

Libro de Resúmenes

**ECO-ETOLOGÍA 2016**

**Congreso Internacional de la Sociedad Española de Etología y  
Ecología Evolutiva**

**Gregorio Moreno-Rueda, Fabián Casas, Eloísa Collantes-Martín, Mar Comas,  
Rodrigo Megía-Palma, David Ochoa, Eliana Pintus, Manuel Pizarro, Senda  
Reguera, José M. Rivas, José L. Ros-Santaella, Francisco J. Zamora-Camacho  
(EDITORES)**



**Granada  
20-23 septiembre 2016**

Recomendación para la cita del libro:

Moreno-Rueda, G.; Casas, F.; Collantes-Martín, E.; Comas, M.; Megía-Palma, R.; Ochoa, D.; Pintus, E.; Pizarro, M.; Reguera, S.; Rivas, J.M.; Ros-Santaella, J.L. & Zamora-Camacho, F.J. (eds.). 2016. Libro de resúmenes de Eco-Etología 2016, Congreso Internacional de la Sociedad Española de Etología y Ecología Evolutiva. Sociedad Española de Etología y Ecología Evolutiva y Universidad de Granada. Granada. I.S.B.N.: 978-84-617-4865-5.

**16:00–17:15 SESIÓN DE COMUNICACIONES ORALES 10  
BIODIVERSIDAD Y CONSERVACIÓN**

**Antipredatory responses of the lizards of Menorca to the scents of snakes: from  
tameness to wariness**

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Antipredatory defenses are maintained when benefit exceeds cost. A weak predation pressure may lead insular lizards to tameness. *Podarcis lilfordi* exhibits a high degree of insular tameness, which may explain its extinction from the main island of Menorca when humans introduced predators. There are three species of lizards in Menorca: the native *P. lilfordi*, only in the surrounding islets, and two introduced lizards in the main island, *Scelarcis perspicillata* and *Podarcis siculus*. Besides, there are three species of snakes, all introduced: one non-sauriophagous (*Natrix maura*), one potentially non-sauriophagous (*Rhinechis scalaris*) and one sauriophagous (*Macroprotodon mauritanicus*). We studied the reaction to chemical cues of snakes of five populations: (1) *P. lilfordi* of Colom, (2) *P. lilfordi* of Aire, (3) *P. lilfordi* of Binicodrell, (4) *S. perspicillata*, and (5) *P. siculus*, ordered by increasing level of predation pressure. We aimed to assess the relationship between predation pressure and the degree of insular tameness regarding scent recognition. We hypothesized that *P. lilfordi* should show the highest degree of tameness, *S. perspicillata* should show intermediate responses, and *P. siculus* should show the highest wariness. Results are clear: neither *P. lilfordi* nor *S. perspicillata* recognize any of the snakes, while *P. siculus* recognizes the scent of *M. mauritanicus*, reacting with typical well-defined antipredatory behaviours. In general, our results suggest that chemical discrimination might be evolutionarily lost sooner than other antipredatory adaptations, such as tail autotomy or escape behaviour.

# Antipredatory responses of the lizards of Menorca to the scents of snakes: from tameness to wariness

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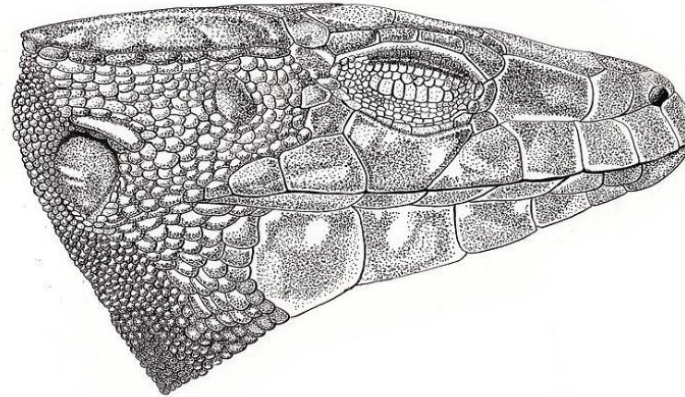


**ECO-ETOLOGÍA-2016**  
**CONGRESO INTERNACIONAL DE LA SOCIEDAD ESPAÑOLA DE ETOLOGÍA Y**  
**ECOLOGÍA EVOLUTIVA**

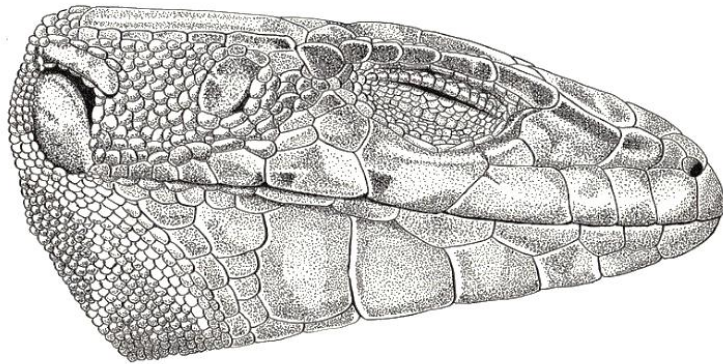
- Defenses of prey and hunting strategies of predators usually **coevolve** in a cost-benefit model
- Some adaptations may be **costly** under a low predation pressure
- **Island tameness**: reduction of antipredatory responses



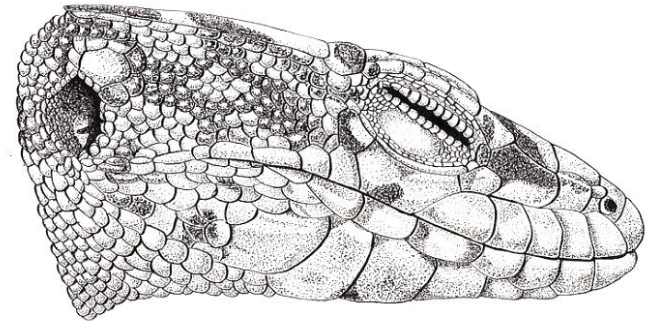
- Three species of lizards in Menorca:



*Podarcis lilfordi* (endemic)



*Podarcis siculus* (introduced)



*Scelarcis perspicillata* (introduced)

- Three species of snakes in Menorca (all of them introduced):



*Natrix maura*

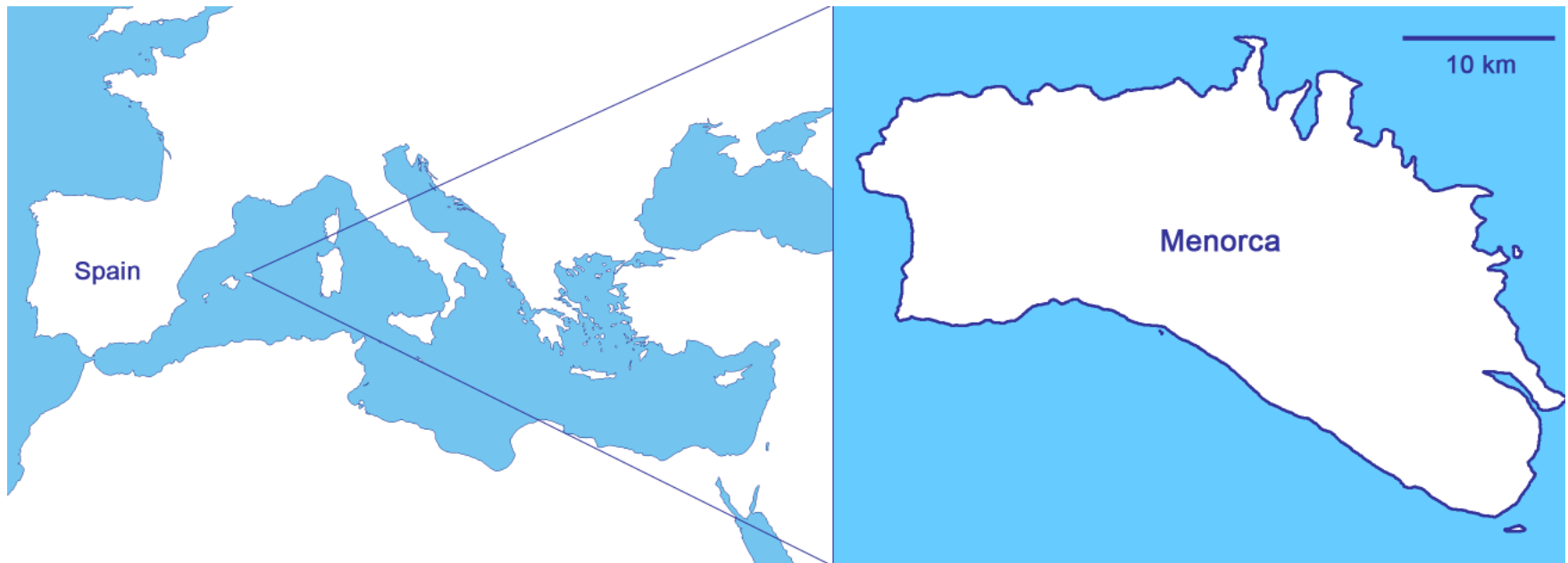


*Rhinechis scalaris*



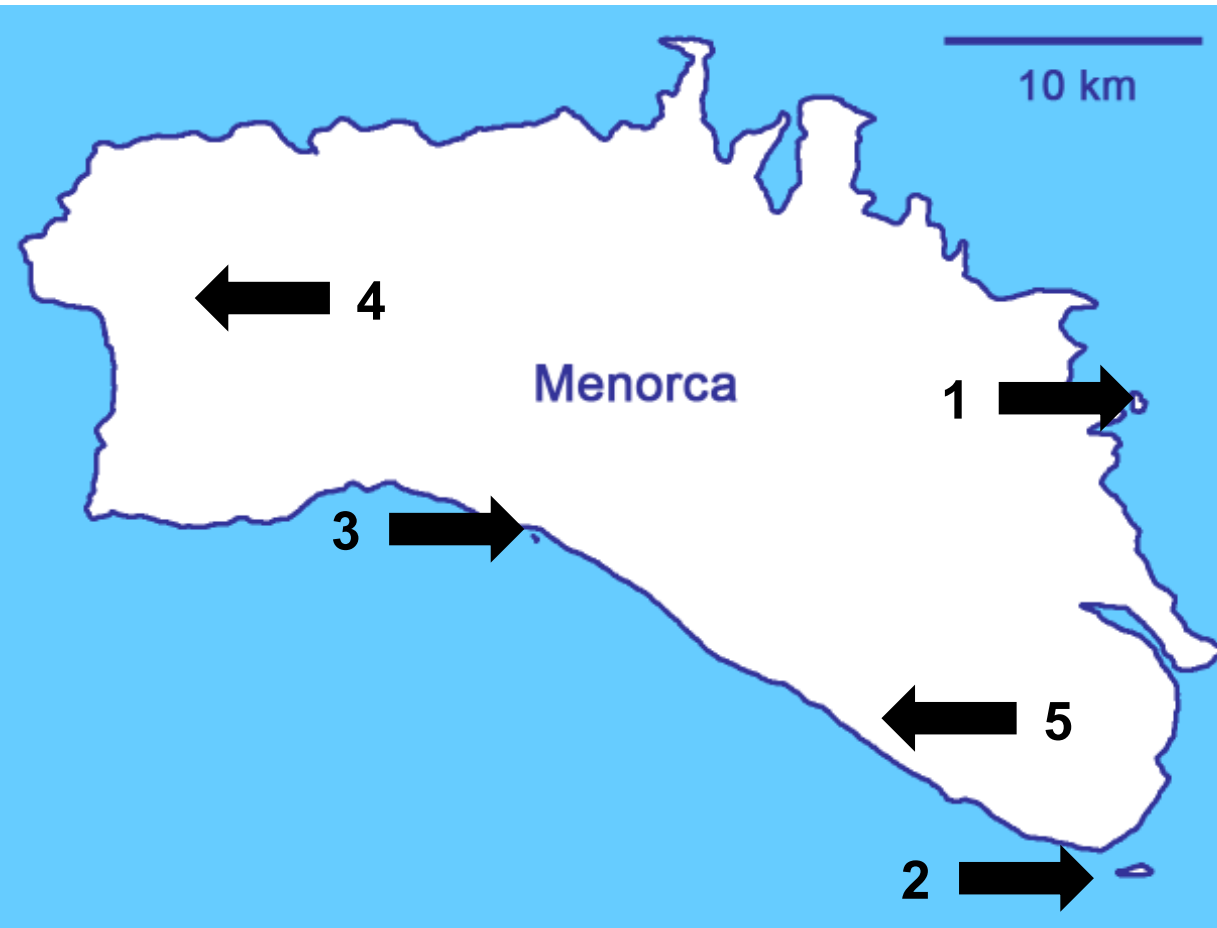
*Macroprotodon mauritanicus*

- We studied the behaviour of lizards against chemical cues of snakes
- 5 populations: different predation pressures





- Five populations:



1. *P. lilfordi* of Colom
2. *P. lilfordi* of Aire
3. *P. lilfordi* of Binicodrell
4. *S. perspicillata*
5. *P. siculus*

Low predation  
pressure



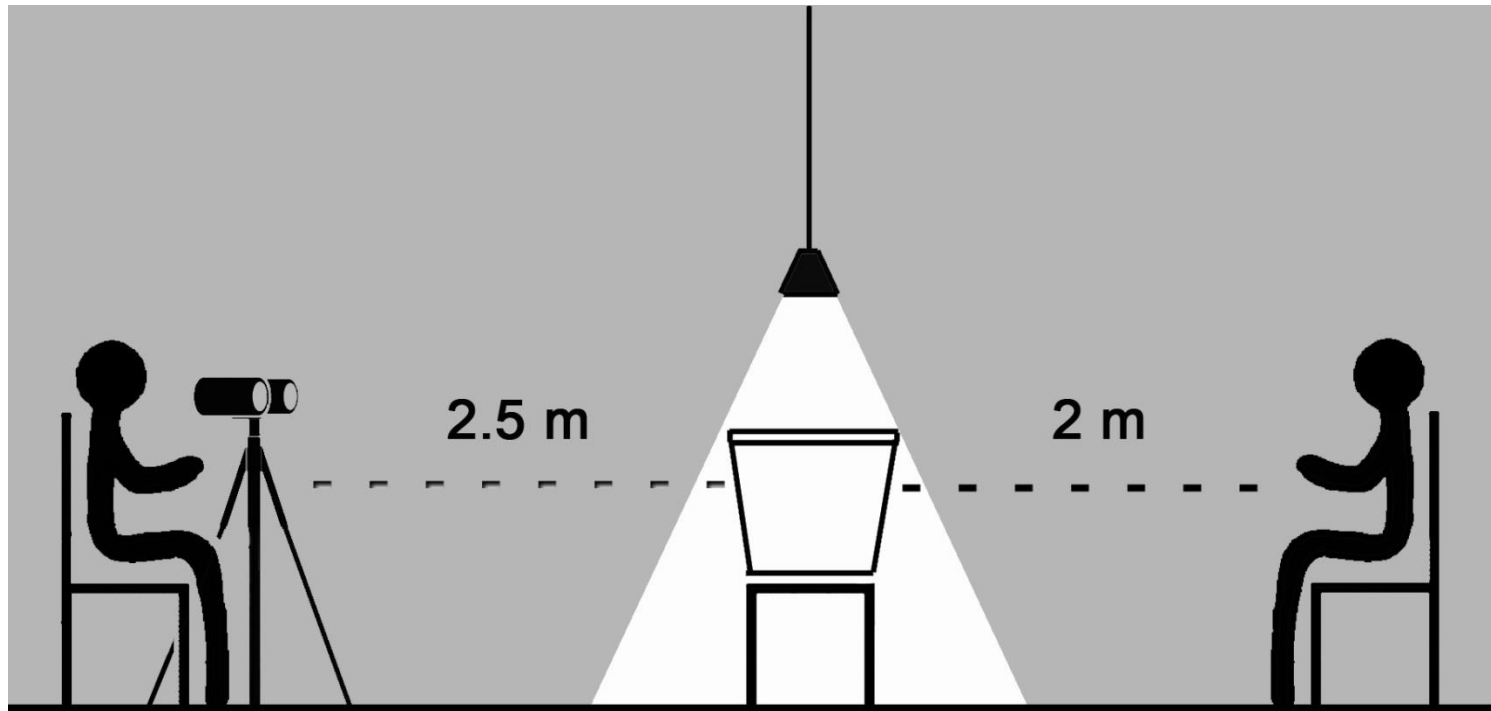
High predation  
pressure

- Five similar experiments (replicated), each:
  - 24 lizards
  - 4 treatments:

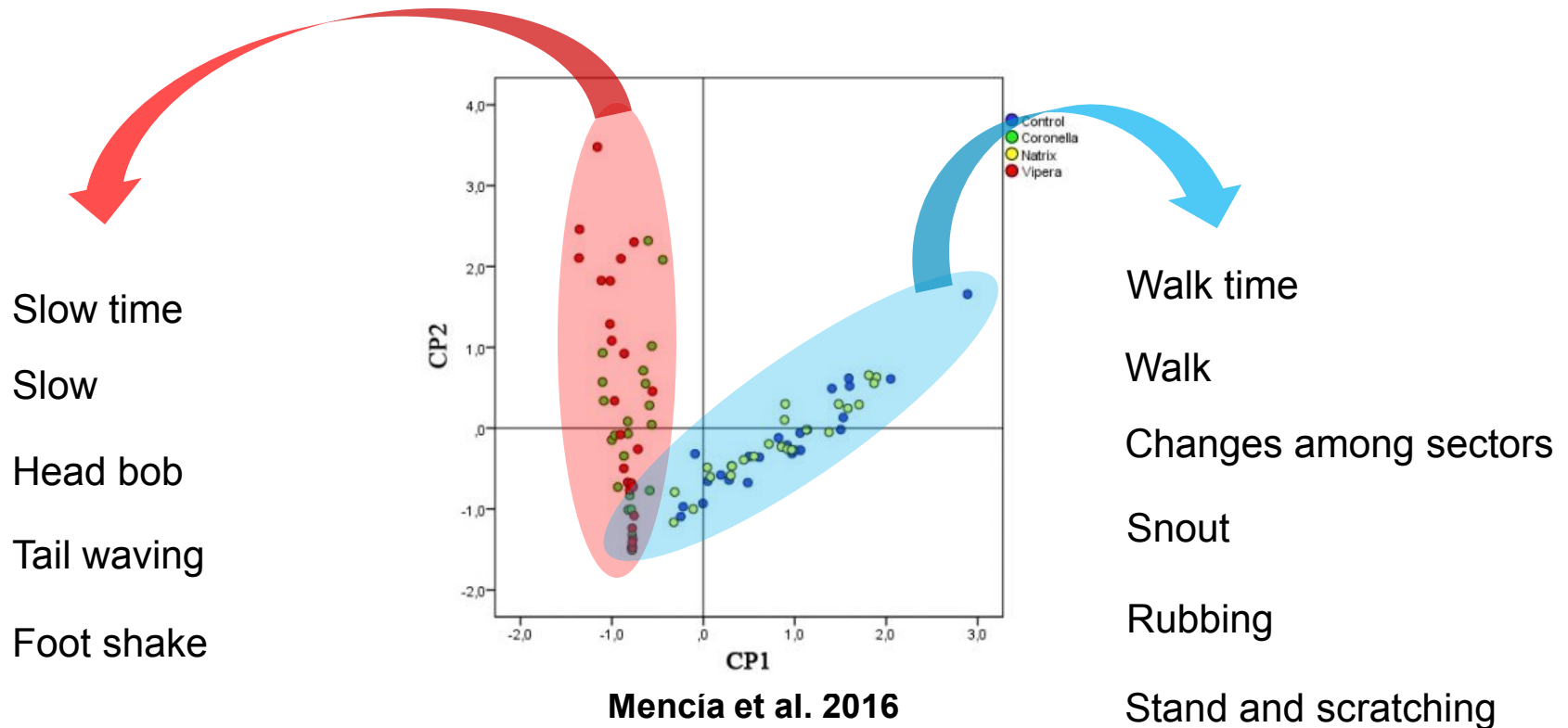


- Repeated measures analysis

- Two observers
- Trials of 15' (24 lizards x 4 treatments x 5 experiments = 480 trials)



- 16 behavioural variables:



Mencia et al. 2016  
(*Iberolacerta galani*)

Walk latency

TF

TF latency

Head rise

No move

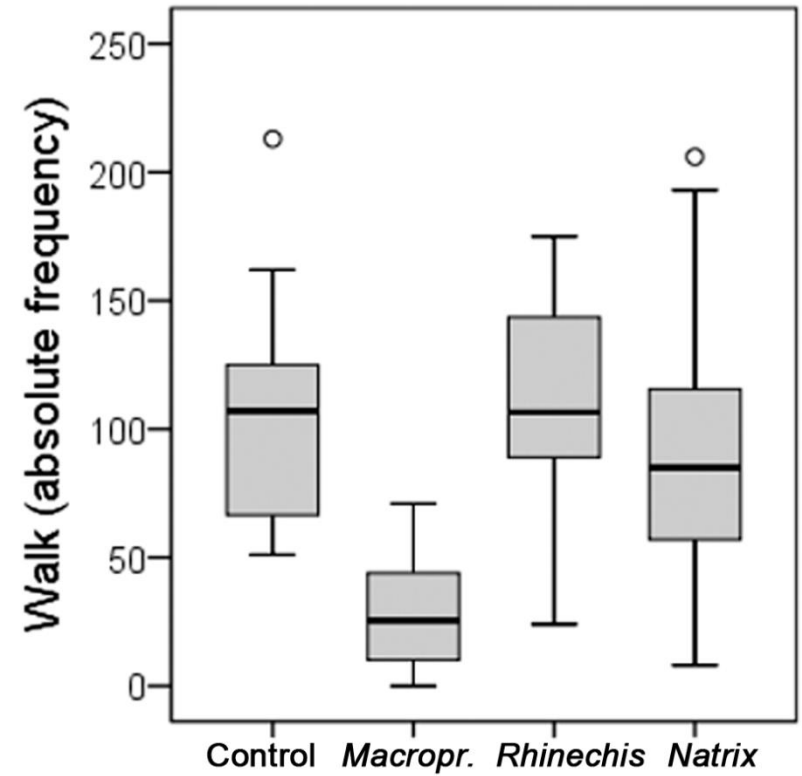
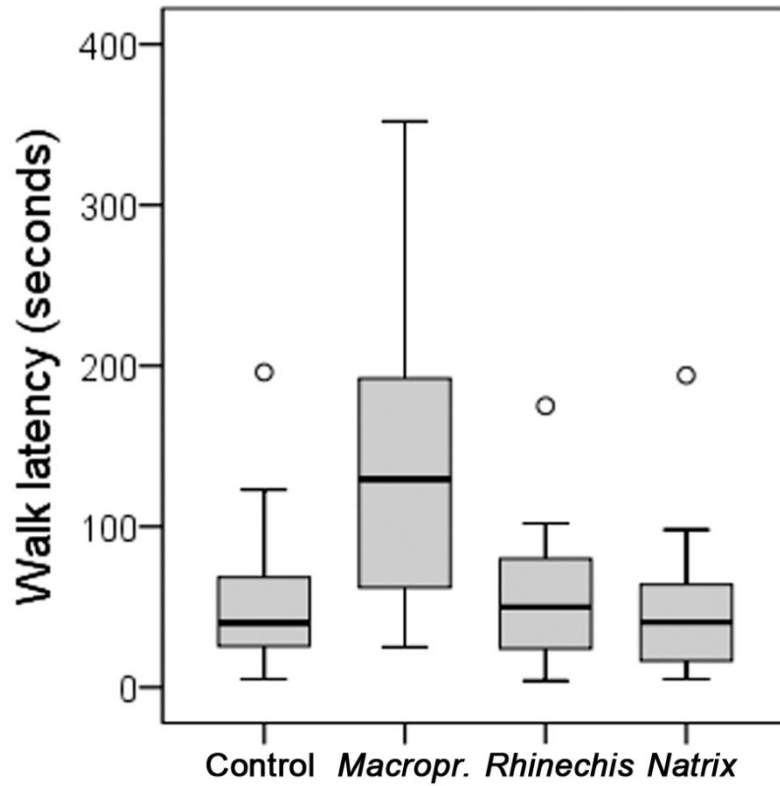
Variable	<i>P. lilfordi</i> Colom	<i>P. lilfordi</i> Aire	<i>P. lilfordi</i> Binicodrell	<i>S. perspicillata</i>	<i>P. siculus</i>
Walk latency	0.2947	0.5185	0.4217	0.1831	<b>0.0002</b>
Walk	0.5142	0.8924	0.4195	0.3331	<b>&lt; 0.0001</b>
Ch. sectors	0.9175	0.196	0.481	0.5467	<b>&lt; 0.0001</b>
Slow	1.0000	1.0000	1.0000	1.0000	<b>&lt; 0.0001</b>
TF latency	0.5455	0.9091	0.3689	0.2078	<b>0.0009</b>
TF	0.1098	0.765	0.244	0.7898	0.5484
Snout	0.1206	0.0944	0.0870	0.0741	<b>&lt; 0.0001</b>
Rubbing	0.2965	0.7012	0.1003	0.1574	0.173
Stand and scr.	0.09043	0.6406	0.4482	0.6823	<b>0.0004</b>
Foot shake	1.0000	1.0000	0.1054	0.3916	1.000
Head bob	1.0000	1.0000	1.0000	1.0000	<b>0.0293</b>
Head raise	0.9268	0.161	0.6116	0.3289	<b>&lt; 0.0001</b>
Tail waving	1.0000	1.0000	1.0000	1.0000	<b>&lt; 0.0001</b>
Walk time	0.9749	0.5621	0.5035	0.4848	<b>&lt; 0.0001</b>
Slow time	1.0000	1.0000	1.0000	1.0000	<b>&lt; 0.0001</b>
No move	0.7879	0.7173	0.4114	0.4362	<b>0.0002</b>

- Only *P. siculus* showed different behaviours between treatments

*A posteriori* paired comparisons for *P. siculus*:

Variable	Control – Macropr.	Control – Natrix	Control – Rhinechis	Macropr. – Natrix	Macropr. – Rhinechis	Natrix - Rhinechis
Walk latency	<b>31.0</b>	2.5	0.5	<b>33.5</b>	<b>31.5</b>	2.0
Walk	<b>49.5</b>	0.0	16.5	<b>49.5</b>	<b>33.0</b>	16.5
Ch. among sectors	<b>44.5</b>	7.5	9.0	<b>52.0</b>	<b>35.5</b>	16.5
Slow	<b>52.5</b>	0.5	17.0	<b>52.0</b>	<b>35.5</b>	16.5
TF latency	27.5	4.0	1.5	<b>31.5</b>	29.0	2.5
Snout	<b>38.0</b>	0.5	7.5	<b>37.5</b>	<b>30.5</b>	7.0
Stand and scratching	<b>31.5</b>	2.0	0.5	29.5	<b>31.5</b>	1.5
Head raise	<b>40</b>	10	20	<b>30</b>	20	10
Tail waving	26.5	0.0	1.5	26.5	25.0	1.5
Walk time	<b>46</b>	3	11	<b>43</b>	<b>35</b>	8
Slow time	<b>52.5</b>	1.0	16.5	<b>53.5</b>	<b>36.0</b>	17.5
No move	<b>37</b>	8	13	<b>29</b>	24	5

Critical value = 29.59 ( $\alpha = 0.05$ )



- Our results reinforce previous findings about the **extrem island tameness** of the native lizard, *P. lilfordi*







Cite this article: Cooper Jr WE, Pyron RA, Garland Jr T. 2014 Island tameness: living on islands reduces flight initiation distance. *Proc. R. Soc. B* 281: 20133019. <http://dx.doi.org/10.1098/rspb.2013.3019>

Received: 18 November 2013  
Accepted: 4 December 2013

**Subject Areas:**  
behaviour, ecology, evolution

**Keywords:**  
antipredatory behaviour, body size,  
escape behaviour, flight initiation distance,  
island tameness, lizard

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## Island tameness: living on islands reduces flight initiation distance

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One of Darwin's most widely known conjectures is that prey are tame on remote islands, where mammalian predators are absent. Many species appear to permit close approach on such islands, but no comparative studies have demonstrated reduced wariness quantified as flight initiation distance (FID; i.e. predator-prey distance when the prey begins to flee) in comparison with mainland relatives. We used the phylogenetic comparative method to assess influence of distance from the mainland and island area on FID of 66 lizard species. Because body size and predator approach speed affect predation risk, we included these as independent variables. Multiple regression showed that FID decreases as distance from mainland increases and is shorter in island than mainland populations. Although FID increased as area increased in some models, collinearity made it difficult to separate effects of area from distance and island occupancy. FID increases as SVL increases and approach speed increases; these effects are statistically independent of effects of distance to mainland and island occupancy. Ordinary least-squares models fit the data better than phylogenetic regressions, indicating little or no phylogenetic signal in residual FID after accounting for the independent variables. Our results demonstrate that island tameness is a real phenomenon in lizards.

### 1. Introduction

Darwin [1] observed that animals on remote oceanic islands often are unafraid of people, permitting close approach. He believed that escape behaviour had diminished where predators were rare or absent on remote islands, which resulted in loss of costly escape responses [2–6] in the absence of strong natural selection to maintain them. Island tameness has been reported anecdotally in birds, lizards and other taxa [6–9]. If Darwin's island tameness hypothesis is correct, predation intensity and escape responses should be diminished on islands compared with the mainland and should also vary with distance from the mainland [10,11]. Mammalian predators are often absent from remote islands [1,7], but

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

William E. Cooper, Jr., Dror Hawlena, and Valentín Pérez-Mellado

**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.

[Traduit par la Rédaction]

### 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 1820; Curio 1966; Blum-

stein 1982; Blumstein et al. 2005; Blumstein & Daniel 2005; Blumstein et al. 2007). 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; Redl et al. 2007).

Cooper et al. 2014

Cooper et al. 2019

- However, chemical recognition did not change with predation pressure!

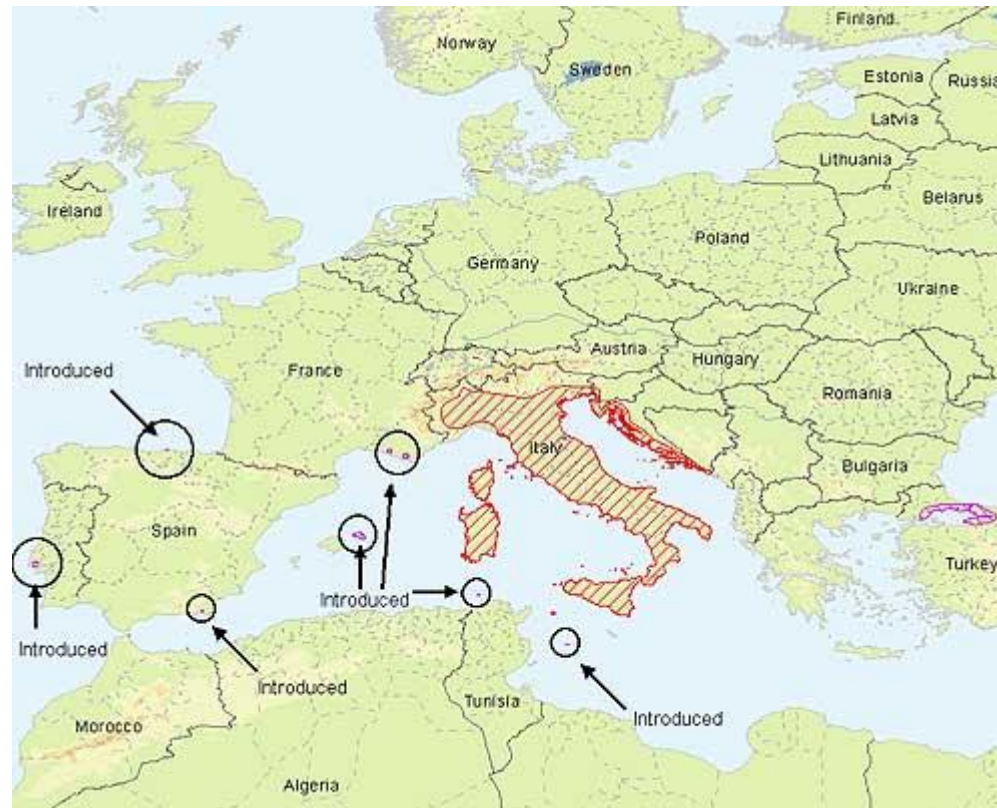
- The lack of recognition of snakes by *S. perspicillata* may be related with their habitat in Menorca



- *P. siculus* recognizes the scent of *Macroprotodon* as a predator and ignores the scent of *Rhinechis*: this reinforces the idea that *Rhinechis* does not predate on lizards



- The ability of *P. siculus* to recognize the predatory snake probably contributed to their colonozation of Menorca, while *P. lilfordi* went extinct





Muchas gracias

Ministerio de Ciencia e Innovación,  
proyecto CGL2012-39850-CO2-02



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