of the genus *Anolis* have provided evidence for the importance of interspecific competition in structuring anole communities and as the driving force behind the evolutionary radiation of *Anolis* lizards in the Caribbean (reviewed in Pacala & Roughgarden 1982; Tokarz & Beck 1987; Losos et al. 1993; Losos 1994; Leal et al. 1998). Competitive interactions also affect the demography of coexisting iguanian lizards (Dunham 1980; Smith 1981). Indirect evidence suggests that competition in anoline and other iguanid lizard communities is exploitative (Dunham 1980; Losos 1994). Case et al. (1994) documented competitive displacement of asexual geckos in tropical Pacific islands by an inadvertently introduced sexual gecko. Staged encounters in the laboratory supported the hypothesis that behavioural

interference is at least partially responsible for the competitive exclusion (Bolger & Case 1992).

Competitive exclusion by behavioural interference is thought to be involved in the spread of the lacertid lizard *P. sicula* in the Mediterranean area. This species of Italian origin has expanded its range, presumably in historical times, to coastal areas and numerous islands along the Adriatic coast of Croatia, where it has apparently replaced the autochthonous species *P. melisellensis*. Distributional data indicate that only one species is present on the numerous smaller islands, and that on the few larger islands (measuring tens to hundreds of square kilometres) where both species are reported to coexist, they occupy distinct habitat types (Radovanovic 1965; Raynor 1989). Based on these observations, Radovanovic (1965) hypothesized that on small islands where the generally more robust *P. sicula* gained a foothold, *P. melisellensis* was replaced by competitive exclusion (reviewed in Nevo et al. 1972; Raynor 1989). Radovanovic tested this notion by introduction experiments on several small islands, and concluded, based on the subsequent abundance of lizards, that competitive exclusion was occurring (Radovanovic 1965). Nevo et al. (1972) found distributional evidence to support this theory on some islands and to refute it on others. Thus, the evidence for the notion that *P. sicula* competitively excludes *P. melisellensis* is equivocal. In addition, the mechanistic basis of the hypothesis, that is that direct behavioural interference is responsible for the putative competitive exclusion, has never been addressed.

We used two complementary laboratory experiments to test the hypothesis that direct behavioural interference occurs between *P. sicula* and *P. melisellensis*, whereby the former obtains an advantage over the latter. Concurrently we assessed the importance of aggression as a mechanism of competitive exclusion. We staged encounters between pairs of newborn *P. sicula* and *P. melisellensis* and compared the resulting behaviour with that shown during staged encounters between pairs of conspecifics. We used newborn lizards because they can be matched for body size and have never been involved in social encounters with other lizards. The first experiment required pairs of lizards to interact briefly and tested whether behavioural interference is manifested through differences in aggression and dominance. In the second experiment the lizard pairs from the first experiment were required to cohabit for several weeks to test whether behavioural interference leads to differences in activity times, microhabitat use and growth rates. This study is not only the first rigorous test for direct behavioural interference between *P. sicula* and *P. melisellensis* but also one of the few behavioural investigations on the mechanistic basis of competitive exclusion.

## METHODS

### Study System

The European lacertid lizards *P. sicula* and *P. melisellensis* provide an ideal system to explore behavioural interference at the interspecies level. Both species have a typical lacertid body shape and are morphologically similar. Although adult sizes vary between locations, adult *P. sicula* are generally larger than adult *P. melisellensis*, the difference being most pronounced in males. The two species also have similar general ecological characteristics (Arnold & Burton 1978; Henle & Klaver 1981; Tiedemann & Henle 1986; unpublished data). Both species forage actively on the ground among grassy vegetation for a wide range of invertebrate prey. Adults of both species have similar preferred body temperatures (i.e. 32–36°C) which they attempt to maintain by basking on small rocks and stone walls, and by shuttling between sunlit and shaded microhabitats. We assume that selected temperatures of juveniles are similar to those of adults (see Castilla & Bauwens 1991). Both species are polygynous and highly territorial (Nevo et al. 1972; Raynor 1989). The behavioural repertoire is qualitatively similar and individuals of both species readily interact with heterospecifics in staged laboratory encounters (unpublished data).

### Collection Sites

We collected adult lizards from Croatia in April 2000, by the method of 'noosing' (Bertram & Cogger 1971). Lizards were abundant in our study area. To ensure that (recent) ancestors of our study animals had not encountered individuals of the other species, we collected adult females at sites where only one of the species is present, but that are otherwise similar in habitat characteristics and faunal composition.

We caught *P. sicula* near Novigrad (45°19′N, 13°33′E) on the Adriatic coast of the mainland of Croatia. The site consisted of a meadow that was partly overgrown by bushes and surrounded by woodland. Other lizards present at this site were *Algyroides nigropunctatus* and *Lacerta bilineata* (Arnold & Burton 1978). We collected *P. melisellensis* near Beli (45°06′N, 14°21′E) on the large island of Cres (ca. 400 km; northern Adriatic, Croatia). We caught lizards on an open meadow bordered by a piled stone wall and surrounded by deciduous woodland (details in Grbac & Bauwens 2001). The lizards *P. muralis, A. nigropunctatus* and *L. bilineata* were also present at this site.

Adults of both species varied in body size, but this variation was less accentuated in the hatchlings used in the study (Table 1).

### Animals and Maintenance

We caught 22 female and 11 male adult *P. sicula*, and 12 female and six male adult *P. melisellensis*. They were transported to and housed at the Institute of Nature Conservation, Brussels, Belgium. The lizards were maintained, two females to each cage with an adult male lizard, in sand-filled terraria (100 × 40 cm and 40 cm high) containing leaf litter and rock shelters. When a female oviposited, we dug up her eggs and placed them individually into 140-ml jars containing moistened vermiculite (−200 kPa) and covered them to prevent evaporative water loss. As part of another study, we

**Table 1.** Mass and snout–vent length (SVL) of male and female *P. sicula* (S) and *P. melisellensis* (M) from our study populations

| | Species | N | Mass (g) | | SVL (mm) | |
|---|---|---|---|---|---|---|
| | | | $\bar{X}\pm$SE | Range | $\bar{X}\pm$SE | Range |
| Female adults | S | 23 | 7.2±0.4 | 4–10 | 69.2±1.4 | 53–78 |
| | M | 12 | 4.9±0.2 | 4–7 | 60.1±1.1 | 55–70 |
| Male adults | S | 13 | 10.5±0.4 | 7–14 | 77.8±1.1 | 68–85 |
| | M | 6 | 6.8±0.3 | 6–8 | 64.9±0.8 | 62–67 |
| Female newborns | S | 111 | 0.44±0.01 | 0.31–0.61 | 26.8±0.1 | 23–30 |
| | M | 73 | 0.40±0.01 | 0.28–0.54 | 25.1±0.1 | 23–27 |
| Male newborns | S | 93 | 0.44±0.01 | 0.33–0.59 | 26.1±0.1 | 22–29 |
| | M | 62 | 0.39±0.01 | 0.28–0.58 | 24.7±0.2 | 23–28 |
| Female study subjects | S | 32 | 1.32±0.03 | 1.02–1.67 | 34.8±0.3 | 32–38 |
| | M | 32 | 1.19±0.02 | 0.88–1.6 | 33.0±0.2 | 31–35 |
| Male study subjects | S | 32 | 1.26±0.03 | 0.99–1.62 | 33.5±0.2 | 30–36 |
| | M | 32 | 1.10±0.03 | 0.82–1.58 | 31.1±0.2 | 29–35 |

Data are presented separately for adult lizards, newborn lizards (0 days) and lizards used as subjects in our study (ca. 6 weeks). See Methods for details of site locations for each species. *N*=number of individuals in a sample.

distributed the eggs from each clutch evenly over two incubators set at $26 \pm 4$ and $28 \pm 4°$C. We checked incubators twice daily for hatchling lizards.

Immediately after hatching, newborn lizards were weighed, measured (SVL) and placed individually in tubs ($20 \times 15$ cm and 25 cm high) within nontransparent walls and containing sand (2 cm depth), leaf litter and a slate shelter. They were maintained in a room at 29°C; 60-W fluorescent tubes positioned 40 cm above the containers provided thermoregulatory opportunities from 0800 to 1800 hours. We sexed lizards when they were 6 weeks old by inspecting the shape of the femoral pores (Arnold & Burton 1978).

During maintenance and experimentation, lizards had access to house crickets, *Acheta domestica*, and water ad libitum, both of which were supplemented with calcium and vitamins, and the light cycle was that of the surrounding area. None of the crickets was ever injured and not eaten.

## Experimental Procedures

We assessed individual differences in growth and behaviour of solitary lizards during the pre-experimental period. When the lizards were ca. 6 weeks old we staged encounters between two conspecific lizards of each of both species (hereafter referred to as 'intraspecific encounters') and heterospecific pairs comprised of one *P. sicula* and one *P. melisellensis* ('interspecific encounters'). We conducted two complementary experiments. The first involved staging interactions over a 20-min period and examining the social behaviour of lizards ('short-term trials'). The second experiment involved staging interactions over 21 days and periodically measuring microhabitat use, levels of activity and body size ('long-term trials'). We stress that the lizards had no social experience prior to these encounters.

For the experiments we used terraria ($100 \times 20$ cm and 40 cm high) lined with sand (5-cm depth) and covered with leaf litter. A retreat site (made of slate) and a water dish were placed at one end of the arena. One 100-W light globe positioned 30 cm above the substrate acted as a heat source (attaining 55°C) on a limited area at the other end of the arena. We used foil to direct the beam of light on to a small ($5 \times 2$-cm) wooden basking site. The limited area of the basking spot precluded both lizards basking at the same time unless they were within 4 cm of each other. To encourage the lizards to use this resource, we maintained our experimental room at ca. 24°C, which is considerably lower than the preferred body temperatures of adults of both study species (ca. 32–36°C: unpublished data).

The light globe heated different areas of the terrarium to different ambient temperatures (recorded using HOBO type temperature data loggers placed on the substrate). To increase structural complexity in the test cages, and delineate sections of different ambient temperature, we placed pairs of cards ($10 \times 4$ cm, positioned 10 cm apart) vertically in the sand base at 20-cm intervals along the length of the terraria. Each section was assigned a relative value that reflected the proximity of its ambient temperature to the preferred body temperature of our study animals (Fig. 1).

### Pre-experimental observations

Lizards were reared in individual cages from hatching until the age of ca. 6 weeks. We measured SVL and body mass at 3–4-day intervals. Five days before staging their short-term trials, we placed the lizards individually into test cages. Lights were switched on between 0900 and 1700 hours. Two days later, we quantified the levels of activity and locations of single lizards every 15 min from 0800 to 1800 hours. Specifically, we scored whether a lizard was hidden or active and, if active, we noted which section of the arena it occupied. From these measurements we calculated growth rates and behaviour of individual lizards when reared in isolation; these provided a
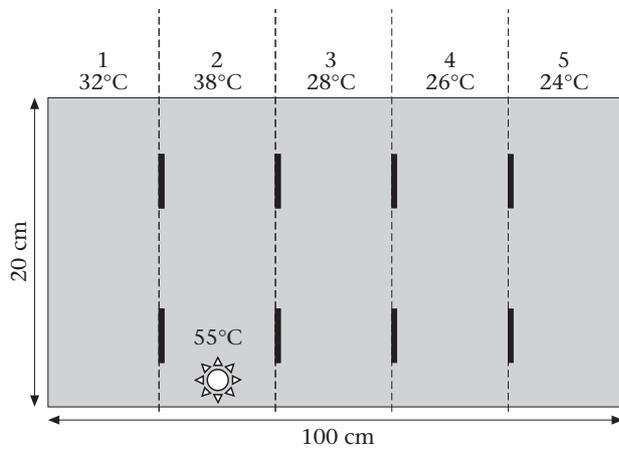
**Figure 1.** A diagram of the experimental set-up delineating the five sections of the arena. The ambient temperatures (as determined with data loggers) attained in each section are shown. The thermal value scores for each section are: area 1=4; area 2=5; area 3=3; area 4=2; area 5=1. Hidden lizards received a score of zero. Lizards that were basking under the heat source were assigned a score of 6.

baseline for assessing growth rates and behaviour during the experimental period (see below).

### Short-term trials

We staged 30 intraspecific short-term trials of each species and 34 short-term interspecific encounters. Individual lizards were used in no more than one short-term experiment. Half of the pairs from each of the three species combinations were comprised of two males and the other half of two females. Pairs of lizards were never from the same litter. Lizards comprising a pair were matched for body mass and length (to within 0.05 g and 0.5 mm). The mean ± SE age of *P. sicula* and *P. melisellensis* used in the short-term trials was $46.4 \pm 0.6$ and

$46.9 \pm 0.7$ days, respectively. Table 1 shows the mean and range in mass and SVL of lizards used in our study. There was no significant variation between species combinations in the difference in size between lizards comprising pairs (Table 2).

We conducted trials between 1000 and 1700 hours in an order that ensured a similar number of trials in the morning and afternoon for intraspecific and interspecific pairs. We observed behaviour from behind a one-way mirror, and recorded it on to audiotape using a dictaphone. To distinguish individuals, we stuck one or two tags ($1 \times 1$ mm) on the lizards' back. The tags were small pieces of adhesive tape, which did not need additional glue. They were easily removed by peeling at the end of the study without any damage to the skin.

Short-term trials were conducted within a 40-cm section of the heated end of test cages. A removable partition divided this area transversely in half such that the heat source fell in equal portions either side of the division. We placed each lizard from a pair alone in one side of the experimental arena and allowed it to acclimate undisturbed for 30 min. We then recorded how long each lizard spent basking (the body was flattened on the substrate and oriented at right angles to the heat source) over 5 min. The difference in basking duration between lizards comprising pairs did not differ significantly between species combinations (Table 2). Therefore, putative between-species variation in basking behaviour during trials probably reflects differences in the social standing of lizards rather than differences in thermal behaviour.

To begin a trial we removed the partition and recorded when two lizards approached to within 4 cm of each other and then when they moved further than 4 cm apart; this was considered to be one encounter. All encounters between lizards were assigned to one of four types and were given an aggression score based on the propensity of lizards to engage in aggressive interactions.

**Table 2.** Difference in individual expression of traits by lizards comprising homospecific and heterospecific pairs

| | Treatment combination | | | | | |
|---|---|---|---|---|---|---|
| | Heterospecific | Homospecific *P. sicula* | Homospecific *P. melisellensis* | df | F | P |
| Short-term trials | N=34 | N=30 | N=30 | | | |
| Mass (g) | 0.02±0.01 | 0.02±0.01 | 0.02±0.01 | 4, 174 | 1.52 | 0.19 |
| Snout–vent length (mm) | 0.9±0.2 | 0.9±0.2 | 0.8±0.2 | | | |
| Basking duration (s) | 9.9±2.9 | 8.5±3.0 | 5.7±2.7 | 2, 88 | 0.36 | 0.70 |
| Long-term trials | N=24 | N=20 | N=20 | | | |
| Mass (g) | 0.03±0.01 | 0.03±0.01 | 0.04±0.01 | 6, 112 | 0.90 | 0.50 |
| Snout–vent length (mm) | 0.8±0.1 | 0.9±0.2 | 0.9±0.2 | | | |
| Growth in mass (g/42 days) | 0.08±0.02 | 0.09±0.02 | 0.09±0.02 | | | |
| Activity index | 0.2±0.04 | 0.3±0.05 | 0.2±0.03 | 2, 56 | 1.55 | 0.22 |
| Location index | 0.2±0.03 | 0.4±0.08 | 0.3±0.04 | 2, 56 | 2.01 | 0.14 |
| Overlap: activity index | 0.5±0.05 | 0.5±0.06 | 0.6±0.05 | 2, 56 | 0.46 | 0.64 |
| Overlap: location index | 4.7±0.28 | 4.6±0.38 | 4.7±0.24 | 2, 56 | 0.26 | 0.77 |

Means are given±SE. Summary statistics from ANOVA or MANOVA (with sex and treatment as factors) are given for the main effect of treatment combination. Interactions between sex and treatment combination were always nonsignificant (P>0.25) as was the main effect of sex (P>0.25). The Wilks' lambda summary statistics are indicated for MANOVA; braces indicate the variables used. Within the heterospecific pairs in the long-term trials, the *P. sicula* was the larger individual in ca. 50% of cases.

(1) Nonconflicting interactions: one lizard walked directly towards the other and neither showed overt aggressive or submissive displays (aggression score=0).

(2) Retreats: one lizard moved directly towards the other, with or without showing aggressive displays, and either lizard moved away from its opponent (aggression score=1).

(3) Display fights: lizards approached one another and then exchanged threat displays (a lizard flattened its body laterally, arched its neck and raised its posture; aggression score=2).

(4) Attack fights: usually began with threat displays but escalated to at least one lizard rapidly running directly towards its opponent and occasionally involved biting (aggression score=3). Biting was observed during only four trials throughout the study and was never severe. On two occasions it involved an attempted bite. On two occasions the lizards made contact with each other but did not puncture the skin and the bite lasted less than 2 s.

Immediately after the first encounter, we also recorded the length of basking by each lizard under the heat source until the trial terminated 20 min later. Since the lizards clearly defended basking sites, we assumed that dominance is positively correlated with duration of basking. A trial was scored as having a clear dominance outcome if a lizard basked under the heat source during a trial for at least 40% longer than its opponent and its opponent retreated from at least 70% of the fights during a trial.

At the completion of their short-term trials, selected lizard pairs were left undisturbed in their test cages; this was the initiation of the long-term trials.

### Long-term trials

We staged 20 intraspecific long-term trials of each species and 24 interspecific long-term encounters. These pairs of lizards were selected from those used in the short-term trials, such that half of the pairs from each of the three species combinations were comprised of two males and the remaining pairs of two females. Lizards comprising a pair were matched for body mass, body length and growth rate. There was no significant variation between species combinations in the difference in size and growth rate between lizards comprising pairs (Table 2).

Long-term trials began immediately after short-term trials and were conducted within the entire test cage. Each pair of lizards remained in their test cage for the next 21 days. Lights were switched on daily between 0900 and 1700 hours. On the day after their introduction, and every 3 days thereafter, we recorded the behaviour of both lizards in a pair. Every 15 min from 0800 to 1800 hours we scored whether a lizard was hidden or active and, if active, we noted which section of the arena it occupied. After the second day of behavioural observations, and at the end of every observation day thereafter, both lizards in a pair were captured and measured (mass, SVL) and immediately returned to their terrarium.

At the end of the study adult lizards were returned to their point of capture, and juvenile lizards were released at the point of capture of their mother.

## Data Analysis

### Short-term trials

For each trial, we counted the total number of encounters observed (E). An overall aggression score (AS) was the sum of the number of encounters in each category multiplied by the corresponding aggression score. To obtain an aggression score per encounter, we divided AS by the total number of encounters observed during the trial (i.e. AS/E). An overall aggression score for individuals comprising heterospecific pairs was calculated as the number of display fights and attack flights initiated multiplied by the corresponding aggression score.

We used two-way ANOVA with species combination and sex as factors to explore differences in the number of encounters (E), aggression score (log[AS]), and aggression score per encounter (AS/E). For the heterospecific trials we used a paired sign test to examine whether *P. sicula* consistently attained a higher aggressive score than *P. melisellensis*. Fisher's exact tests were used to examine between-treatment differences in the probability of trials having a clear dominance outcome.

### Long-term trials

We calculated an index of activity time as the number of periods that a lizard was not hidden divided by the total number of observation periods. For each pair of lizards we calculated overlap in activity time as the number of periods during which both lizards were simultaneously active divided by the total number of observation periods.

We estimated thermal microhabitat use as the number of periods that a lizard was in each section of the terrarium multiplied by the thermal value of that section (see above), and divided by the total number of periods that a lizard was not hidden. For each pair of lizards we calculated the product of the number of periods that both lizards occupied the same section of the terrarium and the thermal value of that section. To calculate overlap in thermal microhabitat use this value was divided by the total number of observation periods that both lizards were not hidden.

We calculated growth rates of individual lizards by regressing the logarithm of SVL against the number of days elapsed since birth. Slopes of these regression lines estimate size-specific growth rates, that is, estimates are independent of size at the beginning of the growth period (Sinervo & Adolph 1989). Coefficients of determination of regression lines were rarely less than 0.90. We opted to estimate growth in SVL rather than mass, because the latter variable is subject to short-term fluctuations in for example feeding status.

We calculated the indices of activity time and thermal microhabitat use for the observation day during the pre-experimental period (i.e. when lizards were housed alone) and for each observation day during the long-term experiment. For each individual lizard we separately estimated growth rate during the pre-experimental period and over the course of the long-term trial. To account for (small) differences in individual growth rates and behaviour during the pre-experimental period, we expressed
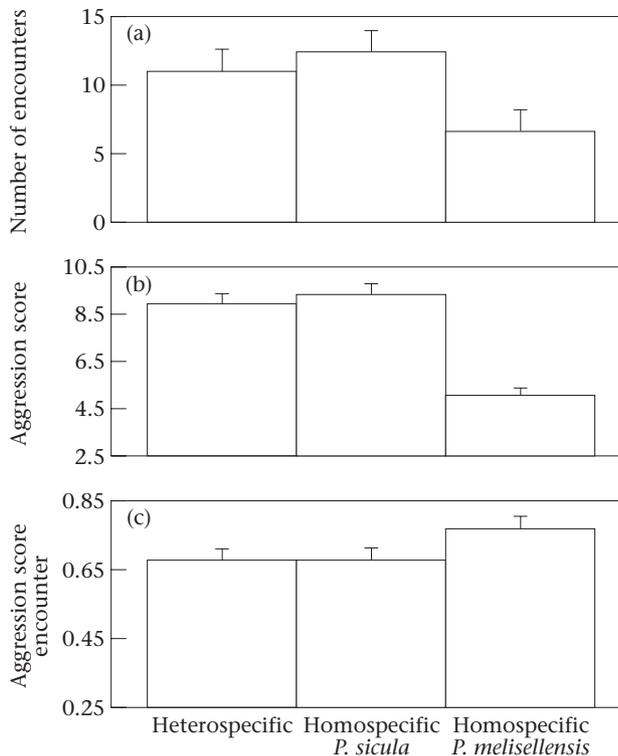
**Figure 2.** Mean+SE values of behaviour recorded during the short-term trials for pairs of lizards: heterospecific, homospecific *P. sicula* and homospecific *P. meliselensis*. (a) Number of encounters, (b), aggression score and (c) aggression score/encounter. See text for formulae used to calculate the indices.

growth and behaviour during the experimental period relative to growth and behaviour during the pre-experimental period by calculating the difference between them. Positive values indicate that expression of the trait was higher during the experimental than during the pre-experimental period; negative values denote a lower expression of the trait during the experimental than during the pre-experimental period.

To test for differences in activity and microhabitat use between *P. sicula* and *P. melisellensis*, we performed repeated measures ANOVAs with species combination and sex as factors and time as the repeated measure. We used the same ANOVA model to analyse the growth data but time was not included as a repeated measure. To examine variation between the species treatments in overlap in activity and overlap in microhabitat use we used repeated measures ANOVA with number of species comprising a combination and sex as factors and time as the repeated measure.

## RESULTS

### Short-term Trials

The number of encounters and the overall aggression score varied significantly between the three types of paired combinations (ANOVA: species combination: encounters: $F_{2,85}=4.20$, $P=0.018$; aggression: $F_{2,85}=3.17$,
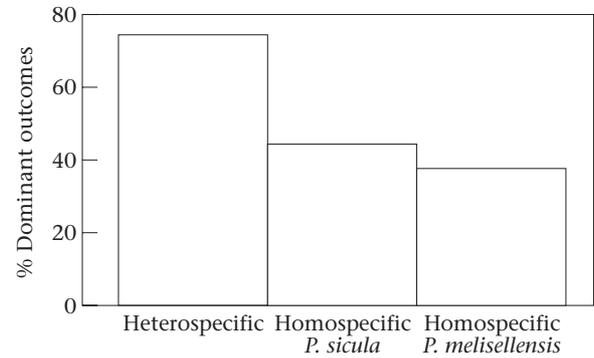


**Figure 3.** Percentage of trials resulting in a clear dominant–subordinate relationship during the short-term trials for pairs of lizards: heterospecific, homospecific *P. sicula* and homospecific *P. meliselensis*.

$P=0.047$; Fig. 2). They were similar in homospecific pairs of juvenile *P. sicula* and heterospecific pairs (Tukey–Kramer honestly significant difference test: mean difference $\leq 0.21$, critical difference $\geq 4.76$). In contrast, homospecific pairs of *P. melisellensis* engaged in fewer encounters and had a lower overall aggression score (Tukey–Kramer honestly significantly difference test: mean difference $\geq 5.81$, critical difference $\geq 4.76$). There was no significant variation between paired combinations in the aggression score per encounter (ANOVA: species combination: $F_{2,85}=1.01$, $P=0.368$; Fig. 2).

During heterospecific short-term trials there was a significant trend for *P. sicula* to have a higher individual aggression score than its opponent *P. melisellensis* (number of trials: *P. sicula* least aggressive 4, *P. sicula* most aggressive 26, *P. sicula* as aggressive as *P. melisellensis* 4; paired sign test: $P<0.001$).

Short-term trials involving pairs of *P. sicula* and *P. melisellensis* were more likely to result in a clear dominant–subordinate relationship than were short-term trials involving pairs of conspecific lizards (Fisher's exact test: $\chi_2^2=6.74$, $P=0.034$; Fig. 3). Of the heterospecific short-term trials that resulted in a clear dominant–subordinate relationship, a larger than expected number (19 out of 24) involved *P. sicula* being the dominant individual (Fisher's exact test: $\chi_1^2=8.2$, $P=0.004$).

### Long-term Trials

Cohabiting with another individual caused lizards to shift their use of thermal microhabitats from that displayed in isolation. However, the magnitude and direction of this change in behaviour varied between species depending on the number of species comprising a pair and the duration of exposure to the opponent lizard (repeated measures ANOVA: number of species × species × time: $F_{6,726}=4.23$, $P=0.003$).

For the first 15 days of the experiment *P. sicula* from heterospecific trials attained higher thermal microhabitat scores than in isolation, whereas *P. melisellensis* from heterospecific trials attained lower thermal microhabitat scores than in isolation (ANOVA: species: $F_{1,176}=5.04$, $P=0.006$; Fig. 4). During the same period there was no
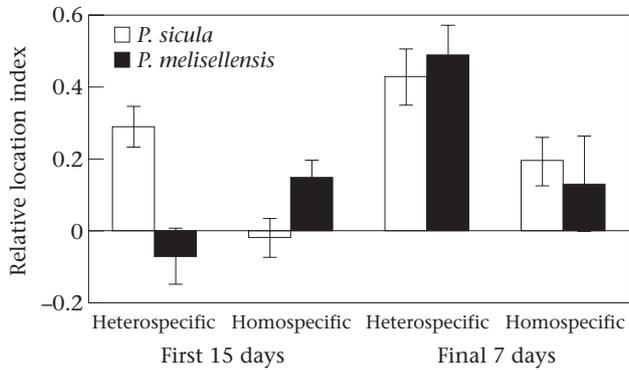
**Figure 4.** Mean±SE thermal microhabitat score of *P. sicula* versus *P. meliselensis* during long-term trials with heterospecific and homospecific pairs. Behaviour during the experimental period was expressed relative to behaviour during the pre-experimental period by calculating the difference between them. Data are presented separately for the first 15 and the final 7 days of the experiment.
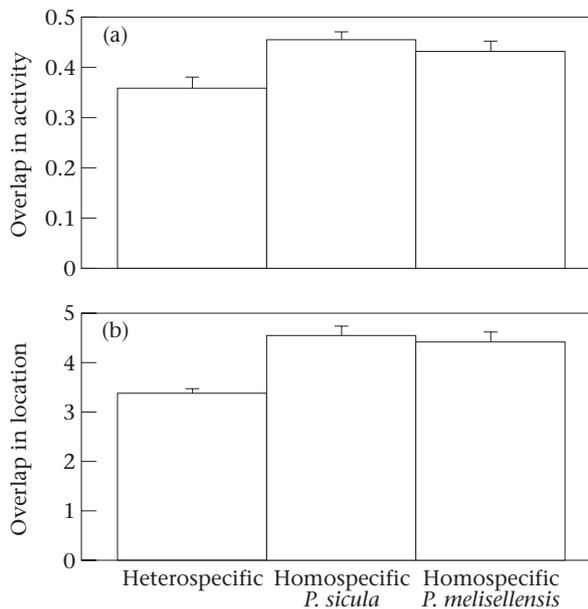


**Figure 5.** Mean+SE values of overlap in (a) activity and (b) thermal microhabitat recorded during the long-term trials for pairs of lizards: heterospecific, homospecific *P. sicula* and homospecific *P. meliselensis*. See text for formulae used to calculate the indices.

significant variation between species comprising homospecific pairs in shifts to thermal microhabitat use (repeated measures ANOVA: species: $F_{1,304}=1.52$, $P=0.221$; Fig. 4). For the final 7 days of the experiment the two species did not differ markedly in the way that they modified their use of thermal microhabitats (repeated measures ANOVA: species: $F_{1,121}=2.60$, $P=0.611$; Fig. 4).

Shifts in microhabitat use by lizards did not reflect changes in how long they were active during trials. There was no significant variation between species in shifts to activity levels between the pre-experimental and experimental periods ($\bar{X} \pm$ SE relative activity index: *P. sicula*: $0.71 \pm 0.015$; *P. melisellensis*: $0.67 \pm 0.016$; repeated measures ANOVA: species: $F_{1,714}=0.61$, $P=0.435$).
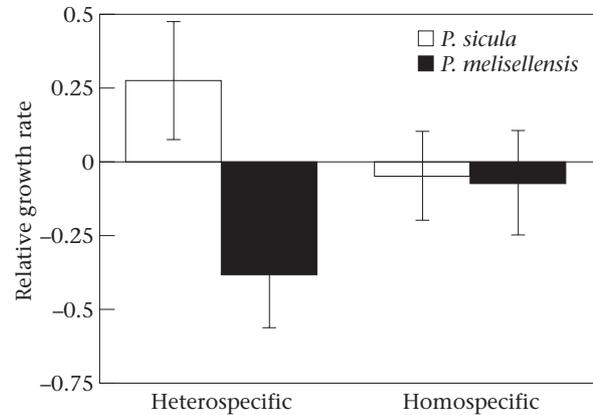


**Figure 6.** Rates of growth ($\bar{X}\pm$SE) in snout–vent length during long-term trials for *P. sicula* and *P. melisellensis* comprising heterospecific pairs. Rates were calculated by regressing the logarithm of size against the number of days elapsed since the beginning of a trial. Growth during the experimental period was expressed relative to growth during the pre-experimental period by calculating the difference between them.

The lizards in a pair were less likely to be active simultaneously if the combination was heterospecific than homospecific (repeated measures ANOVA: species combination: $F_{2,348}=3.55$, $P=0.035$; Fig. 5a). Similarly, there was a lower probability that both lizards in a pair would use a section of the arena at the same time during heterospecific than homospecific trials (repeated measures ANOVA: species combination: $F_{2,348}=4.85$, $P=0.011$; Fig. 5b).

During long-term trials lizards modified their growth in SVL from that in isolation but the magnitude and direction of this change varied between species combinations (ANOVA: number of species × species: $F_{1,124}=3.00$, $P=0.085$), although not significantly so. We conducted further analyses on separate data sets for heterospecific and homospecific pairs. During heterospecific trials *P. sicula* grew faster than in isolation compared with *P. melisellensis* (ANOVA: species: $F_{1,46}=5.88$, $P=0.019$; Fig. 6). A comparison of data for specific pairs of lizards confirms this opposing pattern in relative growth rates between species during heterospecific trials (paired *t* test: $t_{23}=2.42$, $P=0.024$). Relative growth rate during the experiment was faster in *P. sicula* in 18 of 24 pairs (binomial test: $P=0.023$). During the same period there was no significant variation between species comprising homospecific pairs in relative growth rates (ANOVA: species: $F_{1,78}=0.09$, $P=0.922$; Fig. 6).

## DISCUSSION

Studies on demographic characteristics (Dunham 1980; Smith 1981; Alatalo et al. 1985), patterns of resource partitioning (Connell 1961; Schoener 1968; Dickman 1988; Losos 1994) and phylogenetic reconstruction of character evolution (Cotgreave 1994; Losos 1994; Lindeman 2000) have corroborated the existence of competition between species. However, the mechanistic basis of the competitive interactions has rarely been addressed

directly. Specifically, few studies have assessed and provided evidence for the importance of aggression as a mechanism of competitive exclusion (see Tilman 1987; Dickman 1991; Bolger & Case 1992; Niemela 1993). Our study, using staged laboratory encounters, provides clear evidence of behavioural interference between *P. sicula* and *P. melisellensis*. Furthermore, it explicitly shows that the interference ability is asymmetric in favour of *P. sicula*.

Our experiments were designed to control for factors that may be important determinants of the outcome of first encounters between unfamiliar individuals (Stamps & Krishnan 1994; see also Connolly et al. 2001). Specifically, we used socially naïve animals, and staged encounters between pairs that were matched for body size and initial growth rate. The set-up of the experimental arenas forced animals to interact for access to a localized basking site. Both species are territorial and bask (sometimes in small sun flecks) to regulate their body temperature (Avery 1984; Van Damme et al. 1990; Grbac & Bauwens 2001). The body temperatures that ectotherms achieve during activity will affect the rate of biochemical and physiological processes and alter ecologically relevant performance capacities (e.g. Avery 1984; Huey & Kingsolver 1989; Van Damme et al. 1990; Bauwens et al. 1995). Hence, gaining access to a basking site may have important consequences for the ability to capture and process food, and thereby for growth rates. However, we caution that other mechanisms could (directly or indirectly) underlie a reduced growth rate in competing lizards: for instance, stress hormones may be triggered by interference (see Sinervo & Licht 1991 and references within).

Overlap in any niche dimension should be greater among conspecifics than heterospecifics (Oritz & Jenssen 1982; Duncan 1991; Lancaster & Jaeger 1995). Therefore, the most acute ecological competition among individuals is expected to be between conspecifics (Stamps 1977; Oritz & Jenssen 1982; Tokarz & Beck 1987; Duncan 1991; Lancaster & Jaeger 1995; but see Schoener 1975 for effects when exploitative and interference competition is asymmetrical). Our data show that behavioural interference between *P. sicula* and *P. melisellensis* is at least as great as that between conspecifics of these species. Brief encounters between *P. sicula* and *P. melisellensis* were significantly more aggressive and more likely to result in clear dominant–subordinate relationships than were brief encounters between pairs of conspecific *P. melisellensis* (Fig. 3). Furthermore, during prolonged encounters individuals comprising heterospecific pairs were significantly less likely to occupy a thermal microhabitat simultaneously than individuals from homospecific pairs (Fig. 5). Hence, our observations indicate that *P. sicula* and *P. melisellensis* interfere directly for access to a basking site, a spatially localized resource.

Comparing behaviour of individuals comprising heterospecific pairs tests for directionality of aggressive interactions between species (e.g. Bolger & Case 1992; Lancaster & Jaeger 1995). In the present study, these individual contrasts show that behavioural interference is asymmetric in favour of *P. sicula*. During brief encounters

*P. sicula* were significantly more aggressive and more likely to be dominant than their *P. melisellensis* opponents (Fig. 3). When lizards cohabited for longer periods, *P. sicula* used better, and *P. melisellensis* poorer, thermal microhabitats than in isolation (Fig. 4). In addition, *P. sicula* grew faster, and *P. melisellensis* slower, than in isolation (Fig. 6). Importantly, these between-species shifts in microhabitat use and growth were not evident during prolonged encounters with homospecific pairs (Fig. 6). The observed differences in growth rates can be interpreted as a direct consequence of variation in thermal microhabitat use. Greater access to basking opportunities facilitates attainment of body temperatures that maximize energy intake and growth (e.g. Pough 1980; Andrews 1982; Huey 1982; Avery 1984; Niewiarowski & Roosenburg 1993).

Differences in growth rates could have significant ramifications for important components of fitness and the life history of lizards. Slower growth during a lizard's early life can lead to smaller sizes at maturity, the production of fewer offspring per litter, and lighter clutch masses and offspring (e.g. Sinervo et al. 1992; Downes 2001). Increasing in body mass at a slower rate might influence several processes through its effect on body size. For instance, smaller individuals are generally subordinate (Tubbs & Ferguson 1976; Stamps 1984; Metcalfe et al. 1990; Smith 1990; Ryer & Olla 1996; but see below) and may have lower survival probabilities than larger individuals (Werner & Hall 1974; Fox 1975; Ferguson & Fox 1984; Peckarsky & Penton 1989; Downes, in press). Hence, our observations indicate that asymmetric aggressive interactions between hatchlings of our study species reduce an important fitness component (i.e. growth rate) of *P. melisellensis*. This is consistent with the hypothesis that direct behavioural interference by *P. sicula* is the mechanism leading to exclusion of *P. melisellensis*. However, we are reluctant to extrapolate this result to a field situation without quantitative information on the availability of sun patches in natural microhabitats.

The repeatability of these findings in adult lizards depends, at least in part, on the stability of dominance relationships established during the first weeks of life. In several vertebrate species, initial dominance relationships are unlikely to change even if the subordinate member of a dyad grows larger than the dominant member. For instance, in *Anolis aeneus* smaller dominant lizards continue to chase and displace subordinate lizards that have grown 20% larger than themselves (Stamps 1984). Similar results have been obtained in studies of avian nestlings and fish (reviewed in Stamps 1984). *Podarcis sicula* appear to dominate *P. melisellensis* not only during first encounters but also for at least several weeks afterwards (see also Stamps & Krishnan 1994). Furthermore, comparisons of body sizes in adult lizards from our study populations suggest that adult *P. sicula* are considerably larger than adult *P. melisellensis* (see Table 1), and large species are often dominant to smaller species (Schoener 1983). In laboratory experiments, adult *P. sicula* interact aggressively with, and suppress activity levels in adult *P. tiliguerta*, a species that is similar in body size to *P. melisellensis* (Vanhooydonck et al. 2000). Hence, it

seems unlikely that the dominance of *P. sicula* to *P. melisellensis* reported herein for hatchlings would be reversed in adult lizards.

Sympatric species in direct competition often separate themselves by differences in structural niche (e.g. perch diameter, perch height) and, in some cases, by climatic habitat (e.g. open versus shaded areas) or by character displacement (e.g. Pizzimenti & DeSalle 1981; Parmenter & MacMahon 1983; James & Shine 2000). However, despite their similar ecological requirements, *P. sicula* and *P. melisellensis* occur in allopatry throughout most of their range. On the few larger islands where the two species are reported to coexist, two distinct habitat types are present indicating that the species are probably not syntopic (Radovanovic 1959; Nevo et al. 1972; Raynor 1989). This pattern may reflect the strength of the aggression between the species. The proper test of this hypothesis would be to remove species from an area and look at colonization from the other species in the same area. Our results clearly show that interactions can still occur between such species, even given their great geographical separation. The rapid response of lizards towards heterospecific individuals suggests a strong ongoing interaction between the two species. However, we cannot discount the possibility that *P. sicula* react to other species of lizards in much the same way as they do towards *P. melisellensis*.

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