



# Thermoregulation comparisons between a threatened native and an invasive lizard species

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Lizard thermoregulation is costly and is largely behavioural. *Podarcis raffonei*, endemic of few islets of the Aeolian archipelago (southern Italy), is one of the most threatened lizards in Europe, its survival being under threat also due to the presence of the congeneric *P. siculus*, a successful invader characterised by behavioural plasticity and effectiveness and precision at regulating body temperature ( $T_b$ ). We tested whether thermoregulation behaviour diverges between the two species by analysing (i) the heating rates under a standard thermal condition, and (ii) the temperature at which lizards ended basking ( $T_{final}$ ) along a thermal gradient. Overall, we found behavioural differences between the two lizards (i.e. *P. siculus* exhibited lower  $T_{final}$ ), although both species had comparable heating rates and thermoregulated in the same thermal conditions. The invasive *P. siculus* had lower  $T_{final}$  and, since heating rates were similar between species, it expended less time basking than native *P. raffonei*. We speculate that the observed thermal ecology differences could provide a selective advantage to *P. siculus* in the harsh island environment.

**Keywords:** *Podarcis raffonei*, *Podarcis siculus*, lizard, biological invasion, competition

## INTRODUCTION

Ectothermic organisms, such as reptiles, regulate their body temperature ( $T_b$ ), in relation to the external environmental temperatures, within a restricted range close to their physiological optimum (Cowles & Bogert, 1944; Shine & Kearney, 2001; Seebacher, 2005). The extent of the thermoregulation process varies from species to species, within populations, and among different environments, along a continuum from a wide to a narrow thermal range (e.g. Ruibal & Philibosian, 1970; Adolph, 1990; Hertz, 1992) also in relation to climate (e.g. Shine & Madsen, 1996) and microclimate (e.g. Paci et al., 2018). Thermoregulation is largely behavioural in reptiles, including lizards (Spellerberg, 1972; Castilla et al., 1999), and the maintenance of optimal physiological performances is unequivocally habitat-selection-dependent (e.g. Huey, 1991; Reinert, 1993). For instance, body temperature ( $T_b$ ) regulation in lacertid lizards is controlled by (i) adapting activity patterns to the external temperature range, (ii) selecting thermally favourable micro-habitats (e.g., basking spots) and (iii) using postural adjustments that alter the exchange of heat with the environment (Bauwens & Herts, 1996).

Interspecific competitors can temporarily disturb the achievement of optimal  $T_b$  by pushing away from

or exploiting optimal basking places, thus leading to a reduction in performance by direct competition or interference (Cady & Joly, 2003; Luiselli, 2008; Žagar et al., 2015).

In Europe, where the thermal ecology of lizards has been generally intensely studied (e.g. Ortega & Martín-Vallejo, 2019), several threatened species do occur in small Mediterranean islands (IUCN, 2020). In these arid islands, lizard populations generally face extreme scarcity of trophic resources and individual thermoregulation can be affected by strong temporal changes in both abiotic and biotic conditions, thus limiting the time available to forage (see Pérez-Mellado, 1989; Castilla & Bauwens, 1991; Lo Cascio, 2006; Capula & Lo Cascio, 2011; Capula et al., 2014). The IUCN's (2020) Critically Endangered Aeolian lizard, *Podarcis raffonei* (Mertens, 1952), endemic of the Aeolian archipelago in southern Italy (Capula et al., 2002), is the most threatened lizard in Europe (Capula, 2004; Capula & Lo Cascio, 2006, 2011). The continued survival of this species is uncertain due not only to the very small range (Capula et al., 2002), but also to the presence of the congeneric Italian wall lizard *P. siculus* (Rafinesque-Schmaltz, 1810) (Capula et al., 2002), an invasive lacertid accidentally introduced in historical time in the Aeolian Archipelago. It has been hypothesised that *P. siculus* can negatively impact

native lizards, including *P. raffonei*, through competition, displacement and hybridisation (Capula et al., 2002). The overall colonising success of *P. siculus* is considered to be due to quick acclimatisation and adaptability to new environmental conditions propensities, dispersal abilities (Deichsel et al., 2010; Vignoli et al., 2012), and likely to effectiveness and precision at regulating its Tb (Kapsalas et al., 2016; Ortega et al., 2016). Although the constraints of the thermal environment may affect ectotherm species distribution and population density, they have been rarely considered jointly with the possible outcome of interspecific competition, i.e. between invader and native species (Angert et al., 2002).

Preliminary data on field Tb of *Podarcis raffonei* were published by Lo Cascio (2006) and Capula et al. (2014), but up to now the thermo-physiological and thermo-ecological characteristics of this species versus its potential competitor (*P. siculus*) have remained largely unexplored. In addition, no study is available on the thermal ecology of these species under identical environmental quality conditions.

In the present study, by two experiments in controlled arenas, we analyse the thermoregulation characteristics of the two species within the same range of available temperatures. In previous studies, *P. siculus* were more exploratory, bold and neophilic than the sympatric native congeneric lizards (Damas-Moreira et al., 2019). Therefore, it can be hypothesised that *P. siculus* may also differ from *P. raffonei* in thermoregulation performance. Specifically, we tested in comparative experiments (i) the heating rate under standard thermal conditions, and (ii) the temperature at which lizards ended basking ( $T_{\text{final}}$ ) along a thermal gradient. We expect that the possible competitive advantage of *P. siculus* on *P. raffonei* should be, among other factors (Mencía et al., 2017), in thermoregulation traits (Angilletta, 2009) rather than in anatomical adaptations (Camacho et al., 2015). That is: (i) the two congeneric species do not differ in the rate of heating rates due to morphological and anatomical similarities (Gvoždík, 2002), and (ii) *P. siculus* is more efficient than *P. raffonei* in some traits of the thermal biology (i.e. faster achievement of and/or lower Tb to enter activity).

## MATERIALS AND METHODS

### Study species

The Aeolian lizard *Podarcis raffonei* is a small lizard, up to 7.5 cm SVL, that inhabits harsh environments (for instance, in Strombolicchio and La Canna islets), with rocky walls facing the sea and very sparse vegetation. In Vulcano, *P. raffonei* inhabits a human-altered area and some small promontories (Corti & Lo Cascio, 1999). The Italian wall lizard *P. siculus* is a medium-sized (up to 9 cm SVL, Corti et al., 2010) species that ranges throughout Italy south of the Alps, including many islands in the Tyrrhenian Sea, and along the Adriatic coastal area to Montenegro. It is also an invasive species established in several countries outside its native range (Crnobrnja-sailovic et al., 2009).

### Protocol

Lizards were collected from two areas: we sampled *P. raffonei* individuals in May 2017, at the Capogrosso area in the island of Vulcano (Sicily; 38°25'6.98"N, 14°56'32.80"E). For logistical reasons we were unable to catch *P. siculus* individuals from the Aeolian Archipelago. However, since this species is extremely widespread, ecologically generalist and even introduced in different regions of the world, we collected individuals of this species in the same location where *P. raffonei* was hosted (Rome, Latium; 41°54'59.99"N, 133 12°29'16.77"E) also to avoid translocation of an invasive species. The Aeolian lizard population was collected for an ex-situ conservation project headed by the Department of Sciences – Roma Tre University and the Fondazione Bioparco di Roma. After the capture, the individuals were transported to the facilities of the Reptile House at the Fondazione Bioparco di Roma, formerly known as the municipal zoo in Rome. Capture, captive keeping and authorisation for performing studies were given by the Ministry of the Environment and the Protection of the Territory and the Sea (note 0008937; May 2nd, 2017). Sex was determined by the presence/absence of active femoral pores (present in males) and by the width and shape of the head (larger in males). All lizards were adults, females were not pregnant, and each of them was measured for the snout-vent-length (SVL, mm). All individuals were housed in enclosures (1.0 x 1.0 x 0.9 m), with sand as substrate, pine bark as refuges and density set at 5 individuals/m<sup>2</sup>.

### Experiment I – Accumulation of heat

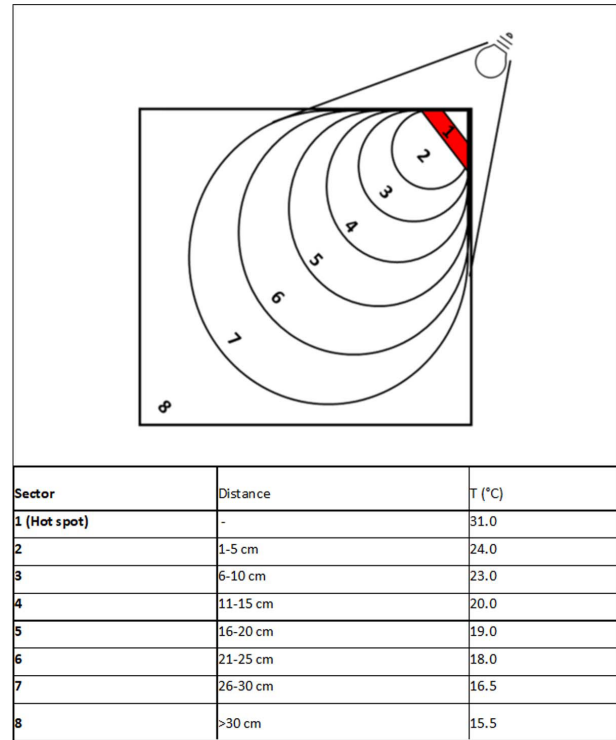
In order to analyse whether there were any differences between *P. raffonei* and *P. siculus* regarding the heating rates, we impeded lizard individuals to adopt any behavioural compensatory mechanism while being tested (Gvoždík, 2002) by placing them into a fauna-box (10 cm x 15 cm), filled with river sand as a substrate, that was positioned within a larger storage box. Above the box an infrared heating lamp (Philips 230-50V) was positioned vertically, supported using a tripod. We measured temperature at the ground inside the fauna-box in five points (four vertices and the centre) by using a digital laser infrared thermometer ( $\pm 0.1$  °C; Seafont AT380) set for the measurement of sandy substrates. The reduced box size allowed obtaining a homogeneous temperature ( $32 \pm 0.3$  °C; mean  $\pm$  SD) within the box to test thermoregulation efficiency of lizards under the same conditions of radiation. The duration of the heat exposure was 10 minutes. The set of temperatures used in our experiment did not exceed 33 °C, in order to not exceed the maximum of the average Tb recorded in the field for *P. raffonei* individuals at Faraglione and at Strombolicchio islets (respectively, 34.7 °C and 33.2 °C) (Lo Cascio, 2006, 2010). For each tested individual, the body temperature at the start of the experiment ( $T_{\text{initial}}$ ) was measured by inserting a K-type thermocouple probe (0.5 mm in diameter) connected to a digital microprocessor thermometer (HD9218, Delta Ohm, Italy) 5 mm into its cloaca (Gvoždík, 2002). After  $T_{\text{initial}}$  recording, the individual was introduced into the fauna box.

During the 10 minutes of test, the cloacal temperature was measured 10 times, once per minute. The time taken to take the individual and measure the cloacal temperature (average = 15 seconds) was homogeneous for the various measurements and among the various individuals, thus it did not bias the thermoregulation process and measurements. After measuring the cloacal temperature, the individual was quickly repositioned in the box. After the 10 minutes of testing, the final cloacal temperature ( $T_{\text{final}}$ ) was measured. We defined as  $\Delta T$  the difference between  $T_{\text{final}}$  and  $T_{\text{initial}}$ . No individual that was housed in the experiments died or lost its tail, thus indicating that the welfare of the captive animals was adequately maintained.

### Experiment II - Thermoregulation behaviour

In order to evaluate differences in the performance of thermoregulation and to evaluate any difference between the two species as for the behavioural regulation of body temperature in thermally heterogeneous habitats (e.g. basking duration, choice of the basking site), experimental arenas were built with a gradient of basking temperatures that could be chosen independently by individuals during the test. Seven individuals were randomly selected for each species and sex. This small sample size was due to the extreme rarity and threatened status of *P. raffonei*. The arena was prepared inside a climatized room with temperatures ranging 15-17 °C. The ambient temperature was selected to have almost inactive animals to be tested. Inside the room, we placed four 1 m x 1 m boxes to house the animals (divided by species and sex) as well as the experimental boxes within which to conduct the tests. The setting of the experimental boxes was dictated by the need to make a basking area that would provide a temperature gradient with a single > 30 °C spot not straightforwardly available to lizards (i.e. raised above the ground). This hot spot was made by placing a piece of cork (10 cm height and 5 cm<sup>2</sup> in upper surface) under a spot lamp (Sera Reptil Alu Reflector 200; diameter 200 mm) carrying a bulb (Solar raptor UV HID-lamp-70 W spot-beam) (Fig. 1). The basking area generated by the lamp heat consisted of a gradient of decreasing temperatures the further away from the hot spot. The temperature gradient was subdivided into eight radial sectors out of which six were evenly spaced (by 5 cm), representing distinct basking sites associated with different temperatures (Fig. 1). Temperature at the ground of the various basking areas was measured by a digital laser infrared thermometer (0.1 °C; Seafont AT380) set for the measurement of sandy substrates both before each experiment and after two hours from turning on the lamps to allow them to reach steady temperature. On top of the cork the temperature was 31.0 °C, 7 °C higher than at the ground (sector 1) (Fig. 1). We set 31.0 °C as maximum temperature following the same reasons as in experiment I. Before starting each experiment, the air temperatures of the room and the experimental arena were recorded. Furthermore, before starting the test, the cloacal temperature ( $T_{\text{initial}}$ ) of each lizard was also measured.

The beginning of the experiment started by



**Figure 1.** Arrangement of the experimental arena. Relative distance from the hot spot (1) and temperature at ground (°C) for each sector (2-8) are also indicated.

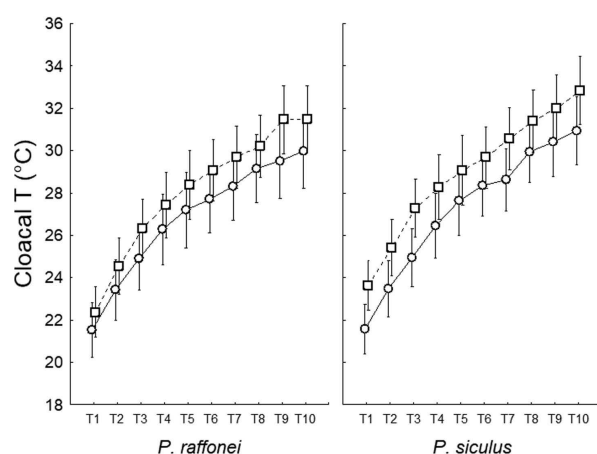
positioning the animal in the furthest point opposite the hot spot (sector 8, at room temperature; Fig. 1). All the various movements and the time spent by the lizards across sectors were recorded. The test ended when the animal left the thermoregulation area and moved to sector 8 for at least one minute. The total duration of the experiment was recorded (total time, seconds). At the end of each test, cloacal temperatures ( $T_{\text{final}}$ ) were recorded. All the experiments were video-recorded with the experimenters being not visible to the lizards. The experiments were conducted between 10:00 AM and 03:00 PM (Rome standard time) and involved two persons (YC and LV).

### Statistical analyses

We built several General and Generalised linear models to test the effect of species, sex, SVL, and basking site on the thermoregulation behaviour of the lizards. To test the rate of heat accumulation, we conducted a GLM (Repeated Measures ANOVA) with the cloacal temperature measured at 1-minute intervals as response variable, species and sex as fixed factors, and the 10 repeated measures of cloacal temperature as the treatment. We tested the effects of (1) species and sex on the basking site (defined as hot spot vs. remaining sectors of the thermal gradient) choice (binomial error distribution and link logit function; dependent variable: basking site; fixed factors: species and sex; covariate:  $T_{\text{final}}$ ); (2) species, sex, basking site on  $T_{\text{final}}$  (normal error distribution; dependent variable:  $T_{\text{final}}$ ; fixed factors: species and sex; covariates: SVL,  $T_{\text{initial}}$ ); (3) species, sex, basking site on  $\Delta T$  (normal error distribution; dependent variable:  $\Delta T$ ;

**Table 1.** Results of the Repeated Measures ANOVA conducted on the rate of accumulation of heat by lizards. The effects of species and sex (group variables) on the cloacal temperature measured at 1-minute intervals (response variable) are shown. R1=treatment (10 repeated measures of cloacal temperature).

Effect	SS	DoF	MS	F	P
Intercept	182862.8	1	182862.8	8121.005	0
Species	21.5	1	21.5	0.953	0.341
Sex	126.1	1	126.1	5.599	0.028
Species*Sex	2.1	1	2.1	0.094	0.762
Error	427.8	19	22.5		
R1	3302.4	10	330.2	261.428	<0.001
R1*species	6.5	10	0.6	0.514	0.879
R1*sex	5.9	10	0.6	0.47	0.908
R1* Species*Sex	5.5	10	0.5	0.434	0.928
Error	240	190	1.3		



**Figure 2.** Experiment on accumulation of heat. Cloacal temperature measured at 1-minute intervals for 10 minutes on males (squares) and females (circles) of *P. raffonei* and *P. siculus*. Vertical bars denote 95 % confidence intervals.

fixed factors: species and sex; covariates: SVL, “total time”,  $T_{initial}$ ); (4) species, sex, basking site on “total time” (normal error distribution; dependent variable: “total time”; fixed factors: species and sex; covariate: SVL). For each model, we estimated the overall fit by means of regression between sum of squares of the total model vs. residuals (multiple  $R^2$ ; for the General Linear Models) and of ratio between degree of freedom and scaled deviance (DoF/SDev; for the Generalised Linear Models). Models with high multiple  $R^2$  or ratio DoF/SDev around 1 were considered as satisfactorily explaining all (random) error variability in the data (i.e. no overdispersion) (Nelder & Wedderburn, 1972). All the models provided a good fit to the data but model (4) that showed a marginal lack of fit (see Supplementary Material). All tests were carried out by using Statistica v 8.0 (Statsoft) with two tails and alpha set at 0.05.

## RESULTS

### Experiment I – Accumulation of heat

The data referring to the individuals tested for the accumulation of heat experiment are summarised in Table S1. There was no significant effect for any of the

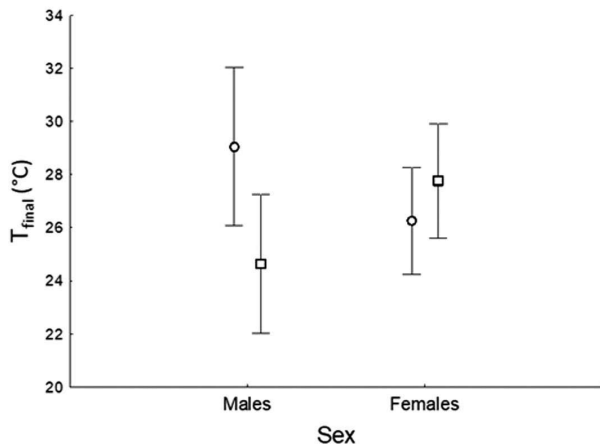
predictors tested in the Repeated Measures ANOVA model except for the sex. The temperatures reached through the one-minute-step did not vary significantly between the two species (Table 1; Fig. 2). Female  $T_b$  was significantly higher than males in the first 3-minutes of treatment before slowing down reaching the same trend as males for the rest of the treatment ( $F_{1,19} = 5.60$ ,  $P = 0.028$ ). On the other hand,  $\Delta T$  was not influenced by sex, species, or interaction species\*sex (for all tests,  $F \leq 0.865$  and  $p \geq 0.360$ ). Similarly, the  $T_{final}$  was not influenced by any of the considered factors and covariates (for all tests,  $F \leq 1.670$  and  $p \geq 0.208$ ).

### Experiment II - Thermoregulation behaviour

A first GLM model showed that species, sexes and their interaction did not influence the choice of the basking site (for all effects,  $Wald \leq 1.663$ ;  $p \geq 0.197$ ). As for  $T_{final}$ , only the basking site ( $F_{1,19} = 14.390$ ,  $p < 0.001$ ) and the interaction term species\*sex ( $F_{1,19} = 5.328$ ,  $p = 0.032$ ) showed an effect (Table S2). Individuals that used the hot spot showed higher  $T_{final}$  ( $29.9 \pm 2.3$  °C) than lizard that thermoregulated in the remaining sectors ( $24.8 \pm 2.4$  °C). Moreover, *P. siculus* males had  $T_{final}$  lower ( $26.36 \pm 2.71$  °C) than *P. raffonei* males ( $29.33 \pm 2.20$  °C) regardless of body size (SVL) and  $T_{initial}$  (Post-hoc test:  $p < 0.01$ ; Fig. 3). There was a positive effect of the basking site on  $\Delta T$  ( $F_{1,18} = 13.132$ ,  $p = 0.001$ ), with individuals basking on the hot spot showing a greater  $\Delta T$  than those basking elsewhere (Table S3). There was a positive correlation between  $\Delta T$  and  $T_{initial}$  ( $F_{1,18} = 20.711$ ,  $p < 0.001$ ), that is the lower the  $T_{initial}$  the more the difference with  $T_{final}$ . No effect of species, sex, SVL, and ‘total time’ on  $\Delta T$  was detected (for all tests  $F \leq 3.121$  and  $p \geq 0.094$ ), whereas a positive effect of the species\*sex interaction term was observed ( $F_{1,18} = 6.769$ ,  $p = 0.018$ ), with  $\Delta T$  being significantly different between the two species: male *P. siculus* individuals accumulated lower  $\Delta T$  than male *P. raffonei*. The ‘total time’ of the experiment duration was significantly different between the sexes (Table S4), with females of both species spending less time basking than males ( $F_{1,20} = 6.055$ ,  $p = 0.023$ ).

## DISCUSSION

Our study consolidates knowledge on how *P. siculus*



**Figure 3.** Experiment of thermal behaviour. Effect of species\*sex interaction on  $T_{final}$  (circles=*P. raffonei*; squares=*P. siculus*). Vertical bars denote 95 % confidence intervals.

appears to be a precise (Van Damme et al., 1990) and accurate (Kapsalas et al., 2016) thermoregulator, and also reveals the ability to enter activity at lower  $T_b$  than *P. raffonei*. These features may not represent direct advantages in interspecific competition. However, it is possible that, by improving the overall effectiveness of thermoregulation, *P. siculus* may have advantages to overcome the thermal challenges of new and/or changing environments (Kapsalas et al., 2016).

As expected, the two study species thermoregulate actively by basking, and the time spent at basking may be considerable for lizards (Avery, 1976). Therefore, lizards that spent less time in basking may invest more time in other activities (for instance, foraging and mating). Thus, minimising the basking time would convey selective advantages in terms of both fitness and survival (for instance, by reducing predation risk due to minimised exposure time). Biophysical models predict that the time spent by lizards in basking may be reduced through physiological or behavioural adjustments of two traits: set-point temperature (= preferred  $T_b$ ) and heating rate (Bakken & Gates, 1975). Although we did not estimate the preferred  $T_b$  in a laboratory photothermal gradient (Gvoždík, 2002), we obtained the temperature at which lizards stop basking in laboratory conditions ( $T_{final}$ ).  $T_{final}$  is therefore proportional to the time spent in basking by a given species, all other things being equal. In our case, *P. siculus* should be advantaged as its  $T_{final}$  was lower than that of *P. raffonei*. Instead, our lizards of both species showed comparable heating rates and thermoregulated in the same thermal conditions. Therefore, we expected that  $T_{final}$  contribute the most to reduce basking time (Huey & Slatkin, 1976).

#### Accumulation of heat

As expected, the temperatures reached at each one-minute step did not vary significantly between the two species indicating that the two species accumulate heat in the same way and do not present significant differences in accumulating body heat (Gvoždík, 2002). The observed intersexual difference is likely due to the sexual size dimorphism in *Podarcis* species (Kaliontzopoulou et al.,

2007), with males significantly larger than females. In fact, a smaller body accumulates heat at a faster rate, all other factors being equal (Avery, 1976).

#### Thermoregulation behaviour

Males of *P. siculus* enter full activity at a lower body temperature than males of *P. raffonei*. This finding would suggest that the lower  $T_{final}$  observed in *P. siculus* may confer a selective advantage over *P. raffonei* during the daily routine activities. The highest  $T_{final}$  was observed in those individuals that thermoregulated in the sector 1 (hot spot), regardless of species and gender. That is, under experimental conditions, *P. siculus* and *P. raffonei* did not show apparent difference in the selection of the hotspot. We also found that *P. siculus* did not thermoregulate faster than *P. raffonei*. Instead, female thermoregulation was shorter than in males irrespective of species. This finding supports the evidence obtained through the experiment on heating rates. The lack of interspecific divergence in basking duration seems to be counterintuitive given the lower  $T_b$  that was needed by *P. siculus* to end basking. We speculate that, since thermal quality of the basking site (i.e. hot spot vs. remaining sectors) influenced  $T_{final}$ , the expected shorter basking time by male *P. siculus* may have been blurred by stochastic choice of basking site. This hypothesis is partly supported by the fact that *P. siculus* males had a higher variance of  $T_{final}$  than those of *P. raffonei*, thus indirectly revealing a higher heterogeneity in basking site (= sector) selection. In nature, where optimal and suboptimal basking sites are likely equally accessible, the advantage of a lower  $T_b$  needed to end basking and entering full activity is expected to also confer a faster thermoregulation process (Kapsalas et al., 2016).

In conclusion, our study pointed out that there are subtle differences in the basking quality and correlated behaviours between an invasive lizard and a threatened endemic species, with potential implications for coexistence dynamics. Obviously, it cannot be excluded that the observed thermoregulation differences between the species may be non-relevant for the interspecific competition outcome. Other factors are possibly involved in giving *P. siculus* a potentially competitive advantage over the native species, like diet strategy, aggressive behaviour, or running speed mediated by  $T_{final}$ . These and other factors are likely to influence overall lizard behaviour and to contribute to the outcome of interspecific interactions. We would urge researchers to perform further field and mesocosm long-term studies on the thermal ecology of these two species, in order to verify whether the observed interspecific differences may influence the respective fitness of the coexisting populations.

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