

Islet tameness: escape behavior and refuge use in populations of the Balearic lizard (*Podarcis lilfordi*) exposed to differing predation pressure

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Abstract: Prey often exhibit reduced escape behavior on islands where predators are absent or scarce. Models of escape and refuge use predict that prey from populations having lower predation pressure have shortened flight initiation distance (FID; distance between a predator and a prey when escape begins), reduced distance fled and tendency to enter refuge, and shortened hiding time before emerging from refuge. By ourselves simulating approaching predators, we tested these predictions for two populations of the Balearic lizard, *Podarcis lilfordi* (Müller, 1927), on the islets of Rei (higher predation pressure) and Aire (lower) adjacent to Menorca. FID, distance fled, and hiding time were shorter and probability of entering refuge was lower on Aire than on Rei, confirming all predictions. All effect sizes were large, indicating major differences in antipredatory behavior between islets. These findings are consistent with data for other lizards on FID and limited data on distance fled and refuge entry. The effect of predation pressure on hiding time is a novel finding. Our results and those of previous studies suggest that relaxation of predation pressure leads to reduced natural selection for maintenance of antipredatory behavior at all stages of predator–prey interactions over a relatively short time span.

Résumé : Les proies ont souvent des comportements de fuite réduits sur les îles où les prédateurs sont absents ou rares. Les modèles de fuite et d'utilisation des refuges prédisent que les proies des populations qui connaissent des pressions de prédation plus faibles ont une distance d'initiation de la fuite (FID; distance entre le prédateur et la proie au début de la fuite) plus courte, une distance de fuite et une tendance à entrer dans un refuge réduites et une période de dissimulation plus courte avant de sortir du refuge. En simulant nous-mêmes l'approche d'un prédateur, nous avons testé ces prédictions chez deux populations du lézard des Baléares, *Podarcis lilfordi* (Müller, 1927), sur les îlots de Rei (pression de prédation plus forte) et Aire (moins forte) adjacents à Minorque. La FID, la distance de fuite et la période de dissimulation sont plus courtes et la probabilité d'entrer dans un refuge moindre sur Aire que sur Rei, ce qui confirme toutes les prédictions. L'importance de tous les effets est grande, ce qui indique des différences majeures dans le comportement antiprédateur entre les îlots. Ces résultats concordent avec les données de FID chez d'autres lézards et avec les données limitées disponibles sur la distance de fuite et l'utilisation des refuges. L'effet de la pression de prédation sur la durée de la dissimulation est une nouvelle observation. Nos résultats et ceux d'études antérieures laissent croire que le relâchement de la pression de prédation mène à une réduction de la sélection naturelle pour le maintien du comportement antiprédateur à toutes les étapes des interactions prédateur–proie sur une période de temps relativement courte.

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Introduction

Animals on islands are often subject to lower predation pressure than mainland populations, resulting in evolution of tameness, a reduction in escape behavior when confronted by people or predators (Darwin 1839; Curio 1966; Blumstein and Daniel 2005). The costs of maintaining morphological, physiological, and behavioral structures that contribute to antipredatory defense is believed to be greater

than the benefits of the defenses when predation events are very rare, leading to reduction and loss of various defensive traits via natural selection (McNab 1994; Van Damme and Castilla 1996; Magurran 1999; Blumstein and Daniel 2005; Rödl et al. 2007).

Antipredatory vigilance, escape, and subsequent hiding in refuge are prominent aspects of antipredatory behavior that might be diminished or lost under relaxed predation pressure on islands. Reduced escape behavior is well known to occur in island birds and lizards (Schallenberg 1970; Lack 1983; Stone et al. 1994). Relatively little is known about effects on vigilance, but macropodid marsupials on islands exhibit reduced vigilance and have lost the group size effect (Blumstein and Daniel 2005). Even the ability to recognize predators decays under relaxed selection (Stankowich and Coss 2007).

Because behavioral antipredatory defense has many components, it may be anticipated that reduced predation pressure may simultaneously affect diverse aspects of defensive behavior. Because this phenomenon has rarely been studied for more than one or two aspects of defense (exceptions are

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Van Damme and Castilla 1996; Blumstein and Daniel 2005), it is unknown whether multiple aspects of escape behavior and refuge use decay simultaneously or nearly so. To our knowledge effects of island life on refuge use have not been studied previously.

Economic models of escape (Ydenberg and Dill 1986; Cooper and Frederick 2007a) apply when a prey has detected an approaching predator and assesses the cost of remaining in its current location and the cost of fleeing. At a given distance from the predator, the cost of remaining (equal to cost of not fleeing) is expected fitness loss owing to predation risk. Costs of fleeing include expected loss of fitness owing to energetic expenditure and risk of injury owing to escape, which may often be trivial, and opportunity costs, the expected loss of fitness that might have been gained by foraging or engaging in social behavior or other activities to increase fitness (Ydenberg and Dill 1986; Cooper and Frederick 2007a). Both cost-benefit models predict flight initiation distance (FID). FID, which is the distance between predator and prey when an escape attempt begins, has variously been called approach distance, flush distance, and flight distance.

The models differ in the criterion used by prey to decide FID. In Ydenberg and Dill's (1986) model, the predicted FID occurs when costs of fleeing and not fleeing are equal. In Cooper and Frederick's (2007a) optimal escape model, the predicted FID is the distance for which the prey's expected fitness after the encounter is maximized. The optimal escape model is an improvement because it allows the prey in many circumstances to improve its fitness during the encounter, which is impossible in Ydenberg and Dill's model (1986), and makes explicit the roles of predation risk, the prey's fitness at the outset of the encounter, and gains in fitness that are possible during the encounter. Both models predict that FID increases as predation risk increases. Predictions of the models have been extensively confirmed for a variety of factors that influence costs of fleeing and of not fleeing in prey representing diverse taxa (reviewed by Stan-kowich and Blumstein 2005).

For prey that have entered refuge, the hiding time (equal to emergence time, which is the time between entering and emerging from the refuge) is predicted by two models that are isomorphic with the escape models discussed in the previous paragraph (Martín and López 1999; Cooper and Frederick 2007b). In these models of refuge use, hiding time replaces distance between predator and prey and the costs are those of emerging and not emerging (Martín and López 1999; Cooper and Frederick 2007b). Thus, both models predict that hiding time increases as predation risk increases. Although hiding time has been studied much less than FID, predictions of both models of hiding time have been verified consistently (reviewed by Cooper 2009a).

Other aspects of escape, including distance fled (the distance that the prey flees before stopping), and probability of entering refuge have not been modeled explicitly. However, it has been proposed that defensive behaviors may be predicted by the escape models with either distance fled or probability of entering refuge substituted for FID (Cooper et al. 2006; Cooper 2007, 2009b). These predictions have been verified for distance fled in some lizards for both costs of fleeing (Cooper and Pérez-Mellado 2004; Cooper et al.

2006) and not fleeing (e.g., Snell et al. 1988; Stone et al. 1994; Martín and López 1996, 2003; Cooper 1997a, 2007; Cooper et al. 2007). Little information is available for probability of entering refuge, but striped plateau lizards (*Sceloporus virgatus* Smith, 1938) were more likely to enter refuge under the greater risk implied by fast than slow predator approach speed and by the second of two successive approaches (Cooper 2009b).

We studied four aspects of escape and refuge use by the Balearic lizard (*Podarcis lilfordi* (Müller, 1927)) on two islets that differ in predation pressure, Rei (higher) and Aire (lower). Because of reduced predation pressure, we predicted that FID, distance fled, and hiding time would be shorter and probability of entering refuge would be lower on Aire than on Rei in accordance with predictions of economic models of escape behavior and refuge use for lower predation risk assessed by prey under relaxed predation pressure.

Materials and methods

Study site and predators

The study was conducted on two islets, Aire and Rei, off the coast of Menorca, Balearic Islands, Spain. Rei is a 4.1 ha islet located in a harbor near the city of Mao; Aire is much larger (29.8 ha) and is located 1 km off the coast of the extreme southeastern tip of Menorca near Punta Prima. Data were collected between 26 April and 8 May 2005 on sunny days when lizards were active. Air temperatures ranged between 20 and 25 °C, but lizards were fully active because basking permitted them to attained body temperatures well above air temperatures. The vegetation in most of our study areas on both islets was sparse, occupying patches surrounded by open ground between plants. On both islets, most of the plants were low bushes or grass, some of which provided cover for the lizards, and flowering species that provide food for the lizards (Pérez-Mellado and Corti 1993). Additional refuges were rocks and holes at the base of a stone fence on both islets, and holes or crevices in the concrete foundations of abandoned building and boards on Rei. There are no obvious differences in availability of refuges at our study sites on the two islets.

The main predators on Aire are birds. Eurasian kestrels (*Falco tinnunculus* L., 1758), which commonly eat lizards in southern Europe (Cramp and Simmons 1980), breed and eat *P. lilfordi* on some Menorcan islets and on Cabrera (Balearic Islands). Kestrels do not nest currently on Aire, but visit the islet frequently. A seagull (*Larus michaelis*, formerly *Larus cachinnans* Pallas, 1811) colony is on Aire, but seagulls are only sporadic predators of lizards (Cramp and Simmons 1982). *Larus michaelis* has not been reported to eat *P. lilfordi* in Cabrera (Araújo et al. 1977) or *Podarcis atrata* Bosca, 1916 in the Columbretes Islands (Catalá et al. 1990; Gomez 1991). Recent examination of more than 400 fecal pellets from *L. michaelis* on the Menorcan islet Colom revealed no remains of *P. lilfordi* (V. Pérez-Mellado, unpublished data). Shrikes (genus *Lanius* L., 1759) that occur on Menorca and some other islets may also be occasional visitors to Aire. No mammalian or ophidian predators are currently present (Pérez-Mellado 1989). At least in part owing to the low predator abundance, lizard density is extremely

high (4099 individuals·ha⁻¹) on Aire (Pérez-Mellado and Corti 1993; Pérez-Mellado et al. 2008). A human family resided on Aire as recently as about 1960, but there have been no permanent residents since then (Pérez-Mellado 1989). However, biologists, personnel who maintain a lighthouse, and boaters attracted by a lighthouse often visit Aire (Pérez-Mellado 1989).

On Rei, kestrels nest (Pérez-Mellado 1989; V. Pérez-Mellado and W.E. Cooper, Jr., personal observation during the study in 2005), and black rats (*Rattus rattus* (L., 1758)) are present (Pérez-Mellado et al. 2008). Rats of the genus *Rattus* are known to eat lizards, and have been implicated in lizard population declines on islands (Recher and Clark 1974; McCallum 1986). Although rats may affect eggs more than adults, they may attract raptors to Rei; the booted eagle (*Hieraaetus pennatus* (J.F. Gmelin, 1788)) is a frequent raptor visitor to Rei that only rarely visits Aire. Shrikes may visit Rei (Cramp and Simmons 1982). Rei was occupied by humans continuously for nearly the last 200 years, during which time dogs and cats occupied it; a cat was sighted on Rei as recently as 1997 (Carreras et al. 2006). There are no permanent human occupants of Rei in 2005, but people have restored some of the buildings and have visited the islet. If human presence caused habituation, this effect would have been greater on Rei than on Aire. Population density on Rei is 403 lizards·ha⁻¹ (Pérez-Mellado et al. 2008), an order of magnitude less than on Aire.

Simulation of attack by investigators

To study effects of predation risk on escape behavior and refuge use, we approached lizards to simulate attacks by predators. Use of human researchers as surrogates for predators is a widely used, effective method for studying both escape behavior (reviewed by Stankowich and Blumstein 2005) in vertebrates (fish — Grant and Noakes 1987; frogs — Cooper et al. 2008, 2009c; lizards — Cooper 1997a; Martín and López 1999; Martín et al. 2003; Cooper and Wilson 2007a, 2007b; birds — Blumstein 2003; Cárdenas et al. 2005; mammals — Blumstein and Pelletier 2005; Stankowich and Coss 2006; insects — Cooper 2006; crabs — Hemmi 2005) and refuge use (reviewed by Cooper 2009a; fish — Krause et al. 2000; lizards — Cooper 1998, 2000, 2009a; Martín and López 1999; Amo et al. 2007; turtles — Martín et al. 2005; birds — Koivula et al. 1995; mammals — Kramer and Bonenfant 1997; Blumstein and Pelletier 2005; crabs — Hemmi 2005).

Simulation of an approaching predator by an investigator permits efficient data collection in lizard studies. Investigators can traverse rough, uneven ground far more easily than can robotic model predators, and their motion is more fluid. An ethical advantage over using natural predators is that the lizards are much less likely to be harmed accidentally by an investigator than intentionally by a natural predator. Possible drawbacks of using human beings to simulate attacks are experimenter bias, failure of a human being to elicit predator-specific defensive responses, and predators are non-antipredatory motivation of prey responses.

None of these potential drawbacks is likely in our study. Experimenter bias is possible whenever the experimenter is aware of predictions, but we minimized any effect of bias

by using standardized methods, including consistent, practiced approach speeds and similar gaits. We selected treatment orders prior to data collection to avoid unconscious selection of treatments to favor predicted outcomes. Predator-specific defensive behaviors occur in chameleons (Stuart-Fox et al. 2006). Although it remains possible that such behaviors occur in *P. lilfordi*, recent tests of another terrestrial lizard (*S. virgatus*) revealed no qualitative differences to approach by researchers, snake models, and a stuffed raptor mounted with wings extended (Cooper 2008). In our other studies, *P. lilfordi* exhibited typical escape behavior for terrestrial lizards (Cooper et al. 2009a, 2009b).

Any concern that motivation for escaping or hiding might be unrelated to potential for injury or mortality because experimenters differ from typical predators of lizards seems implausible to us because numerous studies have confirmed theoretical predictions about FID and hiding time for numerous factors that affect risk of predation (cost of not fleeing) and cost of fleeing in lizards (FID — e.g., Heatwole 1968; Burger and Gochfeld 1990; Martín and López 1996; Cooper 1997a, 1997b, 1997c, 1999, 2000; Cooper et al. 2003, 2006; Cooper and Whiting 2007; hiding time — reviewed by Cooper 2009a). Lizards might have fled to avoid being trampled rather than caught by a predator, but such motivation cannot explain variation in hiding time in refuges when an investigator was motionless some distance from the refuge.

Data collection

We searched for lizards visually while walking slowly through the study sites. We approached only adults. Sex was not determined, but any sex differences in escape behavior and refuge use would be distributed randomly among treatments. The effect would be to increase experimental error without biasing results. After sighting a lizard, an experimenter moved very slowly to a location where the lizard had a clear view of him, then stopped walking and oriented to face the lizard. After several seconds, the experimenter began to approach using a preselected speed that was initially practiced ($n = 10$ per each speed), and periodically checked to prevent drift. The three approach speeds were slow (51.0 ± 1.4 m/min), intermediate (80.8 ± 0.8 m/min), and fast (115.8 ± 3.5 m/min). Only the intermediate approach speed was used for all experiments, except that on the effects of approach speed on FID for which three speeds were used. Starting distance, the distance between predator and prey when the predator begins to approach, affects FID in some birds, mammals, and lizards (Blumstein 2003; Cooper 2005, 2008; Stankowich and Coss 2006). In *P. lilfordi*, starting distance strongly affects FID at the fast approach speed, but not at the intermediate approach speed (Cooper et al. 2009b). In the experiment on effects of approach speed, starting distances were 6–12 m. In this range of starting distances, FID might have increased by at most 0.5 m during fast approach (Cooper et al. 2009b).

In the study of FID, we examined effects of islet population and approach speed. Approach was continuous until a lizard fled, whereupon the experimenter stopped moving immediately and recorded FID to the nearest 0.1 m. In two other experiments, the investigator approached and stopped as in the study of FID, but recorded only (*i*) the distance

fled before stopping to the nearest 0.1 m or (ii) whether or not the lizard entered a refuge or remained outside a refuge when it stopped fleeing. In the other experiment, the investigator continued to approach until the lizard entered a refuge, then began timing the duration of hiding, and moved 6–8 m from the opening of the refuge, and stood immobile there. Hiding time was the number of seconds from entering the refuge until the entire body emerged from the refuge. Hiding time was recorded as 600 s for individuals that did not emerge by then.

We prevented pseudoreplication by walking through a particular area only once during each experiment. Especially on Aire, one or more untested lizards often were visible when the test of another individual was completed. In these cases, we selected the next lizard to be tested from those that differed in appearance from and were not close to the escape path of the previously tested lizard. Because we collected data from the same areas in different experiments, some individuals may have been tested in more than one experiment.

Experimental designs and analyses

Independent groups designs were used in all experiments. The effects of approach speed and islet on FID was tested using a 2×3 factorial design with the three levels of approach speed and two islet populations. Two observers (V.P.M. and W.E.C.) collected the data, which were analyzed using an analysis of variance (ANOVA). The difference between islets in distance fled and hiding time was tested for significance using an ANOVA, and the difference in the proportion of individuals that entered refuge was examined using a Fisher exact probability test. Sample sizes were identical for each approach speed in the Aire population, but because of a miscommunication among us, sample sizes varied greatly among approach speeds on Rei (Fig. 1).

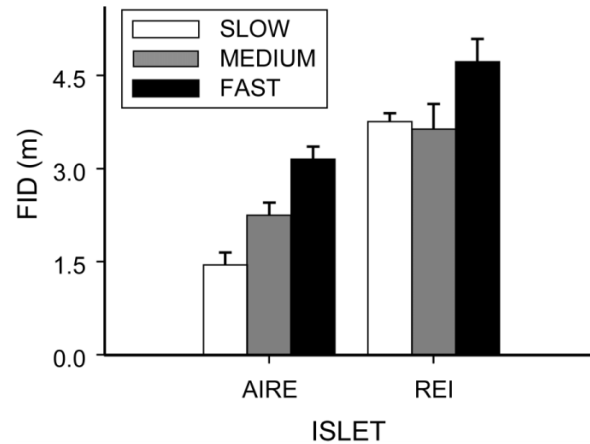
Analyses were conducted using Statistica. Data were examined using Levene's and Kolmogorov–Smirnov tests to ensure that assumptions of an ANOVA regarding homogeneity of variance and normality, respectively, were met. Only violations of the assumptions using raw data and their validity for logarithmically transformed data are reported. After detecting a significant interaction between approach speed and islet, we used Newman–Keuls tests to examine the significance of differences between pairs of means to assess the source of interaction. Except where otherwise noted and justified by directional prediction, all tests were two-tailed with $\alpha = 0.05$. We report effect sizes using η^2 for the ANOVA (Cohen 1992) and $r_{\text{equivalent}}$ for the Fisher exact probability test (Rosenthal and Rubin 2003).

Results

FID and distance fled

Both approach speed and population affected FID (Fig. 1). Because variances of FID were significantly heterogeneous ($F_{[5,109]} = 2.98$, $P = 0.02$), data were logarithmically transformed and verified to have homogeneous variances ($F_{[5,109]} = 1.96$, $P = 0.09$) prior to analysis. The interaction between approach speed and islet population was significant ($F_{[2,109]} = 5.82$, $P = 0.004$). The effect size for the interaction term was relatively small ($\eta^2 = 0.11$). Statistics for the

Fig. 1. Flight initiation distance (FID in m) by adult Balearic lizard (*Podarcis lilfordi*) was affected jointly by approach speed and the islet population, and was consistently greater in the Rei population than in the Aire population. Sample sizes were 20 for each approach speed in the Aire population. On Rei, the sample sizes were 44 for the slow approach speed, 5 for the intermediate approach speed, and 6 for the fast approach speed.



main effects, the significance of which cannot be interpreted apart from the interaction, were $F_{[2,109]} = 18.94$ ($P < 1 \times 10^{-6}$) for approach speed and $F_{[1,109]} = 66.18$ ($P < 1.0 \times 10^{-6}$) for population. The effects sizes were substantial for approach speed ($\eta^2 = 0.35$) and large for islet population ($\eta^2 = 0.61$).

FID was longer for lizards from Rei than from Aire at each approach speed, and greater for Rei at the slowest approach speed than for Aire at the fastest (Fig. 1). FID at each speed in the Rei population was significantly greater than FID for all speeds in the Aire population (Newman–Keuls tests, $P < 0.0063$ each) with two exceptions. FID did not differ significantly between fast approach on Aire, and either slow ($P = 0.19$) or intermediate ($P = 0.36$) approach speeds on Rei.

Using Newman–Keuls tests, differences in FID were significant between each pair of approach speeds on Aire (slow vs. intermediate, $P = 0.0014$; slow vs. fast, $P = 0.00012$; intermediate vs. fast, $P = 0.020$), but FID did not differ significantly between slow and intermediate approach speeds on Rei ($P = 0.97$); FID was only marginally greater for the fast approach speed compared with the slow approach speed (one-tailed test, $P = 0.058$). FID for the Rei population was significantly greater for the fast approach speed than for intermediate approach speed (one-tailed test, $P = 0.026$). The obvious source of interaction is that FID increased steadily as approach speed increased for the Aire population, but did not increase between the slow and the intermediate approach speeds for the Rei population (Fig. 1).

The distance fled was significantly greater on Rei than on Aire ($F_{[1,12]} = 11.63$, $P = 0.0052$); almost four times that on Aire (Table 1). Six of seven distances fled on Aire were less than half the shortest distance fled on Rei. The effect size was extremely large ($\eta^2 = 0.97$).

Refuge entry and hiding time

On Rei 89 of 96 (0.93) lizards entered refuges, whereas on Aire only 13 of 28 (0.46) entered refuges after fleeing.

Table 1. Distance fled and time spent hiding in refuge before emerging for Balearic lizards (*Podarcis lilfordi*) on two islets offshore from Menorca, Balearic Islands.

| Islet | Distance fled (m) | | | | Hiding time (s) | | | |
|-------|-------------------|-----|---------|----------|-----------------|------|--------|----------|
| | Mean | SE | Range | <i>n</i> | Mean | SE | Range | <i>n</i> |
| Aire | 0.6 | 0.2 | 0.2–1.6 | 7 | 26.9 | 6.6 | 3–78 | 14 |
| Rei | 2.2 | 0.4 | 1.4–4.6 | 7 | 241.8 | 42.4 | 30–600 | 18 |

Significantly more lizards entered refuges on Rei than on Aire (Fisher's exact test, $P = 3.4 \times 10^{-7}$). The large effect size was $r_{\text{equivalent}} = 1.00$.

Mean hiding time was approximately nine times longer on Rei than on Aire (Table 1). Variances in hiding time were significantly heterogeneous based on raw data (Levene's test, $F_{[1,30]} = 24.62$, $P = 0.00026$), but variances did not differ significantly based on logarithmically transformed data (Levene's test, $F_{[1,30]} = 0.003$, $P = 0.96$). Based transformed data, the difference in hiding time between islet populations was significant ($F_{[1,30]} = 50.62$, $P < 1.0 \times 10^{-6}$). The large effect size was $\eta^2 = 0.63$.

Discussion

Escape and refuge use by *P. lilfordi* on Aire and Rei

All predictions regarding effects of predation pressure on escape and refuge use were verified. FID and distance fled were longer, probability of entering refuge was greater, and hiding time was longer for *P. lilfordi* on Rei, where predation pressure is higher than on Aire. Furthermore, the effect sizes for differences between islet populations were very large. The effect sizes for islet populations were at, or nearly at, their theoretical maximum values for distance fled and probability of entering refuge (Cohen 1992; Rosenthal and Rubin 2003). Differences between islets accounted for over 60% of the variability in FID and hiding time, despite the interaction between approach speed and islet and the effect of approach speed for FID.

The interaction between approach speed and islet population for FID, although relatively small, was a consequence of the progressive increase in FID as approach speed increased in the Aire population, coupled with a lack of increase between the slow and intermediate speeds and an increase in FID at the highest approach speed in the Rei population. We think that this finding may be an artifact of the small sample size at the intermediate approach speed for Rei. For two of the five observations at the intermediate approach speed on Rei, the FIDs were much shorter than the mean FID at the slower approach speed. Additional observations are needed on the Rei population at the intermediate speed to determine whether or not FID increases between slow and intermediate approach speeds. If it does not, one interpretation would be that Balearic lizards on Rei have high FID even at low approach speed, and further increase FID only during rapid approaches, perhaps abruptly in a step-like manner.

The far greater distance fled on Rei than on Aire is presumably a consequence primarily of the difference in predation risk, but unmeasured differences in distance from refuge between islets could have contributed to this difference. However, on both islets, some lizards were close to refuges

and others were exposed in areas of sparse vegetation several metres from the nearest refuge. Any minor differences in availability of refuge between islets cannot account for the fourfold difference in distance fled. Similarly, although the proportion of lizards that entered refuges was twice as high on Rei as on Aire, we did not measure availability of refuges on the islets. Nevertheless, refuges within a few metres were available to all individuals, suggesting that more frequent entry into refuges on Rei was a consequent of the greater predation risk there.

Comparisons with previous findings

Diminished antipredatory defenses have been reported in lizard populations exposed to reduced predation pressure on islands and elsewhere. The longer FID for lizards on Rei than on Aire adds to mounting evidence for a consistent effect of differences in predation risk between populations on FID (Stone et al. 1994; Blázquez et al. 1997; Diego-Rasilla 2003). FID is shorter on an island than on the mainland in the short-crested spiny-tailed iguana (*Ctenosaura hemilopha* (Cope, 1863)) (Blázquez et al. 1997). In the Galápagos Islands, the tropidurid lizards (genus *Tropidurus* Wied-Neuwied, 1824) had longer FID on islands inhabited by introduced feral cats (Stone et al. 1994). Similarly, the marine iguana *Amblyrhynchus crissatus* Bell, 1825 had longer FID on islands where cats and dogs have been introduced (Berger et al. 2007). Both studies suggest that island tameness acquired during millions of years of greatly reduced predation was reduced or lost owing to exposure to predation in the last few decades.

Our observation that distance fled was greater in a population exposed to higher predation pressure agrees with the report for *Tropidurus* spp. (Stone et al. 1994), but differs from the absence of difference in distance fled between populations at higher and lower elevations in the common wall lizard (*Podarcis muralis* (Laurenti, 1768)) (Diego-Rasilla 2003). Distance to nearest refuge did not differ between the two populations (Diego-Rasilla 2003), but uncontrolled differences in microhabitats and vegetation might have contributed to the lack of difference in distance fled. The finding that probability of entering a refuge is higher in a population at greater risk in *P. lilfordi* corroborates the only other study of this variable in a lizard (Diego-Rasilla 2003). The greater hiding time in a population with higher than lower predation pressure is a novel result that we attribute to greater assessed risk after a given duration spent in refuge for populations exposed to greater risk.

More information that suggests diminution of defenses under reduced predation pressure is available for lacertids than other lizards. In the Iberian wall lizard (*Podarcis hispanica* (Steindachner, 1870)), foot-shaking and tail-vibration responses to chemical cues from a viper were less frequent

in a population from an island where the snakes had been absent for more than a hundred years than on a mainland population (Van Damme and Castilla 1996). These findings suggest that natural selection has reduced certain aspects of defensive behavior in a relatively short time. However, the island lizards retained similar tongue flick rates and started movement bouts as frequently as did mainland lizards (Van Damme and Castilla 1996). In the Balearic lizard (*P. lilfordi*), tails were more difficult to autotomize and the autotomized portions moved less vigorously and for shorter distances and times on one of two islets that experienced lower predation pressure; autotomy was more easily and fully expressed in a mainland populations of Mediterranean lacertids, including *P. lilfordi* (Pérez-Mellado et al. 1997; Cooper et al. 2004).

Together with the findings cited for *P. muralis* (Diego-Rasilla 2003), the effects described in the preceding paragraph indicate that predation pressure experienced by natural populations affects diverse aspects of antipredatory behavior in lacertid lizards, including (i) responses performed when a predator's scent has been detected, but the predator has not been sighted; (ii) aspects of escape behavior including FID and distance fled; (iii) autotomy when overtaken by a predator; and (iv) time spent hiding in refuge. The similar effects of predation risk on FID cited for other lizards suggest that this effect of predation risk applies to diverse lizards, and presumably much more broadly. Evidence from mammalian research suggests that the effects of predation risk apply to vigilance before a predator has been detected (Blumstein and Daniel 2005) and may extend throughout the sequence of responses by prey to presence and actions of the predators (Lima and Dill 1990) during short-term predator-prey encounters.

Extreme island tameness characterized by absence or near absence of escape behavior occurs on isolated islands, such as the Galápagos, where predators have been absent for millions of years. Divergence between the Rei and the Aire populations of *P. lilfordi* is estimated to have occurred 280 000 years ago (Brown et al. 2008), which is ample time for the less extreme decay of various aspects of defensive behavior to occur on different islets of the same island. This is consistent with findings for island-mainland comparisons of changes in only 100 years in another lacertid lizard (Van Damme and Castilla 1996) and thousands of years in macropodids (Blumstein and Daniel 2005). Decay of antipredatory behavior to specific predators that have disappeared has also been reported in mainland deer in several thousand years (Stankowich and Coss 2007). Rates of change in various aspects of defense appear to differ within and between species (Van Damme and Castilla 1996; Blumstein and Daniel 2005). For example, in Australian macropodid mammals, group size effects on vigilance are reduced on islands (although this was not directly attributable to absence of predators), but FIDs are similar on islands and the mainland (Blumstein and Daniel 2005). Quantitative studies are needed to establish the effects of the degree of relaxation of predation pressure and to estimate the rapidity of changes in defensive behaviors.

Two factors other than predation pressure that might account for the observed differences in behavior are interislet differences in population density and in the lizards them-

selves. The higher population density on Aire (Pérez-Mellado 1998) might conceivably have a risk-dilution effect when multiple lizards are in close proximity, which would lead to shorter FIDs. However, lizards that we approached were not close enough to other individuals for risk dilution to have occurred. Balearic lizards on Aire are darker in coloration and are slightly larger than those on Rei (Pérez-Mellado 1998; Pérez-Mellado et al. 2008). Because the darker lizards on Aire are much more conspicuous than those on Rei, greater wariness would have been predicted for lizards on Aire, which is the opposite of our findings. Although one might imagine many scenarios that could lead to differences in wariness, we can think of no credible alternatives to predation pressure that account for the observed differences in antipredatory behavior between the islets.

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