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Hunt or hide: How insularity and urbanization affect foraging decisions in lizards

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Abstract

Foraging decisions should reflect a balance between costs and benefits of alternative strategies. Predation risk and resource availability in the environment may be crucial in deciding how cautious individuals should behave during foraging. These costs and benefits will vary in time and context, meaning that animals should be able to adjust their foraging behaviour to new or altered environments. Studying how animals do this is essential to understand their survival in these environments. In this study, we investigated the effect of both insularity and urbanization on risk-taking and neophobia during foraging in the Dalmatian wall lizard (*Podarcis melisellensis*). Small islets tend to have both a lower number of predators and less resources. Therefore, islet populations were expected to show more risk-taking behaviour and less neophobia in a foraging context. Previous studies on behaviour of urban lizards have yielded inconsistent results, but due to a lack of both predators and arthropod prey in urban habitats, we expected urban lizards to also take more risks and behave less neophobic. We sampled several inhabited and uninhabited locations on Vis (Croatia) and surrounding islets. Risk-taking behaviour was tested by measuring the latency of lizards to feed in the presence of a predator model, and neophobia by measuring the latency to feed in the presence of a novel object. We found that islet lizards do indeed take more risks and were less vigilant, but not less neophobic. Urban and rural lizards did not differ in any of these behaviours, which is in sharp contrast with previous work on mammals and birds. The behavioural differences between islet and island lizards were novel, but not unexpected findings and are in line with the theory of "island tameness". The effect of urbanization on the behaviour of animals seems to be more complex and might vary among taxa.

KEYWORDS
boldness, foraging behaviour, island tameness, neophobia, *Podarcis melisellensis*, urbanization

1 | INTRODUCTION

Natural selection theory predicts that the decisions made by animals should reflect a balance between the costs and benefits of alternative behavioural strategies (Brock, Bednekoff, Pafilis, & Foufopoulos, 2014; Lima & Dill, 1990; Miranda, Schielzeth, Sonntag, & Partecke, 2013). For example, both resource availability and predation risk in the particular environment may determine whether an individual should behave more or less cautious during foraging (Cooper, 2000; Kortet, Hedrick, & Vainikka, 2010; Luttbeg & Sih, 2010). In general, individuals are expected to behave bolder, when the risk is low and the reward is high, and shy when risks and rewards are the other way around (Cooper, Pérez-Mellado, & Hawlena, 2006; Kortet et al., 2010). Such trade-offs might vary over time and contexts. Animals should therefore be able to adjust their behavioural decisions to new or altered environments. Studying in what way and how fast animals do this is a key to understanding their survival in these environments (Lima & Dill, 1990; Sih, Ferrari, & Harris, 2011).

On small islands, the balance between costs and benefits of foraging might change drastically when compared to larger islands or mainland. As mentioned above, the degree of boldness of an individual will depend on both the predation risk and resource availability in his particular environment (Kortet et al., 2010; Luttbeg & Sih, 2010). Predation pressure on islands is often low, due to the absence of predator species (Blumstein & Daniel, 2005; Brock, Bednekoff et al., 2014; Durand et al., 2012; Pafilis, Foufopoulos, Poulakakis, Lymberakis, & Valakos, 2009). In addition, food sources on small islands are often scarce. For example, islands tend to have both lower abundance and diversity of arthropods, which are the main food source for many reptiles and amphibians (Janzen, 1973; Olesen & Valido, 2003). A first consequence of this low predation pressure and food availability on islands should be the loss of costly antipredator behaviours, either due to selection, random genetic drift or phenotypic plasticity (Blumstein, 2002; Blumstein & Daniel, 2005; Cooper, Hawlena, & Pérez-Mellado, 2009). A lack of antipredator behaviour in insular prey species has indeed been described in a variety of taxa and is often referred to as "island tameness" (Cooper, Pyron, & Garland, 2014). Animals on islands often allow closer approach of humans (Blázquez, Rodríguez-Estrella, & Delibes, 1997; Blumstein, 2002; Brock, Bednekoff, Pafilis, & Foufopoulos, 2014; Cooper et al., 2014; Li, Belasen, Pafilis, Bednekoff, & Foufopoulos, 2014 but see Delibes, Blázquez, Soriano, Revilla, & Godoy, 2011), fail to recognize acoustic and olfactory predator cues (Blumstein, 2002; Blumstein, Daniel, & Springett, 2004; Durand et al., 2012) or even actively approach predator decoys (Li et al., 2014). It could therefore be expected that insular prey species will also behave bolder in a foraging context, as the risk is low but the reward is high (Luttbeg & Sih, 2010). The second consequence of the shift in cost–benefit balance on islands should be a decrease in neophobia. More explorative and less neophobic individuals on islands will be able to discover and exploit new resources and might therefore survive better on islands with lower food availabilities (Greenberg & Mettke-Hofmann, 2001; Haemig, 1988; Mettke-Hofmann, Winkler, & Leisler, 2002). However, there have been no studies on neophobia in insular populations so far.

The balance between costs and benefits during foraging will also change when animals colonize urban environments. Urbanization is one of the most drastic alterations of natural habitat caused by humans (Faeth, Warren, Shochat, & Marussich, 2005; Sih et al., 2011; Sol, Lapiedra, & González-Lagos, 2013) and is also a major reason for the decline of many species. Nevertheless, some species have adapted to life in the city and now thrive in urban environments, although requiring specific behavioural adjustments (Audet, Ducatez, & Lefebvre, 2015; Lowry, Lill, & Wong, 2012; Sol et al., 2013). Similar to islands, it has been suggested that predation pressure in urban areas is low, as many of the normal predators will either be absent (Candler & Bernal, 2015; Faeth et al., 2005; Sol et al., 2013; Valcarcel & Fernández-Juricic, 2009) or will have shifted to anthropogenic food sources (Chejanovski, Avilés-Rodríguez, Lapiedra, Preisser, & Kolbe, 2017). Urban animals can therefore afford being bolder, which has been demonstrated in species of various taxa (see Miranda et al., 2013 for a review). On the other hand, some species, particularly small reptiles, might suffer from even higher predation rates in urban environments, due to the lack of vegetation and natural shelter (Chejanovski et al., 2017) or the presence of cats and dogs (Griffin, Netto, & Peneaux, 2017; Koenig, Shine, & Shea, 2002; Lapiedra, Chejanovski, & Kolbe, 2017). Such species will benefit from being less bold in urban habitats. Urban animals are also more frequently exposed to novel, human-made, objects and situations (Candler & Bernal, 2015). Urban populations should therefore show reduced neophobia, especially as the least neophobic individuals will benefit from finding new resources in the city, such as artificial bird feeders (Audet et al., 2015; Miranda et al., 2013; Sol, Griffin, Bartomeus, & Boyce, 2011; Sol et al., 2013; Tryjanowski et al., 2016). Neophobia might also be reduced in many species due to a lower abundance of their normal arthropod prey (Faeth et al., 2005; Griffin et al., 2017). On the other hand, novelty might be associated with danger (e.g., poisonous new food; Sol et al., 2011), which may lead to urban animals behaving more neophobic (Mettke-Hofmann et al., 2002). Studies on the effect of urbanization on neophobia have yielded mixed results (Audet et al., 2015; Griffin et al., 2017; Miranda et al., 2013). Behavioural differences between urban and rural animals might also be a consequence of non-random dispersal. Only the boldest and least neophobic individuals will establish in urban environments, whereas the most shy and neophobic individuals will avoid them (Evans, Boudreau, & Hyman, 2010; Lowry et al., 2012; Sol et al., 2013). The effect of urbanization on behavioural strategies is therefore not straightforward and might differ among species.

Lizards often occur on small predator-free islets in relatively high abundances and often differ considerably from mainland conspecifics in many aspects of their biology, including their behaviour (Brock, Donihue, & Pafilis, 2014; Brock, Bednekoff et al., 2014; Cooper et al., 2014; Olesen & Valido, 2003). Lizards are therefore a widely used model in studies on island biology (see e.g., Blázquez et al., 1997; Cooper et al., 2009, 2014; Li et al., 2014). Several lizard species can also be found in (sub)urban areas, such as gardens, parks and greenbelts. (Perry, Buchanan, Fisher, Salmon, & Wise, 2008). In studies on behavioural adaptation to urbanization, lizards are, however, underrepresented and the few studies on this taxon often show results opposite to studies on birds and mammals. Urban birds and mammals generally behave bolder, while Chejanovski et al. (2017) found urban anoles to be more shy in a foraging context compared to conspecifics from a nearby forest. Moule, Michelangeli, Thompson and Chapple (2015) found no differences in exploratory behaviour and risk-taking between urban and rural skinks. Other studies on the other hand have shown that urban lizards are bolder

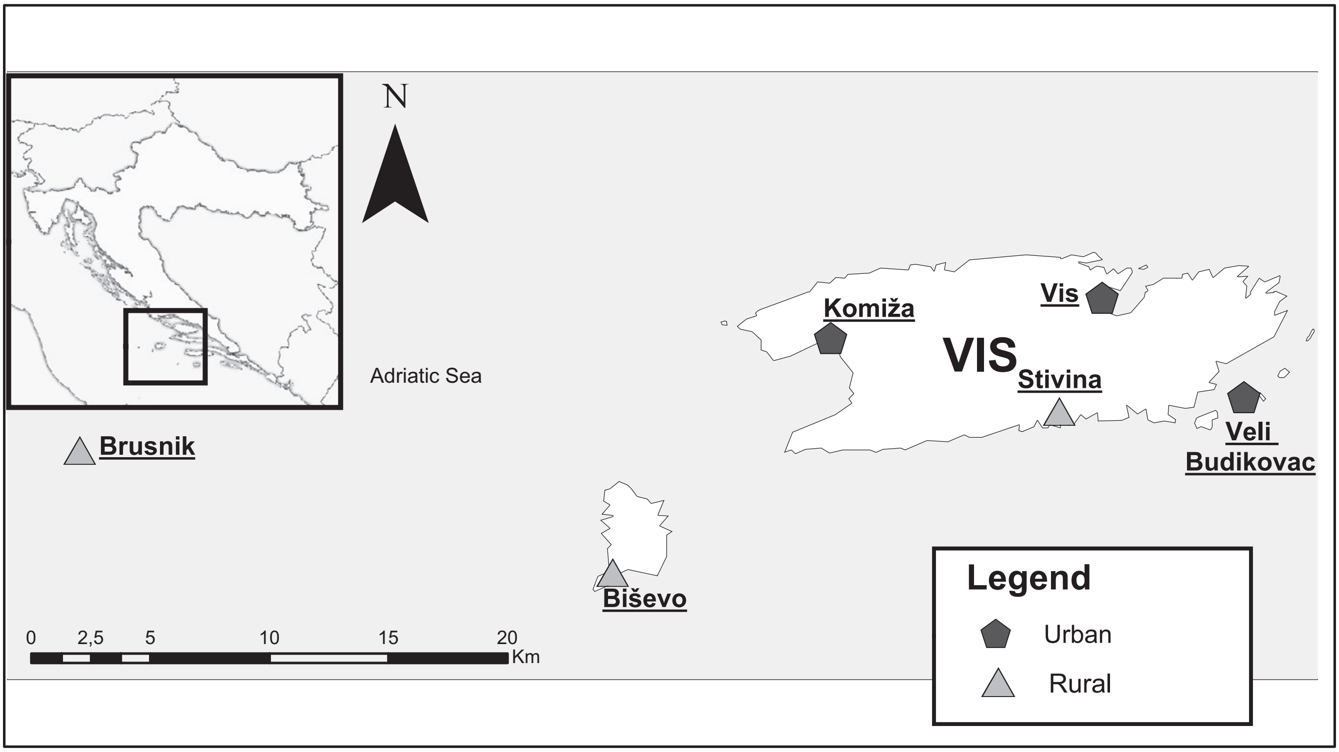

FIGURE 1 Vis and satellite islets, with the locations where lizards were tested on neophobia and risk-taking. Pentagons indicate urban areas, while triangles indicate rural areas

and more explorative (Lapiedra et al., 2017; Pellitteri-Rosa et al., 2017).

In this study, we investigated the effect of both insularity (large island vs. islets) and urbanization (urban vs. rural populations) on the foraging decisions made by the Dalmatian wall lizard *Podarcis melisellensis*, specifically: risk-taking behaviour and neophobia during foraging. While both terms are often used in the context of personality research, we simply refer to risk-taking as the willingness to take risks and neophobia as the fear of novelty (Miranda et al., 2013; Tebbich, Sterelny, & Teschke, 2010), regardless of whether there exists personality variation or not in these traits. Our null hypothesis is that both insularity and urbanization will lead to higher risk-taking and less neophobia during foraging, due to the lower predation pressure and lower food availability and/or exposure to novel food sources in these respective environments.

2 | MATERIALS AND METHODS

2.1 | Study species and location

P. melisellensis (Braun 1877) is a medium-sized insectivorous lizard (SVL: 65 mm, TL: 220 mm) which can be found on many islands on the east Adriatic coast (Speybroeck, Beukema, Bok, & Van Der Voort, 2016). It mainly occurs in Mediterranean scrublands, woodland and abandoned olive orchards (Huyghe, Vanhooydonck, Herrel, Tadić, & Van Damme, 2007), but it also inhabits (sub)urban areas (Baeckens & Briesen, 2017).

The effect of insularity on risk-taking and neophobia was studied by observing the behaviour of *P. melisellensis* on one large island (Vis, 90 km^2), and three small islets (Veli Budikovac, Brusnik and Biševo, all <6 km^2) in the Adriatic Sea near the mainland of Croatia (Figure 1). Four snake species are found on Vis: the four-lined snake (*Elaphe quatuorlineata*), the Balkan whip snake (*Hierophis gemonensis*), the European cat snake (*Telescopus fallax*) and the Leopard snake (*Zamenis situla*) (Jelić et al., 2009; Kryštufek & Kletečki, 2007), while only two of them can be found on Biševo (*H. gemonensis* and *T. fallax*) and none on the two other islets (Jelić et al., 2009). We sampled lizards on Vis and on the small islets in both inhabited and uninhabited areas (further referred to as, respectively, urban and rural lizards). The islet of Veli Budikovac is only inhabited by a few people, but the main building is a restaurant that is frequently visited by tourists during summer. In addition, there is a distinct human impact on the landscape (e.g., human litter, fences and pets.). Therefore, we considered this islet as inhabited, and the lizards as “urban”. The study was conducted during May 2017.

2.2 | Risk-taking tests

A total of 74 lizards were tested for risk-taking and divided into four groups: urban islet (10), rural islet (26), urban island (25) and rural island (13). Lizards were observed in the field between 10:00 and 16:00. Only adult lizards were tested. When a lizard was spotted in the field, it was slowly approached and a plastic petri dish containing five mealworms (*Tenebrio molitor*) was placed well in sight, approximately at a distance of 15 cm of the animal. In addition, we placed a plastic model of a snake next to the petri dish (Figure S1). As *H. gemonensis* and *T. fallax* on these islands do predate on *P. melisellensis* (personal observation), the presence of a snake model should be perceived as an actual risk by the lizard. While lizards combine both olfactory and visual cues when assessing predation risk (Amo, López, & Martín, 2004), we were unable to use olfactory cues in this field study. Nevertheless, previous field studies have shown that the use of a visual predator model should be sufficient to cause antipredator behaviour in lizards (Leal, 1999; Martín & López, 1996; Zani, Jones, Neuhaus, & Milgrom, 2009). Preliminary trials also showed that the snake model elicited higher antipredator behaviour compared to a stuffed rook (*Corvus frugilegus*). The transparent petri dish was closed, meaning that lizards could see but not access the food. Small holes were made in the top of the petri dish to allow detection by chemoreception. In case, the lizard had not fled after placing the petri dish and snake model, which happened in the majority of the cases, it was induced to flee into a nearby refuge (e.g., vegetation, rock and crevice.) by gently extending a hand towards the animal. Timing then began.

Three different indicators for risk-taking were used (Figure S2): (i) the time for the lizard's head to reappear from the refuge, called "appearance time", (ii) the time for the lizard to completely emerge from the hiding place, referred to as "emergence time" (Martín, López, & Cooper, 2003) and (iii) the time for the lizard to touch the petri dish, referred to as "feeding latency". If a lizard did not come out of hiding and/or touch the petri dish after 6 min, the trial was ended and the lizard was given the maximum score of 6 min. As the lizards were never caught, sex could not always be determined with absolute certainty.

Distance between the hiding spot of an individual and the petri dish could influence feeding latencies (Cooper, 2000). However, we believe that variation in distance between refuge and the petri dish was relatively small, both within and among populations.

2.3 | Neophobia tests

A total of 121 lizards were tested and divided into four groups: urban islet (17 control/10 novel), rural islet (14/16), urban island (24/21) and rural island (10/9). The protocol of the neophobia tests was largely similar to that of the risk-taking tests. Again, a lizard was approached in the field, and a petri dish containing five mealworms was placed near it. The lizard was, however, not chased away into a refuge. Neophobia is often tested by placing a novel, preferably conspicuousness and artificial, object near the food of an individual and then noting the latency of the animal to feed (Audet et al., 2015; Tebbich et al., 2010). Therefore, a bright red plastic drinking bottle was placed next to the petri dish with mealworms (Figure S1), and the latency of the lizards to touch the petri dish was timed, further referred to as the "feeding latency". Lizards received the maximum score of 6 min if they did not touch the food within this timeframe. If the lizards touched the petri dish, we also measured how long the lizards investigated the food before losing interest. This is further referred to as "investigation time". Following the same protocol, we also conducted control trials, in which only the petri dish, but no drinking bottle was present, to validate the effect of novelty.

Individual lizards were never tested for both neophobia and risk-taking, as individuals tended to run off after realizing they could not access the food. In addition, we wanted to avoid that the outcome of one test would influence the result of another test (e.g., if a lizard learnt that it could not access the mealworms in the first test, it might be less motivated to try it a second time).

2.4 | Statistical analysis

The program R version 3.4.0. (Ihaka, R. & Gentleman, R., University of Auckland, New Zealand) was used for statistical analyses. We used the R-package "survival", version 2.41-3 (Therneau & Lumley, 2015), and the package "coxme", version 2.2-5 (Therneau, 2015), which are designed to analyse right-censored data (e.g., due to a time limit such as in this study). Mixed effects Cox proportional hazards models were used to test for the effect of island size (large island Vis vs. islets) and urbanization (urban vs. rural). Both island size and urbanization were included as categorical variables, rather than continuous gradients. The interaction between island size and urbanization was included in the model. For the risk-taking data, a series of Spearman Rank Correlation tests showed that only appearance time and emergence time were significantly and strongly correlated (Figure S3). Therefore, we only used appearance time and feeding latency for further analyses. Separate models were used for appearance time and feeding latency. For the neophobia data, treatment (control vs. novel object) was also included in the Cox proportional hazards model.

To test for significant differences in the proportion of lizards touching the petri dish during the risk-taking tests, a binomial generalized mixed model was used, with island size and urbanization included as fixed factors. A similar model was used for the proportion of lizards touching the petri dish during the neophobia tests, with treatment included as an additional fixed factor.

Investigation time was log-transformed to obtain normality and analysed using a generalized mixed model testing the effects of island size, urbanization and treatment.

Non-significant terms were stepwise eliminated from the models. Sampling location was included as random effect in all models.

3 | RESULTS

3.1 | Risk-taking

Lizards from the large island extended their head from their refuge faster (coeff. = 0.66; $z = 2.11$; $p = .04$; Figure 2), but there was no difference in appearance time between urban and rural lizards (coeff. = −0.10; $z = -0.32$; $p = .75$). There was no significant interaction between island size and urbanization (coeff. = 0.85; $z = 1.46$; $p = .14$).

Lizards from the large island were less likely to touch the petri dish in the presence of a predator model, as compared to islet lizards ($z = -2.24$; $p = .02$; Figure 3), and had significantly higher feeding latencies (coeff. = −1.53; $z = -1.98$; $p = .048$; Figure 4). Urban and rural lizards did not differ in their tendency to touch the food ($z = -0.85$;

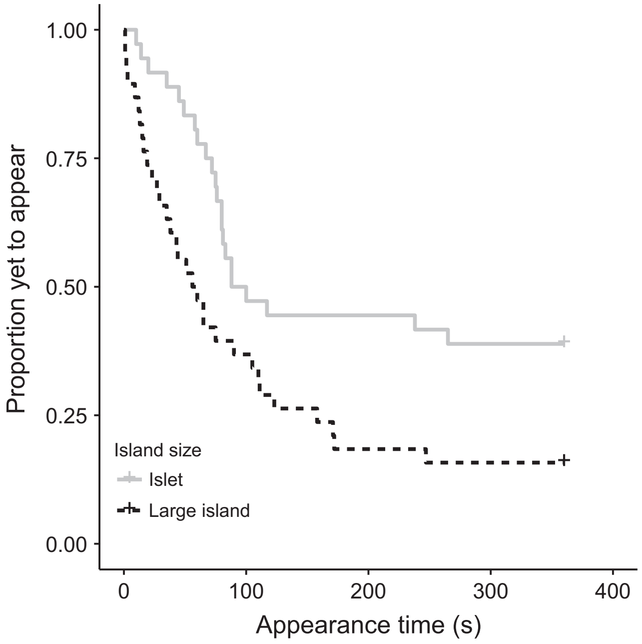

FIGURE 2 Survival analysis comparing the appearance times (the latency for a lizard's head to appear from a refuge in the presence of a predator model) between islet lizards (n = 36) and island lizards (n = 38)

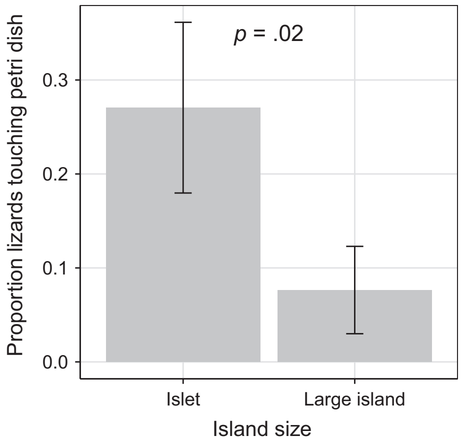

FIGURE 3 Mean proportion of lizards that touched the petri dish in the presence of a predator model for islet lizards (n = 36) and island lizards (n = 38). Error bars indicate standard errors

$p = .40$), nor in feeding latencies (coeff. = −0.52; $z = -0.75$; $p = .45$). There were no significant interactions between island size and urbanization in the proportion of lizards touching the petri dish ($z = 0.50$; $p = .62$), nor in feeding latencies (coeff. = 0.68; $z = 0.44$; $p = .66$). Descriptive statistics are presented in Table S1.

3.2 | Neophobia

There were no significant differences between lizards exposed to novel objects and the control group, nor in the feeding latency (coeff. = −0.27; $z = -0.90$; $p = .37$), the proportion of lizards touching the petri dish ($z = -0.82$; $p = .41$) or the investigation time ($F_{1,35} = 1.37$, $p = .25$). For none of these variables, there were significant interactions between treatment and island size or urbanization (all $p > .05$). Therefore, treatment (control vs. novel) was removed from all models as a factor.

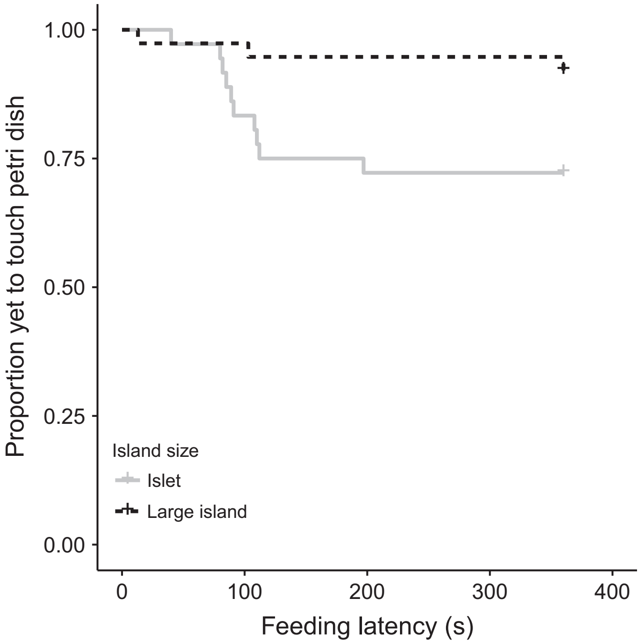

FIGURE 4 Survival analysis comparing the feeding latencies (the latency for a lizard to touch the petri dish in the presence of a predator model) between islet lizards (n = 36) and island lizards (n = 38)

Feeding latency did not differ between lizards from the large island or from the islets (coeff. = 0.01; $z = 0.03$; $p = .98$), nor between rural and urban lizards (coeff. = −0.16; $z = -0.51$; $p = .61$). There was no significant interaction between island size and urbanization (coeff. = 0.335; $z = 0.54$; $p = .59$).

The proportion of lizards touching the petri dish did not differ between island and islet lizards ($z = 0.11$; $p = .91$) or between urban and rural lizards ($z = -0.23$; $p = .56$). There was no significant interaction between island size and urbanization ($z = 0.23$; $p = .82$).

Investigation time did not differ between lizards from the large island and from the islets ($F_{1,3} = 0.29$; $p = .63$), nor between urban and rural lizards ($F_{1,3} = 0.14$; $p = .74$). There was no significant interaction between island size and urbanization ($F_{1,2} = 2.68$; $p = .28$). Descriptive statistics are presented in Table S2.

4 | DISCUSSION

This study investigated the effect of insularity and urbanization on risk-taking and neophobia during foraging in *P. melisellensis*. The behavioural decisions made by a foraging individual depend on the balance between predation risk and resource levels in the environment (Kortet et al., 2010; Luttbeg & Sih, 2010). On both islets and in urban habitats, the risk of predation and the resource availability are usually drastically altered (Blumstein & Daniel, 2005; Faeth et al., 2005; Griffin et al., 2017; Janzen, 1973; Lowry et al., 2012; Olesen & Valido, 2003; Pafilis et al., 2009; Sol et al., 2013). Lizards will, therefore, need specific behavioural adaptations to survive in these environments (Sih et al., 2011).

Small islets tend to have low levels of both predators and food (Blumstein & Daniel, 2005; Janzen, 1973; Olesen & Valido, 2003; Pafilis et al., 2009), prompting insular animals to take more risks in order to get food. In contrast to our expectations, lizards from the large island reappeared faster from a refuge in the presence of a snake model compared to islet lizards. On the other hand, islet lizards were more likely to touch the petri dish with food and did so faster. In hindsight, appearance time might not be an appropriate indicator for risk-taking behaviour, as lizards extending their head out of their hiding spot are still partially hidden and thus relatively safe. Reappearing faster might, however, indicate a higher degree of vigilance in these lizards, as it allows them to observe the potential predator and gather information about its behaviour (Polo, López, & Martín, 2011). Such information might be useful to predict further danger. Islet lizards probably behave less vigilant because predation risk in their habitat is low, and the time spent hiding is better used for foraging. Lower vigilance in island populations has only been demonstrated before in marsupials (Blumstein & Daniel, 2005).

On the other hand, trying to take the food by touching the petri dish represents a greater risk. Lizards had to move away from their safe refuges and actively approach a predator to do this. Therefore, we consider feeding latency a better indicator for risk-taking behaviour. Lower predation pressure on islets is known to lead to the loss of costly antipredator behaviours in a variety of taxa (Blázquez et al., 1997; Blumstein, 2002; Blumstein & Daniel, 2005; Brock, Bednekoff et al., 2014; Cooper et al., 2009, 2014; Durand et al., 2012; Li et al., 2014). In addition, small islets often have a low food availability (Janzen, 1973; Olesen & Valido, 2003), and nutritional state is known to affect risk-taking behaviour (Koivula, Rytkönen, & Orell, 1995; Lima & Dill, 1990; Martín et al., 2003). While insular lizards are known to behave more tame (see e.g., Brock, Bednekoff et al., 2014; Cooper et al., 2014), this is to our knowledge the first observation of islet lizards taking more risks in a foraging context than conspecifics from a larger island.

Food scarcity and the absence of predators should also lead to a decrease in neophobia in islet populations (Greenberg & Mettke-Hofmann, 2001; Mettke-Hofmann et al., 2002). However, islet lizards did not go to the food faster or more often during the neophobia tests than large island lizards. A possible explanation for this might be the lack of neophobia towards the novel object. Lizards exposed to the novel object did not differ in any of the recorded behaviours from lizards in the control group. It is therefore doubtful whether the object was novel enough to cause neophobic reactions. Measuring feeding latencies when exposed to a novel, often artificial and bright coloured, object is a standard protocol for neophobia assays (Audet et al., 2015; Candler & Bernal, 2015; Mettke-Hofmann et al., 2002; Miranda et al., 2013; Tebbich et al., 2010; Tryjanowski et al., 2016). However, this test is normally carried out in laboratory conditions, where animals might already be habituated to being fed by humans. While it is possible that the petri dish itself could be regarded as a novel object, reptiles are often not able to acknowledge transparent barriers (as often seen in terraria, Hernandez-Divers, 2001). Therefore, we doubt the lizards were able to recognize the petri dish as an actual object. Interestingly, lizards from one population (Brusnik) were often attracted to the novel object, even ignoring the offered food in favour of it. Unfortunately, not enough data were collected on this neophilic behaviour. Nevertheless, regardless of the impact of the novel object, the islet lizards should still have been more willing to go to the food and should spent more time investigating the petri dish to get the food, if arthropod prey is indeed scarce on islets (Drakeley, Lapiedra, & Kolbe, 2015; Janzen, 1973; Lima & Dill, 1990; Olesen & Valido, 2003). Future studies should validate whether arthropods are indeed less abundant on these islets.

Urban environments are relatively similar to insular habitats, in terms of reduced predation pressure (Candler & Bernal, 2015; Faeth et al., 2005; Sol et al., 2013; Valcarcel & Fernández-Juricic, 2009) and for lizards often a lower abundance of arthropod prey (Faeth et al., 2005; Griffin et al., 2017). Therefore, it was hypothesized that urban lizards should take more risks and act less neophobic during foraging compared to rural conspecifics, but no significant differences in behaviour were found between urban and rural lizards. The few previous studies on boldness and risk-taking in urban lizards have yielded mixed results (Chejanovski et al., 2017; Lapiedra et al., 2017; Moule et al., 2015; Pellitteri-Rosa et al., 2017). Most studies on birds and mammals, however, seem to confirm that urban animals are indeed bolder (Charmantier, Demeyrier, Lambrechts, Perret, & Grégoire, 2017; Evans et al., 2010; Lowry et al., 2012; Miranda et al., 2013; but see Seress, Bókony, Heszberger, & Liker, 2011; Valcarcel & Fernández-Juricic, 2009). So why do urban lizards differ in their behaviour from urban mammals and birds? One possible explanation might be that urban lizards do not experience the same decrease in predation pressure as urban birds or mammals. Many of their natural predators might still be present, especially mesopredators who thrive in cities due to the absence of top predators (Chejanovski et al., 2017; Faeth et al., 2005). Lizards in (sub)urban areas also suffer from predation by opportunistic predators, such as pets (e.g., cats and dogs) or other introduced species (Griffin et al., 2017; Koenig et al., 2002; Lapiedra et al., 2017). Urban habitats are also structurally less complex, for example less and lower vegetation, more open space and lack of rocks and crevices. (Chejanovski et al., 2017), meaning that lizards are more exposed to predators. Lizards are indeed known to behave less bold in more open habitats (Martín & López, 1995; Vanhooydonck & Van Damme, 2003). All these factors may result in urban lizards experiencing a similar, or even higher, predation pressure compared to rural conspecifics, in which case no differences in risk-taking nor neophobia would be observed, as the costs of being bold and curious are still relatively high (Greenberg & Mettke-Hofmann, 2001). If urban habitats have lower arthropod abundances (Faeth et al., 2005; Miranda et al., 2013), lizards will not be able to compensate predation costs by acting bolder and should therefore behave more careful (Kortet et al., 2010). This might also explain why no differences were found in the time spent investigating the petri dish between urban and rural lizards. We did observe predation on *P. melisellensis* in the city of Vis by a Balkan whip snake (*H. gemonensis;* personal observation) and a hooded crow (*Corvus cornix*; Baeckens & Briesen, 2017), but further research should investigate how predation pressure on lizards differs along an urban gradient. We believe this might explain why urban lizards in general do not behave bolder, while urban mammals and birds do.

An alternative, or even supplementary, explanation might be gene flow between rural and urban areas, which might counter selection for higher risk-taking and lower neophobia in the cities (Lenormand, 2002). While the sampled sites on the large island were at a sufficient large distance from each other, both urban areas are surrounded by rural areas with high abundances of lizards. Such gene flow is less likely to occur between the large island and the islets. Last but not least, it might be that increased risk-taking and lower neophobia are only beneficial after initial arrival in urban environments, when animals still have to switch to alternative resources (Bókony, Kulcsár, Tóth, & Liker, 2012). After establishment, lizards might have already learnt which resources are safe, and selection will once again favour high neophobia and low risk-taking (Bókony et al., 2012; Sol et al., 2013). Previous studies on neophobia in urban animals showed mixed results, and therefore, it is still unclear whether there is a general effect of urbanization on neophobia or not (Audet et al., 2015; Bókony et al., 2012; Candler & Bernal, 2015; Griffin et al., 2017; Miranda et al., 2013; Tryjanowski et al., 2016).

5 | CONCLUSION AND FUTURE PROSPECTS

Islet lizards did take more risks, were less vigilant and more explorative compared to their conspecifics of the large island, as was expected due to the scarcity of food and absence of predators on small islets. The lower vigilance and higher risk-taking in foraging for islet lizards are novel, yet not unexpected, findings. In contrast to our expectations, islet lizards and island lizards did not differ in neophobia, but this was probably due to the general lack of neophobia towards the novel object used in our protocol.

Urban and rural lizards did not differ in any of the studied behaviours, which was in contrast with studies on birds and mammals, but in line with some other studies on lizards. The lack of behavioural differentiation between urban and rural lizards might be a consequence of the still relatively high predation pressure in urban environments. Future studies should investigate if and how predation pressure on reptiles differs between rural and urban habitats, to better understand why some studies do find behavioural differences and others do not. More detailed information on predation pressure and food availability on islets might also have allowed a much deeper interpretation of the observed effect of insularity on lizard foraging behaviour.

As a final remark, we would like to point out that, while significant differences in behaviour were observed among populations of *P. melisellensis*, the underlying reasons for such variation are currently not clear. Divergence in behaviour, both between the large island and islets and between rural and urban areas, might be due to selection (Cooper et al., 2009), behavioural flexibility (Blumstein, 2002) or non-random gene flow (Brodin, Lind, Wiberg, & Johansson, 2013; Miranda et al., 2013). Unfortunately, it was not possible to investigate which mechanisms cause variation among population within the timeframe of our study.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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