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ORIGINAL ARTICLE

Getting ahead: exploitative competition by an invasive lizard

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Abstract

Biological invasions are a contemporary global threat because invasive species can have substantial negative economic and ecological impacts. Invasive species can outcompete native species through two main mechanisms: interference competition (direct, negative interactions like aggression) and/or exploitative competition (indirect, negative interactions resulting from species using the same, limited resources like food). The invasive Italian wall lizard (*Podarcis siculus*) was introduced into Lisbon, Portugal, 20 years ago, and is believed to be locally displacing the native green Iberian wall lizard (*Podarcis virescens*). We experimentally tested for competition between these two lizard species by establishing heterospecific (one pair of each species) and conspecific (two pairs of the same species; control) treatments in enclosures containing a high- and a low-quality refuge. Lizards were fed from food dishes every other day. We tested if species showed interference (aggressive behaviour, stealing food and shelter exclusion) or exploitative competition (tolerance between species but differences in food consumption efficiency). We found evidence for exploitative competition: the invasive species arrived first at food stations, consumed more food and gained more weight than the native species. We suggest that exploitative competition may, in part, explain the observed displacement of *P. virescens* from contact areas with the invasive *P. siculus*. Deciphering the competitive mechanisms between invasive and native species is vital for understanding the invasion process.

Significance statement

To become successful invaders, alien species must often outcompete native species they encounter in a new location. But how can an alien species outcompete a resident with a long evolutionary history in an environment in which the resident is expected to be better adapted? We studied an invasive and native congeneric pair of sympatric lizards to understand how they interact and potentially compete in a controlled environment. The invasive Italian wall lizard and a native congener were very tolerant of each other; however, the invasive species was first to arrive at food, ate more and grew faster, suggesting exploitative competition. This contrasts with previous studies in other introduced locations where the Italian wall lizard was more aggressive towards native lizards, suggestive of interference competition. Our results help explain why the Italian wall lizard is so successful and suggests it may compete in different ways, possibly in response to local environmental conditions and which species it may be competing with, but with the same outcome: the displacement of native species.

Keywords Biological invasions · Interference competition · *Podarcis siculus* · *Podarcis virescens* · Social interactions · Sympatry

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Introduction

Invasive species can have substantial negative impacts on economies, native species and ecosystems (Crooks 2002; Hulme 2007; Walsh et al. 2016). For example, invasive species may negatively impact native species by (1) affecting their development or causing diseases (e.g. Kupferberg 1997; Lymbery et al. 2014; Carmo et al. 2018); (2) altering habitat (e.g. Anderson et al. 2006); (3) through predation or parasitism (e.g. Pintor et al. 2009; Lymbery et al. 2014); (4) hybridisation (e.g. Huxel 1999) or (5) though competition—by being more aggressive (e.g. Holway 1999; Downes and Bauwens 2002) or consuming more food (e.g. Short and Petren 2008; Pintor and Sih 2009). The different evolutionary history and experience of invasive species can facilitate their establishment and may bring together traits that give them an edge over native species adapted to local conditions (Sax and Brown 2000). These traits can ultimately lead to the displacement or even eradication of autochthonous species. Understanding the direct effects and mechanisms through which an invasive species outcompetes a native species is crucial to understanding, managing and minimising their impacts.

The idea that invaders can have an advantage over natives due to their competitive ability is long-standing (Elton 1958). Competition between two species can happen through two main processes—interference and/or exploitation (Miller 1967). Interference competition refers to direct negative interactions resulting from aggressive behaviour. With interference competition, an invasive species may be more aggressive, steal food or exclude others from resources (Michaud 2002; Rowles and O'Dowd 2007; Pintor and Sih 2009; Žagar et al. 2015). Exploitative competition refers to indirect negative interactions resulting from species using the same, limited resources, such as food or water. With exploitative competition, an invasive species does not necessarily interact with another individual or species, but has an advantage in accessing resources. For example, an invasive species may be more efficient at locating and consuming food (Human and Gordon 1996; Petren and Case 1996). Interference and exploitative competition are not mutually exclusive. Therefore, an invasive species that combines both strategies can pose a significant threat to native species (Case et al. 1994; Human and Gordon 1996; Amarasekare 2002). For example, the invasive Argentine ant (*Linepithema humile*) can employ both types of competition against native ants, by foraging more efficiently (exploitative competition) while simultaneously also preying on native ant queens (interference competition), which prevents the establishment of new native colonies (Human and Gordon 1996). Nevertheless, either form of competition can independently result in the displacement or exclusion of species from optimal habitats (Grether et al. 2017).

The Italian wall lizard, *Podarcis siculus*, is a small lacertid native to the Italian Peninsula and Adriatic coast (Senczuk et al. 2017), which has been introduced in multiple locations in the Mediterranean Basin and even Britain and North America (Kraus 2009; Carretero and Silva-Rocha 2015; CABI 2020). It can become quickly established in new areas (Burke et al. 2002; Vervust et al. 2007) and impacts native lizards, leading to their eradication or displacement to low quality habitats (Nevo et al. 1972; Capula et al. 2002; Downes and Bauwens 2002; Herrel et al. 2008). The only experimental study directly testing the mechanism underlying their competitive ability found that *P. siculus* may be displacing the sympatric Dalmatian wall lizard, *Podarcis melisellensis*, through interference competition (Downes and Bauwens 2002). In staged encounters in the laboratory between hatchlings of these two species, *P. siculus* were dominant and more aggressive. Also, when high-quality microhabitats were available, *P. siculus* used them more efficiently than *P. melisellensis*, and heterospecific pairs were less likely to simultaneously occupy the same patch compared to conspecific pairs (Downes and Bauwens 2002). However, even within the same invasive species, different populations might use different competitive strategies depending on local conditions (Amarasekare 2002). The employed competition strategy can depend on the dynamics, availability and abundance of resources (Amarasekare 2002; Perkins and Nowak 2013), or on the specific traits that differ between the invasive and native species (Persson 1985).

A *P. siculus* population in Lisbon (Portugal) was unintentionally introduced from central Italy around 1998, and is currently a high-density population in an urban environment (González de la Vega et al. 2001; Silva-Rocha et al. 2012; CABI 2020). It is likely that *P. siculus* is excluding the native green Iberian wall lizard, *Podarcis virescens*, from more suitable habitat and restricting them to surrounding urban gardens since both species live in close sympatry but not in syntopy (Ribeiro and Sá-Sousa 2018). Also, the displacement of native *Podarcis* spp. after the arrival of *P. siculus* is a common phenomenon (e.g. Nevo et al. 1972; Capula et al. 2002; Herrel et al. 2008). Both *P. siculus* and *P. virescens* are diurnal, feed mainly on terrestrial invertebrates and occupy similar shelters and widely overlap in habitat types such as walls, bushes and sandy substrates (reviewed in Ribeiro 2017). We experimentally tested the hypothesis that *P. siculus* compete with native *P. virescens* by staging interactions in a captive, controlled environment. We predicted that the invasive *P. siculus* would either exhibit interference competition and use aggressive behaviour to steal food (kleptoparasitism) or exclude the native *P. virescens* from food and shelter, and/or use exploitative competition by arriving at food sources first and consuming food more efficiently (Table 1; see "Material and Methods" for details).

Material and methods

Collection and acclimation

During spring 2017, we collected 16 *P. siculus* (8 males and 8 females) and 16 *P. virescens* (8 males and 8 females) adults from the wild at Parque das Nações, Lisbon (38.762131, - 9.094451 and 38.774001, - 9.091770, respectively). Collection sites for each species were 1.6 km apart to ensure individual lizards had not encountered each other before (*Podarcis* lizards have limited home ranges, Verwaijen and Van Damme 2008). Lizards were transported to facilities at CIBIO-InBIO, University of Porto, and acclimated to captivity for 2 weeks. During this acclimation period, animals were kept in individual terraria (200 mm W × 300 mm L × 200 mm H), with indirect natural light and under an artificial light:dark 12:12 h photoperiod (08:00–20:00 h), and with room temperatures of 20–22 ºC during the day. A 50-W heat cable was beneath part of the terrarium, creating a thermal gradient, and allowing lizards to thermoregulate as required, on an individual basis. Lizards had continuous access to water and a small brick shelter, and were fed every other day with three live mealworms.

Experimental protocol

We staged interactions between the two species to test their competitive abilities. We had two experimental treatments: lizards housed with conspecifics (two male and two female *P. siculus*, or two male and two female *P. virescens*) or with heterospecifics (one male and one female of each species). Lizards were housed in groups of four individuals in large experimental tubs (1200 mm W × 1000 mm L × 500 mm H). In the wild, *P. siculus* is naturally larger than *P. virescens* and, therefore, in the heterospecific treatment (species paired together), *P. siculus* was always larger than *P. virescens*. To minimise this difference, we matched individuals that were closest in size (snout-vent length, SVL). The order of body size (SVL) for the heterospecific treatment from largest to smallest was the *P. siculus* male followed by the female, *P. virescens* male, and finally *P. virescens* female (refer to Table S1 in the supplementary material for mean differences in SVL among treatments).

Trials were each 1 week in duration, and were carried out over three consecutive weeks; the conspecific treatment took place within the first 2 weeks (in each week, four tubs had *P. siculus*, and the other four tubs had *P. virescens*), and the heterospecific treatment took place in the third week (all eight tubs had both species). See Fig. S1 in the supplementary material for details. This was done to ensure all lizards experienced the same treatment order throughout the experiment. During the conspecific treatment (week 1 and 2), none of the lizards was held with the same lizard more than once. However, in the heterospecific treatment, all species pairs had been together previously during the conspecific treatment (all species pairs had been together in week 1).

Before the experiment started, each lizard's SVL (to the nearest 0.01 mm with digital calipers) and weight (to the nearest 0.01 g with a digital scale) was measured, and each was uniquely marked. We marked individuals with white TESA® tape to allow easy visual identification. We used four codes: 1 bar, 2 lines, 3 stripes and 2 dots (Fig. 1). At the end of each week, all lizards were again weighed and recoded with tape for the following week. We also checked for scars at the end of each week, but only three *P. siculus* females showed new ventral scars after the conspecific treatments (likely from attempted copulations); consequently, we did not analyse this data. At the end of the week, the lizards were returned to their

Table 1 Predictions in support of interference and exploitative competition for the behaviours and traits we analysed, when both species were housed together (heterospecific treatment). For each type of competition, we expected all four predictions to be supported. *Podarcis siculus* is the invasive species and *P. virescens* the native species

Predictions for interference competition	
Sheltering behaviour	*P. virescens* will hide more than *P. siculus*
Use of the high-quality area	*P. virescens* will use the high-quality area less than *P. siculus*
Stealing food	*P. siculus* will be more likely to steal food from *P. virescens*
Aggression	*P. siculus* will be more aggressive towards *P. virescens*
Predictions for exploitative competition	
Consumption of food	*P. siculus* will consume more food than *P. virescens*
Order of arrival to food	*P. siculus* will arrive to food before *P. virescens*
Weight	*P. siculus* will consequently gain more weight than *P. virescens*
Social tolerance	Both species will tolerate one another

individual terraria, and then were placed into a new, clean tub the following day. We cleaned the tubs with 96% ethanol, and the sand substrate was replaced.

During experiments, we allowed the lizards to freely interact for 1 week (seven full days). During this period, we scored each lizard's activity, use of space, feeding behaviour, basking tolerance and social interactions. We provided lizards with a high- and low-quality shelter, constant access to water and with food (12 mealworms per tub) every other day (Fig. 1). Food was provided from 11:00 to 13:00 h (lizards became active at 10:00 h) on days 2, 4 and 6; lizards were weighed on day 8. We used a medium-grained white sand as a substrate, because both species can live in sandy habitats. Each tub had a heat and light source from 10:00 to 16:00 h every day, placed over the high-quality shelter. The high-quality shelter had eight narrow crevices (providing safety to lizards) and was maintained at 28–30 ºC (30 ºC is close to the preferred temperature maintained throughout the day by both species; Carretero 2015; Sannolo and Carretero 2019), while the low-quality shelter had a wider opening (that *Podarcis* spp. would not typically use) and was maintained at 20–22 ºC. The thermal ecology and climatic envelope of the two species are similar (Garcia-Porta et al. 2019). All tubs were remotely video-recorded continuously with CCTV cameras to minimise any disturbance. The identification codes provided to the lizards were clearly distinguishable in the videos, and allowed blind video scoring by a single individual not familiar with the details of the study, after experiments were completed.

Video scoring

We scored videos by recording behaviours every 15 min (as in Downes and Bauwens 2002) from 10:00 to 16:30 h, resulting in a total of 27 sample points per lizard per day. We scored lizard activity (hidden or active), location in the tub (1, 2 or 3—with 1 corresponding to the high-quality area) and number of contacts between two lizards. The high-quality area is area 1, because it included the high-quality shelter and the heat and light source. The number of contacts was scored as the number of times two lizards were in physical contact (when both bodies were in contact) while basking on the high-quality refuge. Every 15 min, the video was paused, and we recorded this information for each lizard. Activity and location provided information about an individual's sheltering behaviour and use of space, while the number of contacts provided information about their social tolerance to other lizards while basking on the high-quality shelter. In addition, we continuously observed the portion of the videos where lizards were feeding to record the amount of food each lizard ate, the order that lizards arrived at the food dishes and if they stole mealworms from other lizards. Finally, we also continuously scanned all videos over the entire experimental period and recorded any instances of aggression. Videos were essentially scored blindly. See Table 2 for details on behavioural scoring.

Statistical analyses

Prior to statistical analyses, we explored our data to ensure it fitted all model assumptions (such as no influential outliers, overdispersion, collinearity between predictor variables within

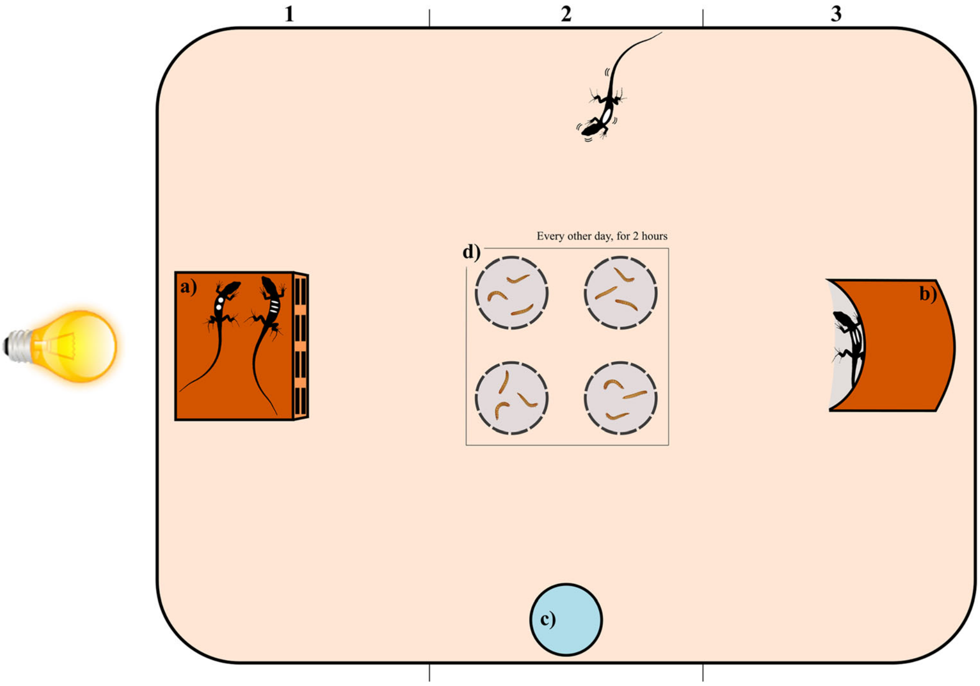

Fig. 1 Schematic representation of the experimental tub. We created a single high-quality refuge consisting of a brick with eight small crevices with a heat and light source above (a), and a low-quality refuge consisting of a brick with only one large opening with no heat or light source (b). A water bowl was placed between both shelters (c). On feeding days (every other day), the food (12 live mealworms) was placed in four transparent dishes (d). In this diagram, lizards with *2 dots* and *3 stripes* are "inactive" in the high-quality area (1) and are not touching each other, the lizard with *1 bar* is moving outside of any refuges, and the lizard with *2 lines* is hiding in the low-quality refuge

Table 2 Behaviours studied during the experiment and how these variables were summarized for use in statistical analyses. Activity, location and social tolerance were scored every 15 min; all the others were scored by continuous observation of the videos

Behaviour	Parameters	Scoring	Variables
Sheltering behaviour	*Activity* If the lizard is concealed (in refuge) or visible in the tub (moving or inactive).	Hidden or active	Sheltering behaviour – We used the number of times "hidden" out of total observations
Use of the high-quality area	*Location* The area of the tub was divided in three equal areas, where 1 corresponds to the high-quality area (that encompasses the high-quality shelter, light and heat source). We observed where the lizard was in the tub at each time point.	Area 1, 2 or 3	Use of high-quality area – We used the number of times in "area 1" out of total observations
Feeding behaviour	*Consumption of food* Number of mealworms each lizard ingested on each feeding day	From 0 to 12	Amount of food
	Weight The change in body mass (g) over the one-week observation period	Weight (± 0.01 g)	Standardized weight: $\frac{(\text{finalweight}-\text{initialweight})}{\text{initialweight}}x100$
	Order of arrival to food dishes The order in which each lizard arrived to the food dishes on each feeding day	1, 2, 3, 4, or NA	Order to food
	Stealing food If the lizard stole food from another	Failed or successful	NA (described qualitatively)
Social interactions	*Social tolerance* If lizard is in contact with another lizard, when basking on the high-quality shelter	In contact with a conspecific or heterospecific	Number of contacts
	Aggression Any aggressive act recorded during the day	Aggression for food, or unrelated	NA (described qualitatively)

a model, data integrity) following Zuur et al. (2010). All analyses, which consisted of generalized and linear mixed effect models (see below for details), were performed in R version 3.4.2 (R Core Team 2017). We did not include SVL in any of our models, because SVL and our factorial variables of species and sex are confounded. Specifically, *P. virescens* was smaller than *P. siculus* ($\beta = -9.74$, $t = -41.15$, $P < 0.001$; results from a linear model performed using the *lm* function in the R package *stats* with sex, species and the interaction between the two as fixed effects), and males were larger than females ($\beta = 8.473$, $t = 35.67$, $P < 0.001$). Also, there was a significant interaction effect between species and sex ($\beta = -6.678$, $t = -19.88$, $P < 0.001$); specifically, *P. virescens* females were the smallest, followed by *P. virescens* males, *P. siculus* females and then male *P. siculus* (i.e. the largest). For all models, α was set at 0.05, and we always ensured models fulfilled their assumptions. To create contrasts between relevant predictor variables, and correct these multiple comparisons with a post hoc Tukey HSD multiplicity adjustment, we used the *lsmeans* R package with the function *lsmeans* (Lenth 2016). We also used the *lsmeans* function to calculate the estimated marginal means ± standard error because it controls for additional fixed effects within our mixed models; we present these data to summarize our findings within the text.

Sheltering behaviour and use of the high-quality area

To examine differences in the proportion of observations a lizard was hiding across treatments, we used a generalized linear mixed effect model (GLMM) with the function *glmer* from the *lme4* R package (Bates et al. 2015). This response variable was proportional (between 0 and 1), so we used a binomial distribution (with a logit link; Crawley 2012). The model included the fixed effects of treatment (conspecific or heterospecific), species (*P. siculus* or *P. virescens*), sex (female or male) and experimental day (continuous from 1 to 7). We initially included the interaction between treatment and species, in this and all models containing both these variables, and then, if the interaction was not significant, we removed the interaction and re-ran the model. We also included lizard identity as a random effect, to control for dependencies in our data due to repeated measures of the same individual over experimental days and treatments. Additionally, we included tub and week as other random factors, to also control for dependencies in these variables within our study. We used a GLMM with the same distribution and variables, as the model described above, to determine if the proportion of observations spent in the high-quality area differed between treatment, species, sex or experimental day.

Consumption of food, order of arrival to food dishes, and weight

To test if the number of food items eaten differed between treatment and species, we used a GLMM with a Poisson distribution. The model included the same variables as described above, but the experimental day variable differed slightly, varying from 1 to 3, because it only included days in which lizards were fed. To analyse the order of arrival to food dishes, we used only data from the heterospecific treatment (in week 3). We used a GLMM with a Poisson distribution to analyse if the order in which an individual arrived at the food dishes (1, 2, 3 or 4) was affected by species (*P. siculus* or *P. virescens*), sex (female or male) or experimental day (from 1 to 3). We also included lizard identity, and tub as random factors in this model. Finally, we used a Gaussian linear mixed effect model (LMM) to examine if lizard weight was influenced by treatment, species, sex or by the interaction treatment × species. We incorporated lizard identity, tub and week as random factors.

Social tolerance

We used a GLMM with a Poisson distribution to analyse whether the frequency with which lizards were in contact varied by treatment and experimental day (continuously varying from 1 to 7). In this model, "treatment" included three levels: conspecific *P. siculus*, conspecific *P. virescens* and heterospecific. This difference was because this data is not tied to a particular individual, or species, and instead is a summary across each experimental day. We also included tub and week as random factors in our model. To account for overdispersion in this model, we also added an observation-level random effect (Crawley 2012).

Results

In all treatments, all lizards spent the night inside crevices within the high-quality shelter, with the exception of one night where one lizard spent the night exposed (a female *P. virescens* housed with conspecifics in week 2). Videos did not reveal in which of the eight crevices the lizards would refuge in overnight, but they often slept in the same crevice (IDM, personal observations before 9 am). Thus, lizards would often aggregate overnight even though there were unoccupied crevices.

Sheltering behaviour and use of the high-quality area

As the experiment progressed, the lizards hid less (Table 3a). We found a significant interaction on the sheltering behaviour between species and treatment (Table 3a): when housed with conspecifics, *P. siculus* hid more often (0.296 ± 0.037) than *P. virescens* (0.183 ± 0.027; Table S3a). In the heterospecific treatment, the sheltering behaviour was not different between species (*P. siculus* 0.257 ± 0.040; *P. virescens* 0.221 ± 0.036). We detected no effect of experimental day, sex, treatment or species on the proportion of observations a lizard was within the high-quality area (Table 3b).

Consumption of food, order of arrival to food dishes, and weight

Lizards ate more as the experiment progressed, and males ate more than females (Table 3c). We found a significant interaction effect on the amount of food eaten between species and treatment (Table 3c): in the conspecific treatment, *P. siculus* and *P. virescens* ate the same amount of food, but in the heterospecific treatment, *P. siculus* ate significantly more than *P. virescens* (Fig. 2; Table S3b). The order of arrival at the food dishes in the heterospecific treatment was not significantly affected by sex or experimental day (Table 3e), but *P. siculus* approached the food dishes significantly sooner than *P. virescens* (Table 3e; Fig. 3).

We also found a significant interaction between treatment and species on the lizards' standardized weight (Table 3d). Specifically, the standardized body weight of *P. siculus* significantly increased between treatments (conspecific, 4.93 ± 1.95%; heterospecific, 8.74 ± 2.07%; thus, a difference of 3.81%), while for *P. virescens*, it was maintained between treatments (conspecific 9.31 ± 1.95%, heterospecific 9.48 ± 2.07%; thus, a difference of 0.17%). For all comparisons, see Table S3 in the supplementary material. Additionally, we analysed if body size (SVL) had an effect on the amount of food a lizard consumed or their order of arrival to food, when lizards were housed with only conspecifics. We found that body size had no effect on the order of arrival to food for either species, but that the larger *P. siculus* ate more (all details in the supplementary material; Table S2).

Stealing food and aggressive behaviour

The low frequency of aggressive interactions and food stealing prevented statistical analysis of this data, and we thus report our observations in Fig. 4. Native *P. virescens* were more likely to attempt to steal food than invasive *P. siculus* during the conspecific treatment (Fig. 4a). However, when in the heterospecific treatment, *P. virescens* attempted to steal food much less frequently, either from conspecifics or heterospecifics (Fig. 4a). In contrast, *P. siculus* attempted to steal food more often when in the heterospecific treatment than when in the conspecific treatment, but these attempts were mostly directly towards conspecifics (Fig. 4a). The majority of aggressive interactions (biting and fights) were related to food (Fig. 4b). When housed with conspecifics, *P. virescens* exhibited the most aggressive interactions (Fig. 4b).

Table 3 Results of our statistical analyses testing if species (*P. siculus*: PS, *P. virescens*: PV), sex (males: M, females: F), treatment (conspecific: C, heterospecific: H) and day had an effect on the studied variables (a–f). In number of contacts (f), the variable of treatment was coded different to the other analyses, specifically as native (Nat), invasive (Inv) or mixed (Mix). Reference levels for each variable are shown in parentheses following variable names. For each model, we present coefficient estimates (β) and their corresponding standard error (*SE*), z-values (*z*) and *P* values (*p*) for fixed effects, as well as variance (σ^2) of random effects and residuals. We also report conditional R^2 for each model. Significant values are indicated in italics

a) Sheltering behaviour	N_{obs} = 672, N_{ind} = 32	$R^2_{conditional}$ = 0.697		
Fixed effects	β	*SE*	*z*	*p*
Intercept (PS, F, C)	*−0.595*	*0.193*	*−3.081*	*0.002*
Day	*−0.043*	*0.008*	*−5.775*	*< 0.001*
Species (PV)	*−0.628*	*0.133*	*−4.728*	*< 0.001*
Sex (M)	−0.199	0.131	−1.521	0.128
Treatment (H)	−0.192	0.192	−0.999	0.318
Species (PV) : Treatment (H)	*0.426*	*0.065*	*6.584*	*< 0.001*
Random effects	σ^2			
Lizard identity	0.129			
Tub	0.095			
Week	0.023			
Residuals	1.000			
b) Use of the high-quality area	N_{obs} = 672, N_{ind} = 32	$R^2_{conditional}$ = 0.002		
Fixed effects	β	*SE*	*z*	*p*
Intercept (PS, F, C)	*−0.080*	*0.029*	*−2.718*	*0.007*
Day	0.003	0.005	0.613	0.540
Species (PV)	−0.022	0.021	−1.016	0.309
Sex (M)	−0.004	0.021	−0.166	0.868
Treatment (H)	0.004	0.023	0.184	0.854
Species (PV) : Treatment (H)	–	–	–	–
Random effects	σ^2			
Lizard identity	< 0.001			
Tub	< 0.001			
Week	< 0.001			
Residuals	1.000			
c) Amount of food	N_{obs} = 288, N_{ind} = 32	$R^2_{conditional}$ = 0.451		
Fixed effects	β	*SE*	*z*	*P*
Intercept (PS, F, C)	*0.673*	*0.186*	*3.610*	*< 0.001*
Food day	0.028	0.044	0.631	0.528
Species (PV)	−0.260	0.176	−1.479	0.139
Sex (M)	*0.396*	*0.168*	*2.360*	*0.018*
Treatment (H)	*0.383*	*0.142*	*2.699*	*0.007*
Species (PV) : Treatment (H)	*−0.724*	*0.164*	*−4.416*	*< 0.001*
Random effects	σ^2			
Lizard identity	0.173			
Tub	0.001			
Week	0.008			
Residuals	1.000			
d) Weight	N_{obs} = 96, N_{ind} = 32	$R^2_{conditional}$ = 0.793		
Fixed effects	β	*SE*	*z*	*p*
Intercept (PS, F, C)	*5.022*	*2.376*	*2.113*	*0.035*
Species (PV)	4.381	2.763	1.586	0.113
Sex (M)	−0.183	2.705	−0.068	0.946
Treatment (H)	*3.812*	*1.189*	*3.205*	*0.001*
Species (PV) : Treatment (H)	*−3.645*	*1.682*	*−2.168*	*0.030*

Table 3 (continued)

Random effects	σ^2			
Lizard identity	53.520			
Tub	< 0.001			
Week	< 0.001			
Residuals	15.083			
e) Order of arrival to food (H treatment)	N_{obs}=92, N_{ind}=32	$R^2_{conditional} = 0.096$		
Fixed effects	β	*SE*	*z*	*p*
Intercept (PS, F)	*0.706*	*0.206*	*3.429*	*0.001*
Food day	0.024	0.083	0.288	0.773
Species (PV)	*0.389*	*0.136*	*2.871*	*0.004*
Sex (M)	− 0.153	0.134	− 1.138	0.255
Random effects	σ^2			
Lizard identity	< 0.001			
Tub	< 0.001			
Residuals	1.000			
f) Number of contacts	N_{obs}=168, N_{ind}=32	$R^2_{conditional} = 0.971$		
Fixed effects	β	*SE*	*z*	*p*
Intercept (Inv)	− 0.214	0.358	− 0.597	0.551
Day	*0.141*	*0.038*	*3.749*	*< 0.001*
Treatment (Mix)	*1.325*	*0.295*	*4.492*	*< 0.001*
Treatment (Nat)	*2.358*	*0.194*	*12.165*	*< 0.001*
Random effects	σ^2			
Observations	0.649			
Tub	0.505			
Week	0.032			
Residuals	1.000			

Social tolerance

In the conspecific treatment, *P. siculus* were observed in contact 399 times. In contrast, *P. virescens* were observed in contact 1207 times. In the heterospecific treatment, lizards were observed in contact 562 times. Of these interactions in the heterospecific treatment, 66 were between *P. siculus*, 169 were between *P. virescens* and 327 were between heterospecifics. The number of observations of lizards in contact while basking increased as the experiment progressed (Table 3f). Within the conspecific treatment, *P. virescens* were observed in contact more frequently than *P. siculus* ($\beta = -2.358$, $z = -12.165$, $P_{\text{corr}} < .0001$). Moreover, the overall number of contacts between lizards in the heterospecific treatment was higher than those observed for *P. siculus* with conspecifics ($\beta = -1.325$, $z = -4.492$, $P_{\text{corr}} < .0001$), but lower than those observed for *P. virescens* with conspecifics ($\beta = -1.032$, $z = -3.719$, $P_{\text{corr}} = 0.001$). For all comparisons, see Table S3 in the supplementary material.

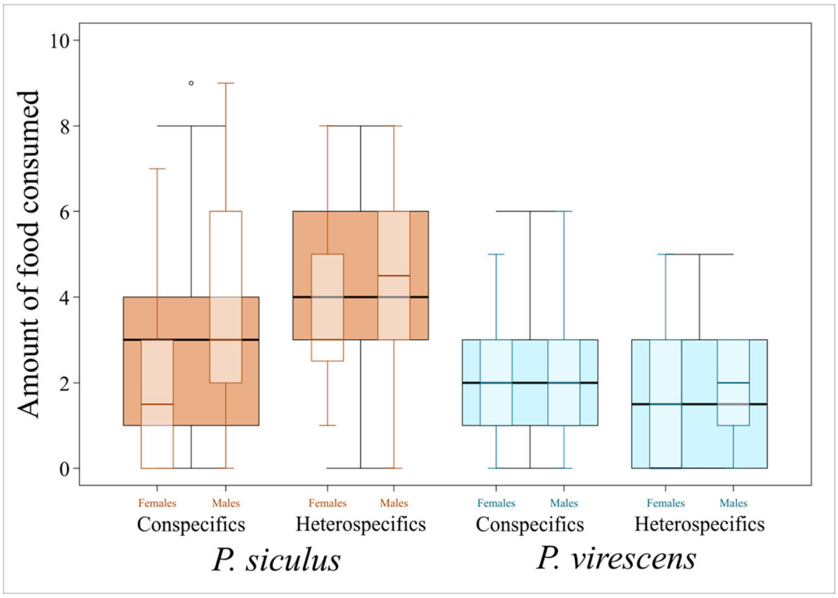

Fig. 2 Average amount of food (number of mealworms) eaten by each species (*Podarcis siculus* in orange and *P. virescens* in blue), and for each sex, for both treatments (conspecifics and heterospecifics). The large darker boxplots show sexes combined. The invasive *P. siculus* in the heterospecific treatment ate significantly more food than all other treatments. This boxplot was made from raw data. The thick horizontal line represents the median, the boxes encompass the quartile ranges and the whiskers represent the minimum and maximum of the data, excluding outliers (points that are 3/2 times the upper quartile). The circle outside of the box and whiskers represents an outlier

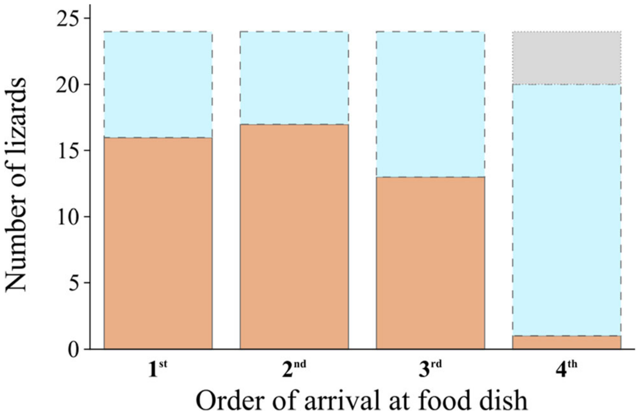

Fig. 3 Order by which species would arrive at the food dishes during the heterospecific treatment. *Podarcis siculus* (orange with solid lines) typically arrived before *P. virescens* (blue with dashed lines). The grey area with dotted lines represents the lizards that did not approach the food dishes. Plots are from raw data

Discussion

We found evidence for asymmetric exploitative competition but not interference competition between the invasive *P. siculus* and native *P. virescens*. Specifically, when both species were together, there were no differences in their sheltering behaviour, use of the high-quality area, in stealing food nor in their aggressive behaviour, all of which would be indicative of interference competition. Instead, *P. siculus* arrived first at the food dishes, ate more food and consequently gained relatively more weight. We also found social tolerance (both species would share shelters and the high-quality area, and be in contact with each other). Together, this is evidence for exploitative competition. Even though it does not depend on direct interactions, exploitative competition can have a significant negative impact on a species. For example, the invasive common house gecko *Hemidactylus frenatus* can rapidly displace the native mourning gecko (*Lepidodactylus lugubris*) across the Pacific basin, solely through exploitative competition (Petren et al. 1993; Case et al. 1994; Petren and Case 1996).

Podarcis siculus modified its feeding behaviour in the heterospecific treatment and started to eat more, compared to the conspecific treatment, while also increasing its weight. This species also had an increased growth rate when with heterospecifics, namely in the presence of *P. melisellensis* during competition experiments (Downes and Bauwens 2002). In our study's heterospecific treatment, the invasive *P. siculus* was first to arrive at the food dishes and consumed more than the native species. In species that live in groups, being the first to arrive at a food source, and eating a greater quantity of food, is common in dominant individuals (Baker et al. 1981; Beauchamp 2013) even if they do not display overtly aggressive behaviour. This pattern has also been documented in invasive Argentine ants (*Linepithema humile*) and in the common house gecko (*Hemidactylus frenatus*) when they are in competition with their respective native counterparts (Petren and Case 1996; Holway 1999). Invasive species can outcompete native species simply by obtaining more, and sometimes better, food (Human and Gordon 1996; Holway 1999), thereby reducing the levels of available resources (Petren and Case 1996). Although *P. virescens* did not lose weight in the heterospecific treatment compared to the conspecific treatment, this may be because there were still relatively large quantities of food available, and, potentially, the duration of our experiment was relatively short (1 week). These effects are likely to be more profound in the wild, especially if food is restricted (such as in summer or in winter because of a limited activity window). Also, an invasive species can dominate invaded areas by establishing high densities, which promotes an increasing foraging voracity (Pintor et al. 2009). Further research

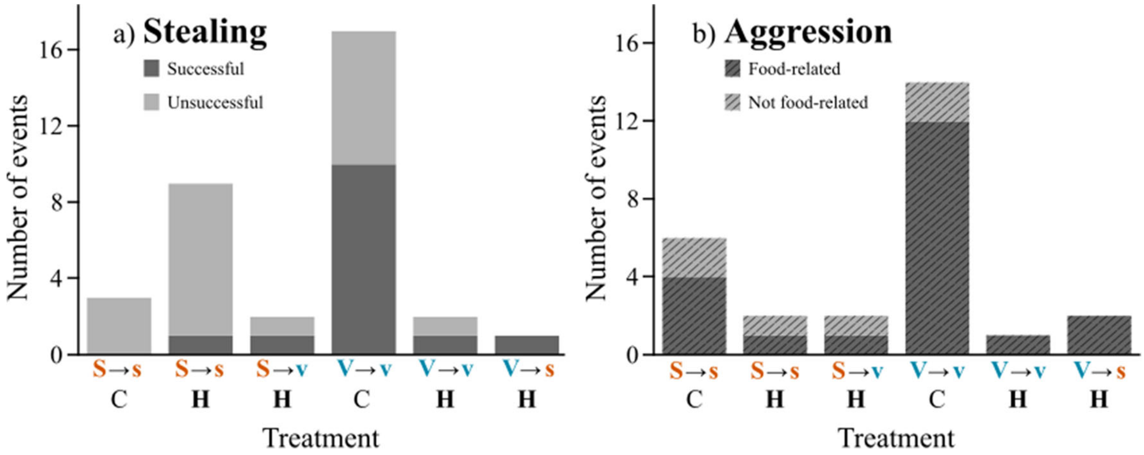

Fig. 4 Number of events of food-stealing (a), and of aggression (b) scored throughout the entire experiment. For each treatment, C = conspecific and H = heterospecific, and the arrow indicates the direction of the behaviour (instigator to recipient). *Podarcis siculus* is represented in orange "S" or "s", and *P. virescens* in blue "V" or "v". In graph (a), dark grey indicates successful food-stealing events, while light grey represents failed stealing events. In graph (b), striped dark grey represents aggression related to food, and striped light grey represents aggression unrelated to food.

should focus on understanding if higher densities of *P. siculus* in the wild could reduce the foraging success of native *Podarcis* spp. and lead to their displacement. In particular, since *P. siculus* is naturally larger than *P. virescens*, this may also influence how they compete.

These results can have major implications for understanding the impact of this invader on native communities. The competitive superiority of exotic species over native species, jointly with the opportunistic use of ecological opportunities derived from human actions, is a major explanation for one of the main paradoxes in biological invasions: how can a species with no evolutionary history in a given location be able to become established, dominant and even displace native species, when the latter had much more time to adapt to local conditions (Sax and Brown 2000)? Two major arguments can explain this competitive superiority. First, invasive species may have a longer history in human-modified ecosystems and therefore they may be better adapted to urban environments than native species (Elton 1958). However, Lisbon is an old European city and the study sites have been intensively used by humans for centuries, and thus, *P. virescens* should not have experienced any less selection from urbanization than *P. siculus* in its native range in Italy. Second, the novel location might have fewer enemies (such as predators or parasites that are not adapted to interact with the introduced species; Roughgarden 1983). But again, this hypothesis provides little explanation, as both species are closely related with similar ecological requirements, and are therefore exposed to similar selective pressures, such as predation. On the other hand, one explanation for the ability of *P. siculus* to exploit food resources in the presence of the native species may be due to the invasive species' personality traits. An invasive species can better exploit food resources by being bolder than native species (Short and Petren 2008) and *P. siculus* has been shown to be not only bolder, but also more exploratory and neophilic than *P. virescens* at the same study site (Damas-Moreira et al. 2019). Also, *P. virescens* may become shier in the presence of the invasive *P. siculus*. Indeed, the native *P. virescens* reduced their frequency of interactions from the conspecific to heterospecific treatment (becoming less aggressive, less socially tolerant and attempting to steal food less), and they were the last to arrive at the food source. This suggests that *P. virescens* adjusted its social behaviour in the presence of *P. siculus*, and may avoid foraging at the same time as the invasive species, as also reported in native geckos (Petren et al. 1993). This may explain why *P. siculus* was not directly aggressive towards the native *P. virescens*. In addition, in Sardinia, the introduced *P. siculus* and the native Tyrrhenian wall lizard (*Podarcis tiliguerta*) sometimes share habitats, but the latter becomes more wary when *P. siculus* is present and may result in habitat segregation (Vanhooydonck et al. 2000). Behavioural responses from native species can be key to understanding the type of competition used by *P. siculus*, and may also help explain its success as an invasive species (Strauss et al. 2006; Langkilde et al. 2017). For example, the native common litter skink, *Caledoniscincus austrocaledonicus*, is able to avoid unknown competitors without prior contact, which reduces the impact or frequency of costly aggressive encounters if they come into contact (Gérard et al. 2016). Therefore, the behaviour of the native species can facilitate the establishment of an invader, by reducing the potential for competition.

While we found evidence for exploitative competition, Downes and Bauwens (2002) documented interference competition of *P. siculus* on *P. melisellensis* in Croatia. This suggests a degree of plasticity, because *P. siculus* may adopt a different competition strategy depending on the context and potentially, the intrinsic properties of the native species. A similar pattern has been documented in squirrels; the invasive grey squirrel (*Sciurus carolinensis*) has largely displaced red squirrels (*S. vulgaris*) in Europe, but the type of competition they employ is not the same across all invaded areas (Wauters et al. 2001; Gurnell et al. 2004). Switches between exploitative and interference competition may be in response to resource availability and population density (Holdridge et al. 2016). In our study, the strategy of exploitative competition may be in response to the behaviour of the other species, the density of lizards, food and resource availability or an interaction of these factors. It would be interesting to test if the behavioural differences we observed between these species in the laboratory are maintained if there is the same density of conspecifics in the heterospecific treatment (as there were in the conspecific treatment). This would help to exclude the possibility that lizards behave differently when housed with a heterospecific, simply because they had less intraspecific competition in the tub. Additionally, we suggest more research is needed to assess the impact of *P. siculus* on native *P. virescens* in the wild. Our study occurred under experimental conditions, which do not fully reflect the situation in the wild where food resources may be more dispersed. Nevertheless, both species have generalist diets, strongly overlapping in prey taxa and prey sizes (Zuffi and Giannelli 2013; Carretero and Salvador 2016). In summary, we found no evidence for competitive interference in our study, while demonstrating that exploitative competition is feasible, and worthy of investigation in the wild. Direct interactions can be costly to both parties because they carry an energetic cost, are stressful and they risk injury. If the costs of interference competition are sufficiently high, the ability to alter behaviour in a manner that favours exploitative competition is an alternative with a potentially high pay off. We suggest that invasive species are a good model with which to test predictions related to competition and the degree to which a species can adjust its behaviour. A species that can plastically adjust its competition strategy to the surrounding environment and displace sympatric native species is likely to be a successful invader.

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Authors' contributions IDM implemented and performed the experiment, and drafted the first manuscript; IDM and JLR analysed the data. All authors conceived and designed the experiment, and substantially contributed to the final version of the manuscript.

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Data and code availability Data and code are available at OSF doi:10.17605/OSF.IO/9YX5H.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval All applicable institutional and/or national guidelines for the care and use of animals were followed. Research was approved by the Macquarie University Animal Ethics Committee (ARA2017/004) and by the Portuguese Institute for Conservation of Nature and Forests (ICNF) (License 428/2017/CAPT).

Consent for publication All authors agree with this publication.

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