

Tiny but "strong": the European Leaf-toed gecko, *Euleptes europaea*, a terrestrial vertebrate able to survive on tiny islets

Michel Jean Delaugerre^a and Claudia Corti^{b,*}

^aConservatoire du littoral, Résidence St Marc, 2, rue Juge Falcone F-20200 Bastia, France ^bSistema Museale di Ateneo, Museo di Storia Naturale dell'Università di Firenze, Museo "La Specola", Via Romana 17, I-50125 Firenze, Italia

Abstract The present paper focuses on the ability of the European Leaf-toed gecko, *Euleptes europaea*, an endemic species of the western Mediterranean, to live in low-nutrient habitats. Its distribution is mainly insular and particularly noteworthy is its ability to live on islets and rocks. This work includes data originating from surveys carried out on 111 islands surrounding the island of Corsica (France) in search of herpetofauna. *E. europaea* is able to survive on the smallest islets, with low habitat complexity, suggesting a pre-adaptation of this species to island life. Moreover, high population densities associated with a low biomass seem to facilitate survival on island.

Keywords Corsica; Gekkota; islands; West Mediterranean; persistence; survival

Introduction

Since Alfred Russel Wallace and Charles Darwin, islands played an important role in the development of scientific thought. Islands and island-like habitats form systems among which species and environmental factors interact in different ways. Although each island system is unique, general mechanisms of colonization, dispersion and speciation can be observed. The theoretical structure of island biogeography (MacArthur & Wilson 1967) was the exciting starting point for further studies which, confirming or refuting the theory, improved the understanding of the mechanisms underlying the composition of insular communities. Most of the studies concern oceanic islands and archipelagos and, although island size and distance from a potential source of colonization are the most studied parameters, little attention has been paid to islands of very small size (Whitehead & Jones 1969; Schoener & Schoener 1982; Pérez-Mellado et al. 2008; Roca et al. 2009; Sillero et al. 2018; Itescu et al. 2020). In the recent decades, the accurate reconstructions of geological and paleo-climatic events shed light on how the past events have shaped the current distribution of living organisms. At temperate and tropical latitudes, reptiles are dominant in the insular sedentary faunas, as it happens in the Mediterranean, where Sauria represent the most widespread island vertebrates. Here they can experience very harsh ecological conditions, sea storms, sea sprays, and summer droughts, as well as limited and unpredictable trophic resources. Many islands inhabited by these reptiles are particularly small and low and exposed to strong surf. On some, not only is there little inhabitable surface but also little or no soil, allowing only

a few vascular plant species to grow. In the Mediterranean region, devoid of large rivers that flow through coastal forests, colonization events by rafting are very unlikely. Furthermore, Mediterranean reptiles, and in particular lizards, are believed to have poor over-water dispersal capacity. Human mediated introductions, well documented for large islands (Corti et al. 1999; Silva-Rocha et al. 2019), are rather questionable on land-bridge islets, since most of them have never been inhabited by man, or at most, little used. As happened for the eastern Mediterranean (Foufopoulos & Ives 1999), the diversity of the island herpetofaunas is closely related to the age of the islands and not to the marine dispersal occurred thanks to a certain distance from a putative source of colonization (e.g., mainland, nearby big island). Itescu et al. (2020) also minimize the importance of distance and report that species richness of land-bridge islets mainly depends on island area rather than island temporal isolation. The distribution pattern observed on the satellite islets of Corsica provides further support for this view. Except for the infrequent recent introduction events (Delaugerre et al. 2017), these islets are not inhabited by "newcomers" such as Tarentola mauritanica and Podarcis siculus that respectively colonised Corsica during the middle or late Neolithic, and in the Middle Ages (Bailon & Rage 2012). These species were not able to reach the islets via marine dispersal (Lanza & Poggesi 1986; Delaugerre & Cheylan 1992) suggesting that even narrow sea channels can represent a barrier for dispersal. Most islets may never have been "colonized" by reptiles, contrary to oceanic islands (Itescu et al. 2020). Their microinsular populations likely originate when the land-bridges between the

^{*}Corresponding author. E-mail: claudia.corti@unifi.it

mainland or main island disconnected during the interglacials (Senczuk et al. 2019). The initial set of species gradually impoverished over time due to island size variations resulting from the sea level fluctuations. The current herpetofaunas are therefore a legacy of paleo climatic history, subsequently driven by extinctions and progressive relaxation of predation and competition. The fauna of small islets might not be balanced in the absence of immigration; it might be gradually relaxing towards extinction at a rate inversely proportional to the size of island (Foufopoulos et al. 2011), as shown for boreal mammals by Brown (1978). Despite the above, are there species that can survive in such extreme conditions? What enables them to persist? To try to answer these questions, we have analysed a dataset relating to 111 islets around Corsica that have been carefully studied over the past 50 years, discussing the tiny European Leaf-toed gecko, Euleptes europaea, which is one of the most tenacious vertebrates living on the Mediterranean islands.

Material and methods

Study system

For the present study we selected the islands according to the following criteria defined by PIM - Initiative pour les Petites Iles de Méditerranée (Médail et al. 2019) presence of vascular plants, at least 2 m from the main island or the closest islet, and separated by a channel at least 50 cm deep (Supplementary Table S1, Fig. 1). A database including 118 Corsican islands was created with unpublished data collected by the authors in the recent decades and information from Lanza & Poggesi (1986) and Delaugerre & Cheylan (1992). Island area and distance from the coast of the nearest greater island were measured using Google Earth Pro. The maximum altitudes were obtained from the Service Hydrographique de la Marine, and the 1: 25 000 maps from the Institut Géographique National or, when missing, from the https://www.geoportail.gouv.fr. Most of the islands are smaller than 1 ha or even 0.1 ha (28%). Elevation of most of



Figure 1. Detailed map of the Lavezzi islands southern Corsica (from GoogleEarth 2020).



Figure 2. An "extreme" islet: "A Botte", north of Ajaccio: 3720 m², elevation = 22 m, mostly bare granite, no soil; plant cover not exceeding 8 m². During winter storms waves crush over the islet. Nevertheless, this islet hosts a relict population of \approx 70 *E. europaea* adults. The islet separated from the mainland some 10 000 years ago. © A. Gauthier.

the islands studied is less than 20 m (average 19.5 ± 17.7 m, median = 15 m). The distance from the closest islet or main island varies from 2 m to 7380 m (median 195 m). Most islands were disconnected from the main island by the post-Pleistocene sea levels rise. Their ages could range from ≈ 2000 to ≈ 15000 years (Lambeck & Bard 2000; Poher et al. 2017; Vacchi et al. 2018). Some younger islets also derive from coastal fragmentation or marine erosion. The most biotically impoverished islets (e.g., the A Botte Islet north of Ajaccio, area 3720 m², plant cover 8 m²; Fig. 2) are mostly bare rocks without soil, home to only a few species of vascular plants. On these islets, marine nutrients supplied by seabirds, such as excretions, regurgitated pellets and prey remnants enrich the terrestrial biota (Garcia et al. 2002; Pafilis et al. 2011; Duda et al. 2020) allowing a non-flying vertebrate the persist on such poor islets.

Study species

The European Leaf-toed gecko, *Euleptes europaea* (Gené, 1839), endemic to the Western Mediterranean, is the only extant species of the genus *Euleptes* (Bauer et al. 1997; Čerňanský et al. 2018). It is the smallest gecko in the western Mediterranean, female average snout-vent-length (SVL) = 40 mm, male average SVL = 37 mm. Adult average weight is 1.7 g in males and 2 g in females; hatchlings weight 0.25 g. Females are usually larger than males

(generally 10-15% larger) but size can vary. On the smaller and most remote islets, there is a general trend towards gigantism in both sexes. Only on very simplified islets, this trend is stronger in males resulting in a reduction or even disappearance of sexual size difference (Delaugerre & Cheylan 1992; Delaugerre et al. 2019). The species is strictly nocturnal and, depending on the climate, active for 8-10 months of the year (Sindaco et al. 2010b). Euleptes is mainly rupicolous and takes refuge in cracks of a few mm in width where the body touches the rock dorsally and ventrally. Roomy cracks, like those found in most granites and schists, can host dozens of individuals in less than one square meter. Special crevices are also used to lay eggs (one or two, once or twice a year depending on altitude and latitude), used by various females for generations (Salvidio et al. 2010). Compared to large islands or to the mainland, smaller islets show a trend towards higher population densities, an estimate obtained using CPUE (Capture per Unit Effort) (Delaugerre & Cheylan 1992). At night Euleptes forages on rocks, on the ground or vegetation. A dispersal distance of 50 linear meters is not unusual (MD, pers. obs.). In the presence of black rats, the gecko shifts its spatial behaviour and forages under plants. In populations living on rat-inhabited islands large geckoes are less numerous (Delaugerre et al. 2019).

The species is mainly found on islands and islets but also on the continental mainland (Fig. 3). In France



Figure 3. Distribution of Euleptes europaea from Delaugerre et al. (2011) modified.

Euleptes lives on the Maritime Alps up to 900 m; on landbridge islets along the coast from Marseilles to Cannes; in Corsica up to 1550 m and, on the Corsican satellite islands. In Italy it is found in Liguria, surroundings of Genoa and on the islands of Tino and Tinetto; in Tuscany, sporadically along its southern coast for about 100 km, on the fossil islands of Monte Calvi, Monte Massoncello, Punta Ala, Uccellina and Monte Argentario, as well as on the Tuscan Archipelago; in Sardinia, on the main island up to 1350 m and on most of its satellite islands. It also occurs off the coast of Tunisia on three islets of the Galite Archipelago (Salvidio et al. 2010). Its reduced presence on islands and a decline of Euleptes populations have been documented at the northern and southern edges of its range (Delaugerre et al. 2011). On the northern edge, a drastic demographic drop was noted for Pomègues and Ratonneau islands (Frioul Islands); a population discovered by Mourgue (1910) was later considered extinct (Mourgue, 1924), also searched in the late 70's but without success (Delaugerre 1981); in 1994 *Euleptes* was "re-discovered" on Pomègues by P. Bayle (unpublished in Salvidio & Delaugerre 2003).

The species still persists on some islands a few meters off the coast of Marseilles (depth below 1 meter) in the past connected to the mainland (< 2000 years ago). *E. europaea* likely became extinct on the coast since that time persisting only on the nearby islands. A marked demographic decline of *Euleptes* on the small steep islets of Grand and Petit Congloué (1910-2000), both without direct human impact, was subsequently reversed following rat eradication in 2000 (Salvidio & Delaugerre 2003). The species has become extinct on Bendor Islet, where remaining natural habitats are rare as human impact is very strong. At the southern edge of its range, *Euleptes europaea* was the only gecko found on the Northern Tunisian islets of Galitone and Aguglia (= La Fauchelle) in the Galite Archipelago, and on the Grand Cani Islet by D'Albertis (1878). The species is now considered extinct on both Galitone and Cani which, in the meantime, have been colonized by *Hemidactylus turcicus* (Delaugerre, Ouni and Nouira, 2011). However, both species coexist on the Toro Islet (S-Sardinia) located at the distribution centre of *Euleptes europaea*.

Statistical analysis

To account for islet complexity we calculated for each island the "biotic capacity Index" (D) by including island area (S) and max altitude (a) in the equation: $D = \log(S^*a)$ (Delaugerre & Dubois 1985; Pérez-Mellado et al. 2008 and references therein). This corrective is particularly powerful and meaningful when dealing with very small islets (e.g., an islet of 1000 m^2 , 3 m high and exposed to strong surf will not support the same number of habitats and species compared to a similar sized island 20 m high). The Student t test was used to compare the geographical features of the islets with and without herpetofauna. The Mann-Whitney U test was used to compare between pairs of species, the D index values of the islets occupied, to verify whether a species is able to persist on smaller and less complex islets better than others. The Capture per Unit Effort (CPUE) was calculated in 21 populations using the ratio between the number of active geckos captured at night by the time devoted to searching (see details in Delaugerre et al. 2019). A linear regression was performed to assess the relationship between the islets complexity (D) and the population densities (CPUE) in 21 populations. The population size has been evaluated on 9 islets by CMR (Capture-Mark-Recapture).

Results

Out of the 118 islands surrounding Corsica, 111 have been visited in search for herpetofauna. The presence of at least one species was recorded on 89 islands. The islands devoid of herpetofauna are smaller and significantly lower and less complex than the islands with herpetofauna (Supplementary Tables S2 and S3). Eleven species live in Corsica, seven of which also occur on its satellite islands: three geckoes, three lacertids and one colubrid snake (Table 1). *E. europaea* is found on eighty-one islands; *Podarcis tiliguerta* on fifty-one; the snake *Hierophis viridiflavus* and the gecko *Tarentola mauritanica* on eight and five islets respectively

Table 1. Distribution of Reptiles and D index of "biotic capacity" on the circum-Corsican islands. N = number of islets where a species is present, average, standard deviation, minimum and maximum of D index.

Species	Ν	$\overline{\mathbf{X}}$	σ	min	max
Euleptes europaea	81	4.99	0.95	2.96	7.59
Podarcis tiliguerta	51	5.31	1.00	3.22	7.59
Hierophis viridiflavus	8	6.92	5.34	5.34	7.59
Tarentola mauritanica	5	6.54	0.83	5.41	7.59
Archaeolacerta bedriagae	3	5.08	0.78	4.18	5.61
Algyroides fitzingeri	1	7.43	/	/	/
Hemidactylus turcicus	1	3.99	/	/	/

Table 2. Results of the Mann–Whitney U test on the biotic capacity of islands with herpetofauna (see Table 1). Z score; * = Level of confidence for directional hypothesis > 95%. Tested only for species occurring on more than 4 islets.

	E. europaea	P. tiliguerta	H. viridiflavus	T. mauritanica
E. europaea	/	/	/	/
P. tiliguerta	1.951*	/	/	/
H. viridiflavus	3.902*	3.410*	/	/
T. mauritanica	2.944*	2.471*	0.587	/

(Table 1). *E. europaea* can live on much smaller and lower islets than the other three species. The other species capable of living in relatively extreme habitats is *Podarcis tiliguerta* which is also present on small islets (Table 2). *Euleptes* is the only terrestrial vertebrate able to survive in the most extreme habitats; in fact, compared to *P. tiliguerta* which is found only on 14% of the islands with a single species, *Euleptes europaea* occurs on 84% of these islands (Table 3).

There is no significant relationship between population density assessed by CPUE and the size and complexity of the islet assessed with the D index (Linear regression n = 21, DF 1.19, $R^2 = 0.039$), nor with the area ($R^2 = 0.031$) or elevation ($R^2 = 0.039$). The population size of *E. europaea* was assessed on 9 islets covering less than 1 ha (Table 4). We estimated that the total population size and biomass of geckos on these islands vary between 65 to 450 individuals, with a low total biomass (114-788 g).

Discussion

The composition of the microinsular herpetofauna is most likely the combined result of 1) ecological constraints, and 2) the Pleistocene relict coastal fauna. If the lack or

Table 3. Herpetological richness and species occurrence on the Corsican islets. The presence of *E. europaea* has probably been underestimated, particularly on 3 out of the 6 islets with a single species where *P. tiliguerta* lives.

species richness	No. of islets with herps	P. europaeus	P. tiliguerta	H. viridiflavus	T. mauritanica	H. turcicus	A. bedriagae	A. fitzingeri
1 sp	43	36	6	/	/	1	/	/
2 sp	34	33	33		1 /		1	/
3 sp	9	9	9	5	2 /		2	/
4 sp	3	3	3	3	2 /		/	1

Table 4. Population size assessed by CMR, related biomass and extrapolated population density of several Corsican microinsular populations of *Euleptes europaea*, from Delaugerre & Cheylan (1992), CEN Corse, pers. comm. and M. Delaugerre, unpubl. data. All the islets are devoid of rats; *Podarcis tiliguerta* lives in the three islets marked with an asterisk; on the remaining islets *E. europaea* is the only non-flying vertebrate.

Islet	Surface (ha)	Population size	Biomass (g)	Biomass (kg/ha)	Population density (ind/ha)
Roscana	0.169	250	438	2.6	1479
Vacca*	0.490	300	525	1.1	612
Porragia				2.4	
piccola*	0.220	300	525		1364
Porragia				0.9	
grande*	0.845	450	788		533
Sperduto				1.0	
grande	0.558	320	560		573
A Botte	0.372	70	123	0.4	188
Palazzu	0.470	75	131	0.3	160
Palazzinu	0.110	65	114	1.0	591
Porri	0.215	165	289	1.3	767

scarcity of fresh water explains the absence of Emys orbicularis and Natrix corsa, the absence of Testudo hermanni almost certainly derives from the lack of inadequate trophic resources. On the other hand, the absence of Podarcis siculus, and the rarity of Hemidactylus turcicus and Tarentola mauritanica are likely explained by their recent colonization of Corsica (Bailon & Rage 2012) and by their inability to cross sea channel to colonize the satellite islands. Algyroides fitzingeri, one of the three Corso-Sardinian palaeoendemic lizards, requires more environmental complexity (e.g., a certain degree of humidity) (Sindaco et al. 2010a), this species is only found on the relatively large Gargalu Island (21 ha; 127 m). On the other hand, the persistence of the other palaeoendemic lizard, Archaeolacerta bedriagae on only three islets of southern Corsica could suggest that from the Pleistocene onwards, most of the coastal distribution of this species has been lost. The latter two lacertids also occur on some of the larger circum-Sardinian islands (Poggesi et al. 1996). E. europaea and P. tiliguerta, which are found respectively on 91% and 63% of the satellite islands of Corsica hosting herpetofauna, dominate over all other species.

The European Leaf toed gecko is able to survive on very small islets characterized by very limited trophic availability. What enables this gecko to live in such extreme conditions? The small biomass combined with the ability to survive in very small populations could be the key to its success. Furthermore, its presence probably has a minimal impact on the islands. Few hundred grams of total biomass (Table 4) seem to be sufficient to allow the persistence of a small viable population. Relictual populations, spatially and genetically isolated for thousands of generations, sometimes count only a few dozen individuals. Euleptes populations may have passed through bottlenecks but seem to well resist inbreeding depression and, despite limited resources, population densities, although variable, are quite high (Table 4) compared to the average value of 158 ind/ha reported by Novosolov et al. (2015) but

see also Buckley & Jetz (2007). Furthermore, the propensity for gregariousness and the absence of dominance of one sex over the other (Salvidio et al. 2010) suggests the absence or negligible aggressive sexual interactions. The geckos' shelters, in narrow and deep crevices, may protect from unfavourable meteorological conditions and potential diurnal predators.

No noticeable changes of the reproductive traits, such as clutch size, egg size, clutch frequency (characters likely genetically fixed), were observed for the studied populations, but a clear reduction of mortality, particularly marked in the first 2 years of life, in almost all the populations (M. Delaugerre, unpubl.).

Body size varies greatly on islands (Delaugerre et al. 2019 and references therein). On the smaller islands, a tendency towards larger geckos is observed in both sexes, only on the less complex islets, this tendency is stronger in males, with a consequent reduction or even disappearance of size sexual dimorphism (usually females are 15-20% larger in SVL than males).

The above could be the result of 1) increased longevity, 2) adaptation to limited trophic resources. Larger individuals can access a wider range of prey. In the most impoverished biota, intraspecific competition for trophic resources would select for larger males thus reducing sexual size dimorphism.

In the presence of the Black rat, geckos shift their spatial behaviour, foraging hidden under the vegetation while "outdoors" on rat free islands (Delaugerre et al. 2019).

Simplified systems, such as small islands, allow to observe interactions between unrelated phylogenetically organisms that can be considered equivalent in the trophic network. During our nocturnal investigations we have observed species such as *Mantis* sp., spiders as *Lycosa* sp., scorpions, *Euscorpius* sp. and even saltwater crabs, which could be considered possible predators of the European Leaf toed gecko, on the other hand *E. europaea* was observed foraging on supralittoral rocks, presumably in search of the marine Isopod *Lygia italica*.

Conclusions

To conclude *Euleptes europaea* shows very few peculiar adaptations to island life except for size on the tiny islets see Salvidio et al. (2010) and Delaugerre et al. (2019). This gecko would seem pre-adapted to island life, thanks to the trait that promotes high population densities and protective shelters that facilitate the survival process on islands (Novosolov et al. 2015). Many populations of *E. europaea* live on "extreme" islets, at the limit of terrestrial life, where other terrestrial vertebrates cannot survive. Despite the small populations which have been isolated for hundreds or thousands of generations, it appears that this gecko has overcome inbreeding depression and other stochastic events.

The disappearance of this species would be a great loss for the Mediterranean fauna. The current climatic trend appears to be particularly unfavourable for the survival of island populations. The prolonged summer drought could pose a particular threat to populations that already live in environments on the edge of survival. Moreover, the expected sea level rise will make many of the low-lying islands disappear in a relative near future (Oppenheimer 2019). The maximum degree of protection must therefore be guaranteed for this endemic species, since habitat destruction, the introduction of alien species and any poorly considered conservation action could lead to the disappearance of some populations. Island populations are important not only because they can be considered evolutionary units but also because they are of great help in unveiling the strategies that allow an organism to survive in extreme contexts.

Acknowledgements

We would like to thank the Réserves naturelles des Bouches de Bonifacio, de Scandola and des Iles du Cap Corse and Marta Biaggini, Pietro Lo Cascio, Nicolas Nègre-Santucci and Olivier Bonnenfant for having assisted us during fieldwork; Christophe Mori (University of Corsica) for the assistance during the statistical analysis. Permits for handling protected species have been issued by *Arrêtés Préfectoraux (Haute-Corse and Corse du Sud)*.

Supplementary material

Supplementary material is available online at: https://doi.org/10.6084/m9.figshare.12593468

References

- Bailon S, Rage JC. 2012. Données fossiles et mise en place de l'herpétofaune actuelle de la France: In: Atlas des Amphibiens et Reptiles de France. Biotope MNHN. Chirat France; pp 33–39.
- Bauer AM, Good DA, Branch WR. 1997. The taxonomy of the southern African leaf-toed geckos (Squamata: Gekkonidae), with a review of old world. Proceedings of the California Academy of Sciences. 49(14):447–497.
- Brown JH. 1978. The theory of insular biogeography and the distribution of boreal birds and mammals. Great Basin Naturalist Memoirs. (2):20.
- Buckley LB, Jetz W. 2007. Insularity and the determinants of lizard population density. Ecology Letters. 10(6):481–489.
- Čerňanský A, Daza JD, Bauer AM. 2018. Geckos from the middle Miocene of Devínska Nová Ves (Slovakia): new material and a review of the previous record. Swiss Journal of Geosciences. 111(1–2):183–190.
- Corti C, Masseti M, Delfino M, Pérez-Mellado V. 1999. Man and herpetofauna of the Mediterranean islands. Rev Esp Herp. 13:83–100.
- D'Albertis E. 1878. Parte narrativa. Crociera del Violante comandato dal Capitano-Armatore Enrico d'Albertis durante l'anno 1876. Ann Mus Storia Nat Genova. 11:11–324.
- Delaugerre M. 1981. Le point sur la répartition géographique de *Phyllodactylus europaeus* Gené. Bull Soc Herpet Fr. 18:14–16.
- Delaugerre M, Cheylan M. 1992. Atlas de répartition des batraciens et reptiles de Corse. Ajaccio Parc naturel régional de Corse: Ecole pratique des hautes études.
- Delaugerre M, Dubois A. 1985. La variation géographique et la variabilité intrapopulationnelle chez *Phyllodactylus europaeus* (Reptilia, Sauria, Gekkonidae). Bulletin du Muséum national d'histoire naturelle Section A, Zoologie, biologie et écologie animales. 7(3):709–736.

- Delaugerre M-J, Ouni R, Nouira S. 2011. Is the European Leaftoed gecko *Euleptes europaea* also an African? Its occurrence on the Western Mediterranean landbrige islets and its extinction rate. Herpetology Notes. 4:127–137.
- Delaugerre M-J, Sacchi R, Biaggini M, Cascio PL, Ouni R. 2019. Coping with aliens: how a native gecko manages to persist on Mediterranean islands despite the Black rat? Acta Herpetologica. 14(2):89–100.
- Delaugerre M-J, Thibault JC, Beuneux G. 2017. Le renouvellement récent des faunes de vertébrés sur l'île de Cavallo (archipel des Lavezzi, Corse). Ecologia Mediterranea. 43(2): 207–217.
- Duda MP, Glew JR, Michelutti N, Robertson GJ, Montevecchi WA, Kissinger JA, Eickmeyer DC, Blais JM, Smol JP. 2020. Long-Term Changes in Terrestrial Vegetation Linked to Shifts in a Colonial Seabird Population. Ecosystems [Internet]. [accessed 2020 Feb 25]. http://link.springer.com/10.1007/ s10021-020-00494-8.
- Foufopoulos J, Ives AR. 1999. Reptile extinctions on land-bridge islands: life-history attributes and vulnerability to extinction. The American Naturalist. 153(1):1–25.
- Foufopoulos J, Kilpatrick AM, Ives AR. 2011. Climate Change and Elevated Extinction Rates of Reptiles from Mediterranean Islands. The American Naturalist. 177(1):119–129.
- Garcia LV, Maranon T, Ojeda F, Clemente L, Redondo R. 2002. Seagull influence on soil properties, chenopod shrub distribution, and leaf nutrient status in semi-arid Mediterranean islands. Oikos. 98(1):75–86.
- Itescu Y, Foufopoulos J, Pafilis P, Meiri S. 2020. The diverse nature of island isolation and its effect on land bridge insular faunas.Borregaard MK, editor. Global Ecology and Biogeography. 29(2):262–280.
- Lambeck K, Bard E. 2000. Sea-level change along the French Mediterranean coast for the past 30 000 years. Earth and Planetary Science Letters. 175(3):203–222.
- Lanza B, Poggesi M. 1986. Storia naturale delle isole satelliti della Corsica. L'Universo. 66(1):198.
- MacArthur RH, Wilson EO. 1967. The theory of island biogeography. Princeton, NJ: Princeton University Press.
- Médail F, Petit Y, Paradis G, Hugot. 2019. Flore et végétation vasculaires des petites îles et îlots du littoral de Galeria à Porto (Réserve naturelle de Scandula et environs, Corse occidentale). J Bot Soc Bot France. 88:13–118.
- Mourgue M. 1910. Habitats nouveaux de *Phyllodactylus europaeus* et de *Spelerpes fuscus*. Feuil J Nat. 5(41):482.
- Mourgue M. 1924. Note succinte sur les espèces de *Lacerta muralis* des îles du Golfe de Marseille. Bulletin de la Société Linnéenne de Lyon. 3:55.
- Novosolov M, Rodda GH, Feldman A, Kadison AE, Dor R, Meiri S. 2015. Power in numbers. Drivers of high population density in insular lizards. Global Ecology and Biogeography.
- Oppenheimer M, Glavovic BC, Hinkel J, van de Wal R, Magnan AK, Abd-Elgawad A, Cai R, Cifuentes-Jara M, DeConto RM, Ghosh T, Hay J, Isla F, Marzeion B, Meyssignac B, Sebesvari Z. 2019. Sea Level Rise and Implications for Low-Lying Islands, Coasts and Communities. In: IPCC Special Report on the Ocean and Cryosphere in a Changing Climate [H.-O. Pörtner, D.C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama, N.M. Weyer (eds.)].
- Pafilis P, Foufopoulos J, Sagonas K, Runemark A, Svensson E, Valakos ED. 2011. Reproductive Biology of Insular Reptiles: Marine Subsidies Modulate Expression of the "Island Syndrome." Copeia. 2011(4):545–552.
- Pérez-Mellado V, Hernández-Estévez JÁ, García-Díez T, Terrassa B, Ramón MM, Castro J, Picornell A, Martín-Vallejo J, Brown R. 2008. Population density in *Podarcis lilfordi* (Squamata, Lacertidae), a lizard species endemic to small islets in the Balearic Islands (Spain). Amphibia-Reptilia. 29(1):49–60.
- Poggesi M, Agnelli P, Borri M, Corti C, Finotello PL, Lanza B, Tosini G. 1996. Erpetologia delle isole circumsarde. Biogeographia (ns). 18:583–618.

- Poher Y, Ponel P, Médail F, Andrieu-Ponel V, Guiter F. 2017. Holocene environmental history of a small Mediterranean island in response to sea-level changes, climate and human impact. Palaeogeography, Palaeoclimatology, Palaeoecology. 465:247–263.
- Roca V, Foufopoulos J, Valakos E, Pafilis P. 2009. Parasitic infracommunities of the Aegean wall lizard Podarcis erhardii (Lacertidae, Sauria): isolation and impoverishment in small island populations. Amphibia-Reptilia. 30(4):493–503.
- Salvidio S, Delaugerre M. 2003. Population dynamics of the European leaf-toed gecko (*Euleptes europaea*) in NW Italy: implications for conservation. Herpetological journal. 13(2):81–88.
- Salvidio S, Lanza B, Delaugerre MJ. 2010. Euleptes europaea (Gené, 1839). In: Fauna d'Italia. Vol. 45. C. Corti, M. Capula, L. Luiselli, Razzetti, R. Sindaco. Milano: Edizioni Calderini de Il Sole 24 ORE; p. 869.
- Schoener TW, Schoener A. 1982. The ecological correlates of survival in some Bahamian *Anolis* lizards. Oikos.:1–16.
- Senczuk G, Castiglia R, Colangelo P, Delaugerre M, Corti C. 2019. The role of island physiography in maintaining genetic diversity in the endemic Tyrrhenian wall lizard (*Podarcis tiliguerta*). J Zool. 309(2):140–151.

- Sillero N, Biaggini M, Corti C. 2018. Analysing the importance of stepping-stone islands in maintaining structural connectivity and endemicity. Biological Journal of the Linnean Society. 124(1):113–125.
- Silva-Rocha IR, Salvi D, Carretero MA, Ficetola GF. 2019. Alien reptiles on Mediterranean Islands: A model for invasion biogeography. Cowie R, editor. Diversity and Distributions. 25(6):995–1005.
- Sindaco R, Corti C, Delaugerre MJ. 2010a. Algyroides fitzingeri (Wiegmann, 1834). In: Fauna d'Italia. Vol. 45. C. Corti, M. Capula, L. Luiselli, Razzetti, R. Sindaco. Milano: Edizioni Calderini de Il Sole 24 ORE.
- Sindaco R, Paggetti E, Corti C. 2010b. Genere *Euleptes* Fitzinger, 1843. In: Fauna d'Italia Reptilia. Bologna: Edizioni Calderini de Il Sole 24 Ore Editoria Specializzata S.r.l; p. 257.
- Vacchi M, Ghilardi M, Melis RT, Spada G, Giaime M, Marriner N, Lorscheid T, Morhange C, Burjachs F, Rovere A. 2018. New relative sea-level insights into the isostatic history of the Western Mediterranean. Quaternary Science Reviews. 201:396–408.
- Whitehead DR, Jones CE. 1969. Small islands and the equilibrium theory of insular biogeography. Evolution. 23(1):171–179.