

Coping with aliens: how a native gecko manages to persist on Mediterranean islands despite the Black rat?

MICHEL-JEAN DELAUGERRE^{1,*}, ROBERTO SACCHI², MARTA BIAGGINI³, PIETRO LO CASCIO⁴, RIDHA OUNI⁵, CLAUDIA CORTI³

¹ Conservatoire du littoral, Résidence St Marc, 2, rue Juge Falcone F-20200 Bastia, France. *Corresponding author. Email: m.delaugerre@conservatoire-du-littoral.fr

² Dipartimento di Scienze della Terra e dell'Ambiente, Università degli Studi di Pavia, via Taramelli 24, I-27100, Pavia, Italia

³ Sistema Museale di Ateneo - Museo di Storia Naturale dell'Università di Firenze, Sede "La Specola", Via Romana 17, I-50125 Firenze, Italia

⁴ Associazione Nesos, via Vittorio Emanuele 24, I-98055 Lipari (ME), Italia

⁵ Tunisia Wildlife Conservation Society, Faculté des Sciences de Tunis, Université Tunis El Manar II Tu-2092, Tunisia

Submitted on: 2019, 14th April; revised on: 2019, 16th June; accepted on: 2019, 24th June
Editor: Uwe Fritz

Abstract. How a native gecko manages to coexist with an alien rodent in the Mediterranean since thousands of years? What kind of eco-ethological adaptations or evolutionary adjustments enables this gecko to persist? The present study explores the interaction between the endemic European Leaf-toed gecko (*Euleptes europaea*) and the alien Black rat (*Rattus rattus*). In the last 30 years, we compared 26 populations inhabiting "rat" and "rat-free" islands and islets in Tunisia, Sardinia, Corsica and Southern France. Geckos' populations can persist despite the occurrence of rats. In the presence of rats: 1) geckos' average body size tends to decrease towards medium-sized individuals; 2) geckos shift their spatial behaviour avoiding to forage "in the open"; 3) geckos' body condition is not affected by the presence of rats. Moreover, shortly after rats' eradication, geckos' population structure seems to change and larger sized geckos prevail while the spatial behaviour is much more conservative. The mechanisms driving the interactions between the two species still need to be explained. Rats could represent a stressor for geckos, compete for space, be pest vectors and even predators. Coexistence of natives and aliens requires adaptive plasticity and evolutionary adjustments. In contexts where the risk of reinvasion is high, eradication programs need to be carefully evaluated, since the arrival of "new rats" on an island could have much more damaging effects on the insular biota than those caused by the eradicated population.

Keywords. Behavioural shift, disturbance, ecological plasticity, evolutionary processes, predation, rat eradication, *Euleptes europea*, *Rattus rattus*.

In memory of Michel Pascal (1947-2013)

INTRODUCTION

The long term dynamics of insular biota reflect the interplay between recurrent immigration and extinction events (Brown and Lomolino, 2000). Mainly because of human expansion on global scale, the natural phenomenon of sea dispersal has been greatly amplified favouring introductions and even biological invasions (Simberloff

et al., 2013). In the last centuries, with a speeding up in the last decades human-induced dispersal of species has implied: a) huge acceleration of the introductions' rate; b) great number of species involved; c) remote origins of some propagules; d) possible genetic modifications originated from captive breeding and farming activities. Insularity-associated features, such as high sensitivity to climate and sea level changes, high rate of speciation, immigration and extinction processes, naiveté of native species, make insular biota particularly fragile (Moser et al., 2018).

Over the last decades, conservation biology has emphasized the detrimental effects of introduced species (mostly mammals) on insular ecosystems, but little attention has been paid to the understanding of the eco-ethological adaptations that enable a native species to persist despite the presence of aliens (Martin et al., 2000; Hoare et al., 2007; Ruffino et al., 2009). In systems with novel combination of species (native and introduced ones) that do not show co-adaptation, rapid evolutionary changes may occur (Berthon, 2015; Mooney and Cleland, 2001; Strauss et al., 2006; Sax et al., 2007; Stuart et al., 2014). On islands, in particular, morphological, ecological and behavioural shift are more easily detectable than in more complex systems (Simberloff, 1974).

Within the Mediterranean, reptiles, notably lizards, are good tools to investigate insular evolution. These herpetological communities, which are currently found on continental islands and on many land-bridge islets, origin from the neighbouring continents or large islands before their isolation, dating back to the sea level raise of the last interglacials. Trans-marine dispersal is less frequent in the Mediterranean arid islands (Foufopoulos and Ives, 1999).

Most of the endemic herpetofauna still remains on some big islands (e.g., Corsica, Sardinia) and relative satellite islands, while on other major Mediterranean islands the endemic herpetofauna has been completely replaced by human-introduced species, and endemic species persist only on some of their satellite islands (Corti et al., 1999; Silva-Rocha et al., 2018, 2019).

In the present work we investigated the interaction between the native European Leaf-toed gecko *Euleptes europaea* (Gené, 1839) and the alien Black rat, *Rattus rattus* (Linnaeus, 1758) on some small islands of the Western Mediterranean. The European Leaf-toed gecko, a Western Mediterranean endemic species listed in Appendix II of the European Habitat Directive, is a very old inhabitant of this region, presumably since several million years ago (Müller, 2001). This species underwent a process of historic extinction or steep demographic decline along the North-Western (Provence, France) and Southern (Tunisia) edges of its range (Delaunay et al., 2011). The Black rat colonized the Western Mediterranean approximately 2000-2400 years ago (Thibault et al., 1987; Vigne and Valadas, 1996; Ruffino and Vidal, 2010). Thus, the coexistence between the two species might last since hundreds of geckos' generations and thousands of rats' generations, since *Euleptes* lives longer than rats (Salvidio et al., 2010 and ref. therein). According to Ruffino et al. (2009), in the Western Mediterranean, 74% of the islands between 1 and 5 ha (and 99% of islands larger than 30 ha) are colonized by Black rats. Among the human introduced spe-

cies, rats can dramatically impact on island biodiversity (Recher and Clark, 1974; Atkinson, 1985; Courchamp et al., 2003; Bennett et al., 2005) and Black rats in particular, have caused rapid extinctions on islands, as reported for New Zealand and the Hawaiian Archipelago (Townes et al., 2006; Drake and Hunt, 2009). Alien rats can predate and compete with native species and modify islands' food chains (Traveset and Richardson, 2006). The worldwide success of the Black rat as colonizer is due to its ability to exploit a large range of habitats and resources (Jones et al., 2008), as well as to shift to seasonal resources (Caut et al., 2008). This plasticity is crucial to survive in poor insular ecosystems, characterized by strong resource variation.

On small islets *E. europaea* and *R. rattus* are often the only sedentary vertebrates. They are both nocturnal, good climbers on rocky substrates, and they both forage on rocky outcrops and on low vegetation.

Rat eradication programs are often focused on one or few emblematic species (Capizzi et al., 2010), without a comprehensive understanding of insular assemblages. Investigating the possible interactions between the European Leaf-toed gecko and the Black rat the present work could provide useful data for long-term insular conservation plans.

In particular, we explored the effects of the Black rat on the Leaf-toad gecko population structure (analysed on the basis of the relative proportion of size classes), body condition and habitat use, comparing populations living on islands colonized by rats and islands free of rats. Because we expect rats to interfere with geckos' habitat use, feeding habits and thermoregulation, geckos living on islands on which also rats live should show: 1) population structure with smaller-sized individuals resulting from a shorter lifespan; 2) poor body conditions; 3) modification of spatial behaviour by minimizing or even avoiding foraging in open spaces.

MATERIAL AND METHODS

Ecological or evolutionary responses of native species to aliens cannot be easily distinguished from the pre-existing ecological differences (Strauss et al., 2006). However, even if each micro insular population differs from the others (e.g., due to age of isolation, presence of competitors and/or predators, etc.), any detectable trend can provide strong correlative evidences.

Study species

Euleptes europaea is a small gecko (average snout-vent length, hereafter SVL, 38 mm; average adult weight 1.2 g; hatching weight 0.25 g) endemic to the Western Mediterranean, mostly found on islands in rocky habitats. It is strictly noctur-

nal, spending daytime in narrow rocky crevices (opening 2–4 mm wide) where dorsal and ventral parts of the body are in contact with the rock. These crevices are also used for egg laying (Salvidio et al., 2010). Achieving its sexual maturity at the age of 3 years (Salvidio and Delaunay, 2003), it might live 6 to 8 years in the wild and its maximum longevity in captivity attains 21 years (F. Molle in Mertens, 1970).

It feeds on flying and ground dwelling invertebrates. On islets, densities are higher than on the mainland and population size ranges from several hundreds to only few dozen adults. This gecko is able to live on tiny islets (hundreds of square meters) characterized by the presence of few vascular plants, where it represents the only sedentary vertebrate (Delaunay and Cheylan, 1992). Body size greatly varies on islets with trends towards gigantism, dwarfism and variation of the sexual size difference (Delaunay and Cheylan, 1992; Salvidio et al., 2010).

Rattus rattus (average weight 170 g), is a good climber, both on rocks and trees, but not a long lasting swimmer and therefore considered with poor marine dispersal capacities (≤ 500 m) (Cheylan, 1988; Ruffino et al., 2009). In the Mediterranean, rats feed mainly on plants, avoiding or rarely eating halophilous and nitrophilous ones (Cheylan, 1988; Cassaing et al., 2007). Black rats and *Euleptes europaea* are both nocturnal and share the same habitat.

Study sites and data collection

We focused on islands characterized by simple ecosystems, where strong interactions between the target species are more likely to occur, namely small islands characterised by seasonal shortage of food availability for rats, and higher probability of encounters between the two species. We selected 26 islands and islets (Table 1) throughout most of the Leaf-toed gecko range (Fig. 1). Islands were classified as “rat” vs “rat-free”, depending on the presence or absence of rats; islands where rats were eradicated were considered as “rat-free”. The presence of rats was detected thanks to at least one of the following evidences: direct sightings, fresh and/or old faeces, remains of chewed olive seeds or plants, rats’ nests, rats’ urine scent. Past presence/absence of rats on islands was investigated through literature and observations made by locals. Nine islands (the largest ones) were inhabited by rats probably since their early colonization (Abdelkrim et al., 2009), whereas 13 islands (the smallest and most remote ones, without edible plants) were presumably never inhabited by rats. On Lavezzi Island (Corsica) we collected data before and after rat eradication (performed in 2000): the island was considered as “rat” before the eradication and as “rat-free” after eradication (Table 1). Five islands with “transient” rat populations (i.e., small islets close to a colonization source but lacking resources to support a permanent rat population) were treated as “rat”, because rat frequency on these islands is unknown.

Sampling methods

Observations were carried out in spring, summer and autumn from July 1983 until August 2016. Sampling sessions (n

= 47) consisted of 1 up to 6 nights per island (Table 1). Active geckos were searched using battery-powered lamps starting one or two hours after dusk and lasted until dawn. Total sampling effort achieved more than 380 hours (Table 1). Geckos behaviour was classified as follow: “in the open” when found on bare rocks, on the ground or on plants; “under cover” when found hidden by the vegetation at the base of rocks (Fig. 2). Distance from the ground (height of the first sight) was also measured. Geckos were carefully caught by hand and temporarily stored in bags; sex and adulthood was determined according to Delaunay and Dubois (1985). Snout-vent length (SVL) of 1795 individuals was measured to the nearest 0.01 mm using a digital calliper, weight (W) of 424 adults was recorded to the nearest 0.01g using a digital scale. Geckos were released in the area of original sighting. Body condition index (BCI) was calculated as from Bonnet and Naulleau (1994). Spatial behaviour of 1012 geckos (i.e., “in the open” or “under cover”), recorded for 24 sampling sessions carried out on 17 islets, was assessed for one hour “catch per-unit-effort” (CPUE).

Statistical analyses

Population structure. In order to assess whether the populations structure of *E. europaea* was affected by the presence of rats, we compared gecko’s size between islands with and without rats. Since Leaf-toed geckos’ size varies among islands independently of rats, we firstly normalized body sizes by dividing each measure by the greatest observed value in order to have all values in the 0–1 range (Legendre and Legendre, 2012). Each individual was classified depending on its inclusion in the quartile of the distribution of the normalized body size as “small” (1st and 2nd quartiles), “medium” (3rd quartile), and “large” (4th quartile). Geckos’ population structure was assessed by computing the proportion of individuals per size class. Different population structures were computed for spring and autumn. Sample size included 1871 individuals from 24 islets (Mean values $\pm$ SE: 78 ± 16); islands with less than 10 individuals measured (San Bainzu, Piana and Porro) were excluded. Data were analysed using permutational multivariate analysis of variance, PERMANOVA (Anderson, 2001; McArdle and Anderson, 2001) on the basis of Euclidean distances among islands’ population structures. The PERMANOVA allows the multivariate information to be partitioned according to the full experimental design without any *a priori* assumption regarding the distributions of the original variables. The predictors were rat occurrence (yes/no), season (spring/autumn), number of reptile species, number of sampling sessions (to account for repeated measures within an island), and island size. P-values were obtained by permutation, and the number of permutations was set to 9999.

Body condition. The effect of rat occurrence on the body condition of geckos was assessed using a linear mixed model in which the BCI was the dependent variable; rat occurrence, sex, and season were the fixed effects, whereas the island was the random factor accounting for repeated measuring.

Spatial behaviour. Linear mixed models were also used to investigate the effect of rat occurrence on the habitat use by geckos. In a first analysis we checked if Leaf-toed geckos avoided

Table 1. Map identification numbers (see Figure 1) of the study islands, geographical region, surface, presence (“rat”) or absence (“rat-free”) of the Black rat, and number of reptile species. For each island we also indicate sampling dates (and number of sampling nights), sampling effort (in minutes), number of geckos measured (n Biometry), number of geckos for which activity data were recorded (n Activity).

n°	Islet/island	Region	Surface (ha)	Rat status	N sp reptiles	Year (month): n nights	Sampling effort (min)	n Biometry	n Activity
1	Gallo	N_Tunisia	8.9	rat	2	2008 (05):3	1320	49	/
				rat		2010 (07):1	270	/	30
2	Toro	Sardinia	13.22	rat free	3	2015 (06):1	195	34	45
3	Carpa	Sardinia	0.4	rat	2	2011 (09):1	430	50	67
4	Porco	Sardinia	4.8	rat	4	2012 (05):1	285	44	55
5	Spargiotto	Sardinia	11.13	rat free	3	2014 (05):1	360	66	79
6*	Lavezzi	Corsica	62.73	rat	3	1986 (08):1	390	50	/
				rat free		2010 (06):3	550	40	41
				rat free		2011 (06):3	427	67	41
				rat free		2012 (06):2	720	66	/
7	Porraccia Grande	Corsica	1.25	rat free	2	1985 (08):1	600	50	/
8	Porraccia piccola	Corsica	0.61	rat free	2	1986 (08):1	410	59	/
9	Sperduto grande	Corsica	0.92	rat free	1	1984 (10):2	785	40	/
				rat free		1986 (08):1	330	81	/
				rat free		2011 (06):1	435	43	43
10	Toro grande	Corsica	1.62	rat free	2	1986 (08):1	360	59	/
				rat free		2005 (04):1	200	50	/
				rat free		2012 (07):1	140	/	52
				rat free		2014 (07):1	250	48	59
11	1st islet NE of Toro piccolo	Corsica	0.11	rat free	1	1986 (08):1	240	15	/
12*	Vacca	Corsica	0.65	rat free	2	1985 (08):3	1395	95	/
				rat free		2012 (07):1	165	8	15
13	Roscana	Corsica	0.2	rat free	1	1986 (08):1	720	94	/
				rat free		2008 (10):3	2258	125	/
				rat free		2012 (09):2	824	122	/
14	Locca	Corsica	0.79	rat	2	2010 (04):1	90	/	10
15	Mezzumare	Corsica	35.66	rat	3	2012 (08):1	213	15	18
16	A Botte	Corsica	0.52	rat free	1	2010 (09):3	630	35	43
				rat free		2011 (06):6	990	/	62
17	Gargalu	Corsica	20.06	rat	4	1985 (04):2	1060	50	/
				rat		1990 (07):2	505	19	/
18	Palazzu	Corsica	0.47	transient	1	1986 (08):1	225	26	/
19	Palazzinu	Corsica	0.1	transient	1	1985 (07):2	490	34	/
20	Porri	Corsica	0.27	rat free	1	1983 (07):2	590	32	/
				rat free		1986 (07):1	335	69	/
21	Brocciu	Corsica	1.11	transient	1	2012 (06):1	132	30	60
22	Giraglia	Corsica	10.35	rat free	4	2000 (09):1	360	38	/
				rat free		2012 (08):2	406	33	33
				rat free		2012 (10):1	230	/	50
				rat free		2014 (07):1	230	/	19
				rat free		2014 (10):1	190	36	38
				rat free		2015 (08):1	220	/	32
23	Saint Ferreol	Provence	0.45	rat	2	2016 (05):1	700	23	40
24	La Tradière	Provence	1.05	rat	2	2016 (05):1	460	23	37
25	Rascas	Provence	0.76	transient	2	1985 (09):1	290	50	/
26*	Gabinière	Provence	3.42	transient	2	2003 (10):1	345	69	/
				transient		2016 (05):1	187	37	43

* On Lavezzi Island (n. 6) rats were eradicated in 2000; on the Toro islets (n. 10 and 11) in 1992, after 2-4 years of presence on the islets; on Vacca (n. 12) in January 2011, after having been detected in July 2010; on Gabinière (n. 26) rats were present in 1937, eradicated in 1966, rats re-invaded the island in 2010 and were eradicated again in 2014. The islets San Bainzu, Piana and Porro, all inhabited by rats, were excluded from the analysis because less than 10 geckoes were measured.

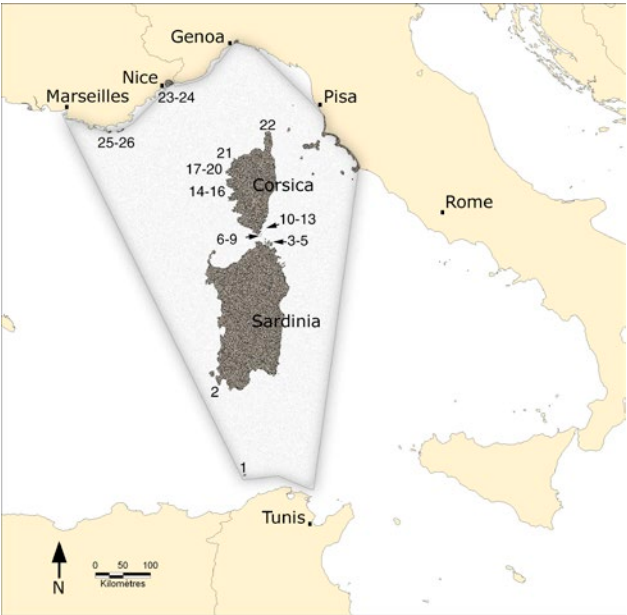


Fig. 1. Geographic range of *Euleptes europaea* and studied populations. Numbers refers to Table 1.



Fig. 2. Vegetation (mostly *Lotus cytisoides*) covering the base of the granite boulders inhabited by *Euleptes europaea* on Spargiotto Islet (Maddalena Archipelago). May 2012.

“in the open” microhabitats on islands with rats: the catch per unit effort (CPUE) was the dependent variable, while rat occurrence, habitat type (“in the open” vs “under cover”), island size and the number of reptile species were the fixed predictors. We also added the rat occurrence $\times$ habitat type interaction to account for differential habitat use between “rat” and “rat-free” islands. We could not include in the model the season as all but three islands were sampled in spring, and the island entered the model as random effect to control for double measuring within island (i.e., CPUE in open and close microhabitat). Sample size

included 16 islands for which we collected more than 10 individuals ($n = 1001$, Mean values $\pm$ SE: 62 ± 10) for computing CPUE indexes for both “in the open” and “under cover” microhabitats. In a second analysis we checked if the height above the ground of the first sighting differed in islands with or without rats, using rat occurrence, season, number of reptile species, island size, and the rat occurrence $\times$ season as fixed predictors. As in the previous analysis, the islands entered the model as random effect, and geckos observed “under cover” were excluded. The sample for this last analysis included 469 geckos from 14 islands.

Analyses were performed using the package lme4 (Bates et al., 2014) in R ver. 3.2.4 (R Core Team, 2018), and otherwise stated, data reported are means $\pm$ standard error.

RESULTS

Population structure

The PERMANOVA showed that the population structure significantly varied in response to rat occurrence, season, number of reptile species living on the island, but was invariant in respect to the sampling effort (Table 2). In particular, a) the structure of geckos’ populations living on the islands with rats showed a larger proportion of medium-sized individuals and a lower proportion of large-sized geckos compared to populations occurring on “rat-free” islands (Fig. 3a); b) irrespective of rat occurrence, smaller geckos were frequent in spring, while larger ones prevailed in autumn, and the relative abundance of medium-sized individuals did not vary between seasons (Fig. 3b); c) the greater was the number of reptile species on the island, the smaller was the frequency of larger geckos and the higher the number of medium-sized individuals (Fig. 3c). Moreover, large geckos were more frequent on islets rather than on islands (Fig. 3d).

Body condition

Body condition of the Leaf-toed geckos did not differ between “rat” and “rat-free” islands (0.0292 ± 0.0005

Table 2. Results of permutational ANOVA for the variability of the population structure of the Leaf-toed geckos in response to rat occurrence, season and number of reptile species after having been controlled for island size and number of sampling years. P-values are computed with 9999 permutations.

Variable	df	F	R ²	P
Rats	1,24	3.916	0.08	0.0374
Islet size	1,24	3.775	0.08	0.0374
Season	1,24	10.69	0.23	0.0010
N. reptiles	1,24	3.975	0.08	0.0336
N. replicates	1,24	0.0033	<0.01	0.9958

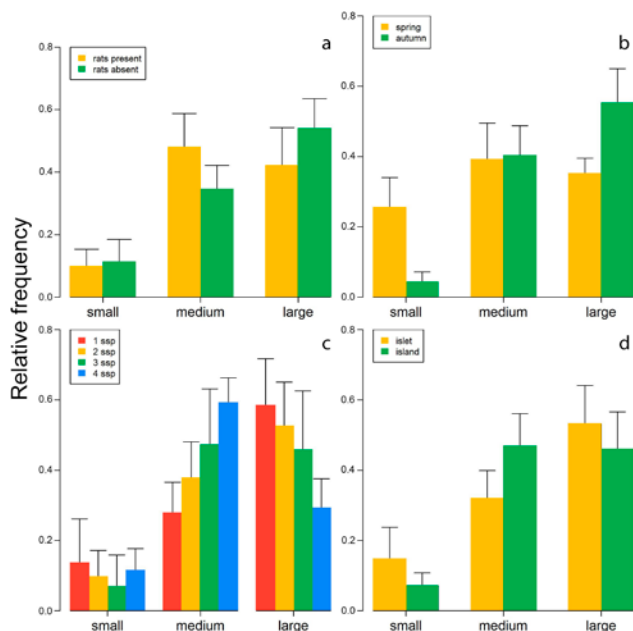


Fig. 3. Variation of the population structure of the European Leaf-toed gecko on 22 Mediterranean islands in response to (a) rat occurrence (present in yellow, absent in green), (b) season (Spring in yellow, Autumn in green), (c) number of reptile species living on the islands (1 sp. in red, 2 spp. in yellow, 3 spp. in green, 4 spp. in blue), and (d) island size (islet: < 10,000 m² in yellow, island: > 10,000 m² in green). Bars = 95% confidence interval.

and 0.0285 ± 0.0002 respectively, $F_{1,5} = 0.0053$, $P = 0.94$), either between males and females (0.0282 ± 0.0003 and 0.0292 ± 0.0004 respectively, $F_{1,413} = 2.545$, $P = 0.11$), or season (autumn: 0.0269 ± 0.0004 ; spring: 0.0295 ± 0.0003 , $F_{1,5} = 0.608$, $P = 0.46$) (Table 3). By contrast, the random effect (island) was highly significant (L-ratio $\chi^2 = 24.0$, d.f. = 1, $P < 0.001$), and the effect ($\sigma = 0.0021$) accounted for 32% of the total variance, suggesting that body condition is highly dependent on the island features.

Spatial behaviour

Leaf-toed geckos were more active on “rat-free” islands than on “rat” islands (values of CPUE being 7.85 ± 2.35 and 6.33 ± 2.30 , respectively), but this difference was significantly depending on the habitat (rat occurrence $\times$ habitat type interaction: $F_{1,24} = 11.99$, $P = 0.0019$, Table 4). Geckos on “rat-free” islands were active “in the open” rather than “under cover” ($P = 0.057$), while the opposite occurred on “rat” islands ($P = 0.0091$, Fig. 4), suggesting that the Leaf-toed geckos actually avoid insecure micro-habitats in presence of rats. All other predictors were not significant (see Table 4 for details). The random effect of islands (L-ratio $\chi^2 = 2.92$, d.f. = 1, $P = 0.09$) was not sig-

Table 3. Results of the linear mixed model for the variability of the body condition index of male and female Leaf-toed geckos in response to rat occurrence. Only fixed effects are reported.

Predictor	df	F	P
Rat occurrence	1,6	0.0053	0.94
Season	1,6	0.608	0.46
Sex	1,5	2.545	0.11

Table 4. Results of the linear mixed model for the variability of the activity of Leaf-toed geckos in response to rat occurrence (df have been calculated using the Satterthwaite approximation). Only fixed effects are reported.

Predictor	df	F	P
Open vs close habitats			
Rat occurrence	1,12.7	0.781	0.39
Habitat type	1,24.9	1.344	0.26
N. reptile species	1,8.5	0.629	0.45
Island size	1,8.3	0.802	0.39
Rat occurrence $\times$ Habitat type	1,24.9	11.99	0.0019
Height above ground			
Rat occurrence	1,14.9	1.068	0.32
Season	1,22.3	0.659	0.42
N. reptile species	1,2	0.142	0.74
Island size	1,4.4	2.168	0.21
Rat occurrence $\times$ Season	1,19.2	2.446	0.13

nificant, suggesting that CPUE was not affected by island features other than rat occurrence and habitat.

By contrast, the height from the ground where the geckos were observed “in the open” was not affected by the rat occurrence (“rat-free” islands: 47.6 ± 2.6 ; “rat” islands: 32.6 ± 6.5), either by season (autumn: 51.7 ± 5.0 ; spring: 44.3 ± 2.7) or by their interaction (Table 4). Similarly, the effects of both island size and the number of reptile species were also negligible (see Table 4 for statistics).

We report some additional observation on the spatial behaviour. Before rat eradication, on Lavezzi Island in 1982, on 112 sightings $\approx 85\%$ of geckos were active under plant cover; in 1986 ($n = 50$) the proportion was $\approx 80\text{--}85\%$ (MD pers. obs.). Ten years after rat eradication, the percentage of geckos active under plant cover was lower but still high: 67% in 2010 ($n = 41$), 68% in 2011 ($n = 41$). On the remote Vacca Islet, rats were detected for the first time in 2010 and eradicated by the Bouches de Bonifacio Natural Reserve in less than one year (O. Bonnenfant pers. com.). We do not know the activity pattern before eradication, but in July 2012, 87% of geckos were observed in the open. Analogously, few miles away,

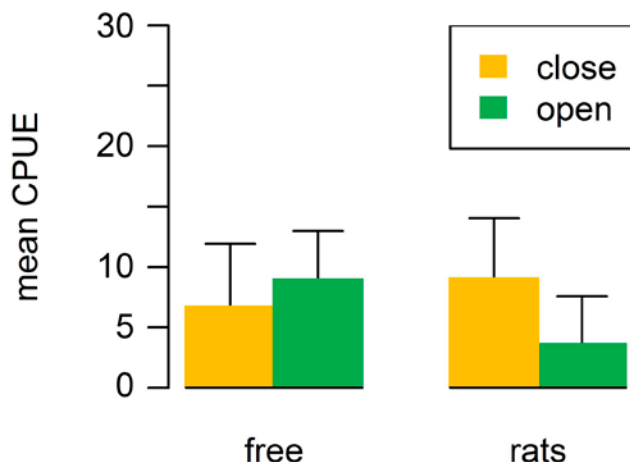


Fig. 4. Variation of the foraging mode of the European Leaf-toed geckos, “in the open” (open) and “under cover” (close) in response to the presence of rats. The relative activity of geckoes was obtained from sightings of one hour of “catch per-unit-effort” (CPUE) on 15 islets. Bars = 95% confidence interval.

rats invaded the Toro Islands where they have stayed for about 4 years, until 1992, when eradication occurred (Thibault, 1992). In April 2005 ($n = 50$) $\approx 90\%$, in July 2012 ($n = 52$) 96% and in July 2014 ($n = 59$) 93% geckos were observed in the open.

DISCUSSION

Two out of the three predictions on how the Black rat may influence the activity and demography of *Euleptes europaea* were confirmed by our results: a) in the presence of rats smaller sized geckos prevail, and b) geckos are less active “in the open”; c) by contrast, no significant effect on body condition was found.

Transition to populations characterized by smaller sized individuals could be caused by selective predation on larger geckos. On Ohinau Islet in New Zealand, juveniles of the giant gecko *Hoplodactylus duvaucelii* are more vulnerable to predation by *Rattus exulans* (Hoare et al., 2007), likely because adult geckos are similar in size to the Pacific rat. Conversely, a 170 g Black rat could easily predate European Leaf-toed geckos of any size (from 0.3 to 2 g). If this would be the case, a random predation of any size class could ultimately also result in a shortage of the larger sized geckos. In the Mediterranean, despite some detailed studies on this topic (Cassaing et al., 2005; Pérez-Mellado et al., 2008; Petralia et al., 2010; Ruffino et al., 2011), direct predation of *Rattus rattus* on Sauria was never observed, although predation on lizards has been supposed to occur in other regions (Caut et al., 2008;

Gasc et al., 2010); ascertained (Harper and Bunbury, 2015; Thibault et al., 2016; Clapperton et al. 2019) or observed for other rat species (Townes et al., 2006). Abundance of lizards (and Tuataras) has been related to the presence of rats but the mechanisms still deserve to be explained and likely could involve competitive processes less obvious than predation (Townes et al., 2006).

Other Vertebrates or invertebrates living on the studied islands could interact with the Leaf-toed gecko as possible competitors and/or predators such as: the ant *Crematogaster scutellaris*, competing for rock crevices and predating hatching geckos (Delaugerre, 1981); introduced cows, grazing on vegetation used by geckos foraging “under cover”, e.g., on Lavezzi (Delaugerre and Brunstein, 1987); the bird *Monticola solitarius* and the ant *Tapinoma erraticum* predating *E. europaea* respectively on Lavezzi (Delaugerre and Cheylan, 1992) and Porraggia Grande islands (Delaugerre and Brunstein, 1987) and perhaps the Western Whip snake *Hierophis viridiflavus*, that on Giraglia Island has been observed to have nocturnal habits (Delaugerre, 2013). However 73% of the studied islands, host just one or two reptile species (Table 1), the second species being typically a *Podarcis* (diurnal) lizard, that is unlikely a predator of the Leaf-toed gecko. On the remaining 27% islands, the presence of three or four (just on three islands) reptile species is equally distributed between rat and rat-free islands.

Alternatively, rats may affect gecko’s population structure by interfering with their growth process. Survival of geckos can be reduced by increased physiological stress, which ultimately may cause physiological shifts in life history strategy and demographic fitness components (Rödl et al., 2007; Trompeter and Langkilde, 2011; Narayan et al., 2013). Rats could act as stressors for geckos just roaming around. Moreover, geckos could be subjected to infections carried by black rats (Prenter et al., 2004), often infested by the adult nematode *Mastophorus muris* (Cassaing et al., 2005). According to Lafferty et al. (2010), native geckos of the central Pacific islands might serve as paratenic hosts of *M. muris*; this stage being the most incline in affecting host fitness (Kuris, 2003).

Rats might also interact with geckos in a more indirect way, for instance inducing vegetation changes. *Lotus cytisoides*, for example, is a plant that provides high quality shelters for geckos and for a lot of invertebrates (geckos’ preys) and it is consumed by rats (Cassaing et al., 2005; Ruffino et al., 2011). Behavioural shift in microhabitat use might be costly for geckos, since they would be forced to forage under plant cover with consequently limited access to bare rock surfaces more favourable for nocturnal thermoregulation (thigmothermy).

Information gathered on Lavezzi before and after rat eradication seems to confirm an influence of the presence of rats on geckos' population structure. Before rat removal, as observed for other islands with rats, geckos' size class structure was skewed towards medium-sized individuals. A decade after eradication (three geckos generations) we observed an upward trend towards larger sized individuals, even if the sample size of some size classes is too small to perform a statistical test.

Rats seem to change geckos' population structure without affecting body condition of individuals. Indeed, geckos' body condition was not influenced by the presence of rats, sex or season. However, we found a strong significant random effect of islands, suggesting that body condition in both males and females strongly depends on some island features rather than on the presence of rats.

Activity, assessed by the catch per unit effort, did not vary just according to rat occurrence, but also depending on the microhabitat. In the presence of rats, geckos avoided to forage "in the open" and were more active "under cover", probably to avoid disturbance and/or predation risk induced by the ground-dwelling rodents (Whitaker, 1973; Hoare et al., 2007). On Lavezzi Island, the "under cover" was the most common mode both before and after rat eradication, even if the percentages of geckos active "under cover" decreased ten years after eradication. This pattern (even if related to one island) may suggest a certain persistence of an avoidance behaviour likely resulted from a prolonged coexistence with rodents. Though in geckos as well as in most reptiles, young individuals cannot learn through parental care or imitation, the acquisition of a novel behaviour might take long time. Unlike how observed for the New Zealand *Hoplodactylus duvaucelii* who recovered its arboreal habitat six months after rat removal (Hoare et al., 2007), Lavezzi *Euleptes* gecko did not show a similar behavioural plasticity. Dealing with antipredator behaviours on islands Blumstein (2002) reported that «experience dependant behaviours change rapidly following isolation» (and the loss of predator), «whereas more hard wired behaviours may persist for many generations.» Does *Euleptes* geckos have acquired an avoidance behaviour over the last 2000 years while coexisting with Black rats? Or, does this behaviour date back to the Pleistocene when geckos coexisted with mammals nowadays extinct (e.g., the Tyrrhenian field rat, *Rhagamys orthodon*, M. Masseti and G. Cheylan (pers. comm.)? However, geckos' behavioural changes due to the presence of rats seem to be very variable (Hoare et al., 2007; Krebs et al., 2015).

As suggested by our results, geckos may benefit from rat eradication in most contexts but a lot of caution should be paid when undertaking rat eradications on islands that likely can be reinvaded (Harris et al., 2011;

Savidge et al., 2012). Once settled on an island, a rat population may repel new invading rats through aggressive interactions, as observed by Granjon and Cheylan (1989) and Abdelkrim et al. (2009) who found that the Lavezzi population was founded by a single colonization event without further gene flow. Hence, eradication might entice new invaders to settle in a competition-free ecosystem.

Moreover, island "old-resident" rat populations are adapted to exploit seasonal resources adjusting home range, demography and intraspecific interactions (Cheylan, 1988; Clark, 1980; Cassaing et al., 2007; Ruffino et al., 2011; Pisanu et al., 2011). New invading rats (e.g., mainland rats), not familiar with the island conditions, might severely affect the local biota. Observations carried out on the Corsican Toro islands 2-4 years after rat invasion, besides the well-known detrimental effects on the Cory's shearwater and on the Pallid swift, revealed that rats preyed almost to extinction *Silene vellutina* (Caryophyllaceae) (Thibault, 1992), a rare endemic plant that elsewhere was not (or only marginally) consumed by "old-resident" rats.

Since several eradication actions have 'failed', and reinvasions occurred (Cheylan and Granjon, 1987; Howald et al., 2007; Russell et al., 2010; Savidge et al., 2012; Sposimo et al., 2012; Ragionieri et al., 2013), the urge to learn from failures led to the proposal to adopt the metapopulation (Russell et al., 2008) or the eradication units approach (Robertson and Gemmell, 2004) by considering first islands' assemblages and relative reinvasion sources in order to properly guide eradication programs. Native island species must cope with an increasing number of biological invasions; understanding the mechanisms of invasions, as well as the interaction between native species and long coexisting aliens, may be crucial to adopt proper conservation actions.

ACKNOWLEDGMENTS

We would like to thank: Joanne Monks (born Hoare), who kindly granted us to borrow part of the title and structure of the paper (Hoare et al., 2007); Initiative Petites Iles de Méditerranée (PIM), APAL (Tunisia), CEN Corse, Réserves naturelles des Bouches de Bonifacio, de Scandola et des Iles de la Pointe du Cap Corse, Parc naturel régional de la Corse, Parco Nazionale dell' Arcipelago de La Maddalena, Parc National de Port-Cros; the colleagues and friends who helped during field work: A. Abiadh, Ch.-H. Bianconi, V. Bosc, D. Brunstein, M.H. Casalonga, G. Deso, Y. Donno, A. Gaio, O. Gerriet, F. Grita, N. Nègre-Santucci, O. Patrimonio, J. Renet.

Our study was improved by valuable discussions with Gilles Cheylan, Marc Cheylan, Marco Masseti, Michel Pascal and Jean-Claude Thibault.

Permits to handle protected species were issued by the Dreal (Corse and PACA) and by the Ministero dell'Ambiente e della Tutela del Territorio e del Mare (U. prot. DPN 0010637B 16/05/2009, 0017564 12/08/2010, 0044068 04/12/2012 and 0001805 04/02/2015) and the Parco Nazionale dell'Arcipelago di La Maddalena. The access to Giraglia Island was authorized by the Préfet de Haute-Corse.

REFERENCES

- Abdelkrim, J., Pascal, M., Samadi, S. (2009): Genetic structure and functioning of alien ship rat populations from a Corsican micro-insular complex. *Biol. Invasions* **11**: 473-482.
- Anderson, M.J. (2001): A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* **26**: 32-46.
- Atkinson, I.A. (1985): The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas. *Conservation of Island Birds* **3**: 35-81.
- Bates, D., Mächler, M., Bolker, B., Walker, S. (2014): Fitting linear mixed-effects models using lme4. *ArXiv*:1406.5823.
- Bennett, P.M., Owens, I.P.F., Nussey, D., Garnett, S.T., Crowley, G.M. (2005): Mechanisms of extinction in birds: phylogeny, ecology and threats. In: *Phylogeny and Conservation (Conservation Biology)*, pp. 317-336. Purvis, A., Gittleman, J., Brooks, T., Eds, Cambridge University Press, Cambridge.
- Berthon, K. (2015): How do native species respond to invaders? Mechanistic and trait-based perspectives. *Biol. Invasions* **17**: 2199-2211.
- Blumstein, D.T. (2002): Moving to suburbia: ontogenetic and evolutionary consequences of life on predator-free islands. *J. Biogeogr.* **29**: 685-692.
- Bonnet, X., Naulleau, G. (1994): Utilisation d'un indice de condition corporelle (BCI) pour l'étude de la reproduction chez les serpents. *Comptes Rendus de l'Académie Des Sciences. Série 3, Sciences de La Vie* **317**: 34-41.
- Brown, J.H., Lomolino, M.V. (2000): Concluding remarks: historical perspective and the future of island biogeography theory. *Global Ecol. Biogeogr.* **9**: 87-92.
- Capizzi, D., Baccetti, N., Sposimo, P. (2010): Prioritizing rat eradication on islands by cost and effectiveness to protect nesting seabirds. *Biol. Conserv.* **143**: 1716-1727.
- Cassaing, J., Derré, C., Moussa, I., Parghentanian, T., Bocherens, H., Cheylan, G. (2005): Le régime alimentaire du rat noir *Rattus rattus* dans les îles d'Hyères analysé par la biochimie isotopique et les contenus stomacaux. *Sci. Rep. Port-Cros Natl. Park, Fr.* **21**: 85-115.
- Cassaing, J., Derré, C., Moussa, I., Cheylan, G. (2007): Diet variability of Mediterranean insular populations of *Rattus rattus* studied by stable isotope analysis. *Isotopes in Environmental and Health Studies* **43**: 197-213.
- Caut, S., Angulo, E., Courchamp, F. (2008): Dietary shift of an invasive predator: rats, seabirds and sea turtles. *J. Appl. Ecol.* **45**: 428-437.
- Cheylan, G. (1988). Les adaptations écologiques de *Rattus rattus* à la survie dans les îlots méditerranéens (Provence et Corse). *Bull. Ecol.* **19**: 417-426.
- Cheylan, G., Granjon, L. (1987). Ecologie du rat noir à Lavezzi (Corse du Sud): abondances, déplacements et reproduction. *Travaux Scientifiques—Parc Naturel Régional et Réserves Naturelles de Corse* **12**: 71-91.
- Clapperton, K., Maddigan, F., Chinn, W., Murpy, E. (2019): Diet, Population Structure and Breeding of *Rattus rattus* L. in South Island Beech Forest. *New Zeal. J. Ecol.* **43**: 1-8.
- Clark, D.B. (1980): Population ecology of *Rattus rattus* across a desert-montane forest gradient in the Galápagos Islands. *Ecology* **61**: 1422-1433.
- Corti, C., Böhme, W., Delfino, M., Masseti, M. (1999): Man and lacertids on the Mediterranean islands: conservation perspectives. *Natura Croatica* **8**: 287-300.
- Courchamp, F., Chapuis, J.-L., Pascal, M. (2003): Mammal invaders on islands: impact, control and control impact. *Biol. Rev.* **78**: 347-383.
- Delaugerre, M. (1981). Sur l'histoire naturelle de *Phyllodactylus europaeus* Gené, (Gekkonidae, Sauria, Reptiles): Port-Cros : étude d'une population naturelle. *Trav. Sci. Parc. Nation. Port-Cros* **6**: 147-175.
- Delaugerre, M., Brunstein, D. (1987): Observations sur la flore et la faune de plusieurs îlots du sud de la Corse (archipels des Lavezzi, des Cerbicales et côte sud-orientale). *Travaux Scientifiques—Parc Naturel Régional et Réserves Naturelles de Corse* **12**: 1-17.
- 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**: 709-736.
- Delaugerre, M., Ouni, R., Nouira, S. (2011). Is the European Leaf-toed gecko *Euleptes europaea* also an Afri-

- can? Its occurrence on the Western Mediterranean landbridge islets and its extinction rate. *Herpetol. Notes* **4**: 127-137.
- Delaunier, M.-J. (2013). Going out tonight? When insular *Hierophis viridiflavus* breaks the Whip Snakes Rules. *Acta Herpetol.* **8**: 47-52.
- Drake, D.R., Hunt, T.L. (2009): Invasive rodents on islands: integrating historical and contemporary ecology. *Biol. Inv.* **11**: 1483-1487.
- Foufopoulos, J., Ives, A.R. (1999). Reptile extinctions on land-bridge islands: life-history attributes and vulnerability to extinction. *Am. Nat.* **153**: 1-25.
- Gasc, A., Duryea, M.C., Cox, R.M., Kern, A., Calsbeek, R. (2010): Invasive predators deplete genetic diversity of island lizards. *PLoS One* **5**: e12061.
- Granjon, L., Cheylan, G. (1989): Le sort de rats noirs (*Rattus rattus*) introduits sur une île, relevé par radio-tracking. *Comptes Rendus de l'Académie Des Sciences. Série 3, Sciences de La Vie* **309**: 571-575.
- Harper, G.A., Bunbury, N. (2015): Invasive rats on tropical islands: Their population biology and impacts on native species. *Global Ecol. Conserv.* **3**: 607-627.
- Harris, D.B., Gregory, S.D., Bull, L. S., Courchamp, F. (2011): Island prioritization for invasive rodent eradications with an emphasis on reinvasion risk. *Biol. Inv.* **14**: 1251-1263.
- Hoare, J.M., Pledger, S., Nelson, N.J., Daugherty, C.H. (2007): Avoiding aliens: Behavioural plasticity in habitat use enables large, nocturnal geckos to survive Pacific rat invasions. *Biol. Conserv.* **136**: 510-519.
- Howald, G., Donlan, C.J., Galván, J.P., Russell, J.C., Parkes, J., Samaniego, A., Wang, Y., Veitch, D., Genovesi, P., Pascal, M., Saunders, A., Tershy, B. (2007): Invasive Rodent Eradication on Islands. *Conserv. Biol.* **21**: 1258-1268.
- Jones, H.P., Tershy, B.R., Zavaleta, E. , Croll, D.A., Keitt, B.S., Finkelstein, M.E., Howald, G.R. (2008): Severity of the Effects of Invasive Rats on Seabirds: A Global Review: Effects of Rats on Seabirds. *Conserv. Biol.* **22**: 16-26.
- Krebs, É, Abba, A., Gillet, P., Eudeline, R., Gauthier, J., Le Quilliec, P., Lorvelec, O., Martinerie, G., Vidal, É, Buisson, É. (2015): Réponses des populations de reptiles à l'éradication du Rat noir (*Rattus rattus*) sur l'île de Bagaud (Parc national de Port-Cros, Var, France). *Rev. Ecol.-Terre Vie.* **70**: 99-109.
- Kuris, A.M. (2003): Evolutionary ecology of trophically transmitted parasites. *J. Parasitol.* **89**: S96-S100.
- Lafferty, K.D., Hathaway, S.A., Wegmann, A.S., Shipley, F.S., Backlin, A.R., Helm, J., Fisher, R.N. (2010): Stomach Nematodes (*Mastophorus Muris*) in Rats (*Rattus rattus*) Are Associated with Coconut (*Cocos nucifera*) Habitat at Palmyra Atoll. *J. Parasitol.* **96**: 16-20.
- Legendre, P., Legendre, L.F. (2012): Numerical ecology. Elsevier B.V., Amsterdam.
- Martin, J.-L., Thibault, J.-C., Bretagnolle, V. (2000): Black rats, island characteristics, and colonial nesting birds in the Mediterranean: consequences of an ancient introduction. *Conserv. Biol.* **14**: 1452-1466.
- McArdle, B.H., Anderson, M.J. (2001): Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* **82**: 290-297.
- Mertens, R. (1970): Ueber die Lebensdauer einiger Amphibien und Reptilien in Gefangenschaft. *Zool. Gart.* **39**: 13-209.
- Mooney, H.A., Cleland, E.E. (2001): The evolutionary impact of invasive species. *P. Natl. Acad. Sci. USA*, **98**: 5446-5451.
- Moser, D., Lenzner, B., Weigelt, P., Dawson, W., Kreft, H., Pergl, J., Pyšek, P., van Kleunen, M., Winter, M., Capinha, C., Cassey, P., Dullinger, S., Economo, E.P., García-Díaz, P., Guénard, B., Hofhansl, F., Mang, T., Seebens, H., Essl, F. (2018): Remoteness promotes biological invasions on islands worldwide. *P. Natl. Acad. Sci. USA*, **115**: 9270-9275.
- Müller, J. (2001): A new fossil species of *Euleptes* from the early Miocene of Montaigu, France (Reptilia, Gekkonidae). *Amphibia-Reptilia* **22**: 341-348.
- Narayan, E.J., Cockrem, J.F., Hero, J.-M. (2013): Sight of a Predator Induces a Corticosterone Stress Response and Generates Fear in an Amphibian. *PLoS One* **8**: e73564.
- Pérez-Mellado, V., Hernández-Estévez, J.Á., García-Díez, T., Terrassa, B., Ramón, M.M., 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**: 49-60.
- Petralia, E., Messina, A., Petralia, A., Siracusa, A.M. (2010): Stato della popolazione di *Rattus rattus* (Linnaeus, 1758)(Rodentia, Muridae) nella Riserva Naturale Integrata "Isola Lachea e Faraglioni dei Cicli" di Acicastello (Catania, Italia). *Bollettino Accademia Gioenia Sci. Nat.*, **43**: 12-22.
- Pisanu, B., Caut, S., Gutjahr, S., Vernon, P., Chapuis, J.-L. (2011): Introduced black rats *Rattus rattus* on Ile de la Possession (Iles Crozet, Subantarctic): diet and trophic position in food webs. *Polar Biol.* **34**: 169-180.
- Prenter, J., MacNeil, C., Dick, J.T., Dunn, A.M. (2004): Roles of parasites in animal invasions. *Trends Ecol. Evol.*, **19**: 385-390.
- R Core Team. (2018). R: A language and environment for statistical computing. <https://www.r-project.org/>

- Ragionieri, L., Cutuli, G., Sposimo, P., Spano, G., Navone, A., Capizzi, D., Baccetti, N., Vannini, M., Fratini, S. (2013): Establishing the eradication unit of Molar Island: a case of study from Sardinia, Italy. *Biol. Inv.* **15**: 2731-2742.
- Recher, H.F., Clark, S.S. (1974): A biological survey of Lord Howe Island with recommendations for the conservation of the island's wildlife. *Biol. Conserv.* **6**: 263-273.
- Robertson, B.C., Gemmell, N.J. (2004): Defining eradication units in pest control programmes. *J. Appl. Ecol.* **41**: 1032-1041.
- Rödl, T., Berger, S., Romero, L.M., Wikelski, M. (2007): Tameness and stress physiology in a predator-naive island species confronted with novel predation threat. *P. Roy. Soc. B-Biol. Sci.* **274**: 577-582.
- Ruffino, L., Bourgeois, K., Vidal, E., Duhem, C., Paracuellos, M., Escribano, F., Sposimo, P., Baccetti, N., Pascal, M., Oro, D. (2009): Invasive rats and seabirds after 2,000 years of an unwanted coexistence on Mediterranean islands. *Biol. Inv.* **11**: 1631-1651.
- Ruffino, L., Russell, J.C., Pisanu, B., Caut, S., Vidal, E. (2011): Low individual-level dietary plasticity in an island-invasive generalist forager. *Popul. Ecol.* **53**: 535-548.
- Ruffino, L., Vidal, E. (2010): Early colonization of Mediterranean islands by *Rattus rattus*: a review of zooarcheological data. *Biol. Inv.* **12**: 2389-2394.
- Russell, J.C., Beaven, B.M., MacKay, J.W.B., Towns, D.R., Clout, M.N. (2008): Testing island biosecurity systems for invasive rats. *Wildlife Res.* **35**: 215.
- Russell, J.C., Miller, S.D., Harper, G.A., MacInnes, H.E., Wylie, M.J., Fewster, R.M. (2010): Survivors or reinvaders? Using genetic assignment to identify invasive pests following eradication. *Biol. Inv.* **12**: 1747-1757.
- Salvidio, S., Delaunerie, M. (2003): Population dynamics of the European leaf-toed gecko (*Euleptes europaea*) in NW Italy: implications for conservation. *Herpetol. J.* **13**: 81-88.
- Salvidio, S., Lanza, B., Delaunerie, M.J. (2010): *Euleptes europaea* (Gené, 1839). In: *Fauna d'Italia Vol. 45 (Reptilia)*, pp. 258-270. Corti, C., Capula, M., Luiselli, L., Razzetti, E., Sindaco, R., Eds, Edizioni Calderini de Il Sole 24 ORE, Milano.
- Savidge, J.A., Hopken, M.W., Witmer, G.W., Jojola, S.M., Pierce, J.J., Burke, P.W., Piaggio, A.J. (2012): Genetic evaluation of an attempted *Rattus rattus* eradication on Congo Cay, U.S. Virgin Islands, identifies importance of eradication units. *Biol. Inv.* **14**: 2343-2354.
- Sax, D.F., Stachowicz, J.J., Brown, J.H., Bruno, J.F., Dawson, M.N., Gaines, S.D., Grosberg, R.K., Hastings, A., Holt, R.D., Mayfield, M.M. (2007): Ecological and evolutionary insights from species invasions. *Trends Ecol. Evol.* **22**: 465-471.
- Silva-Rocha, I., Montes, E., Salvi, D., Sillero, N., Mateo, J.A., Ayllón, E., Pleguezuelos, J.M., Carretero, M.A. (2018): Herpetological History of the Balearic Islands: When Aliens Conquered These Islands and What to Do Next. In: *Histories of Bioinvasions in the Mediterranean*, pp. 105-131. Queiroz, A.I., Pooley, S., Eds., Springer International Publishing, Cham, Switzerland.
- Silva-Rocha, I., Salvi, D., Carretero, M.A., Ficetola, G.F. (2019): Alien Reptiles on Mediterranean Islands: A Model for Invasion Biogeography. *Divers. Distrib.* **25**: 995-1005.
- Simberloff, D., Martin, J.L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., Vilà, M. (2013): Impacts of biological invasions: what's what and the way forward. *Trends Ecol. Evol.* **28**: 58-66.
- Simberloff, D.S. (1974): Equilibrium theory of island biogeography and ecology. *Annu. Rev. Ecol. Syst.* **5**: 161-182.
- Sposimo, P., Spano, G., Navone, A., Fratini, S., Ragionieri, L., Putzu, M., Capizzi, D., Baccetti, N. (2012): Rodent eradication on Molar Island and surrounding islets (NE Sardinia): from success to the riddle of reinvasion. *Aliens* **32**: 33-38.
- Strauss, S.Y., Lau, J.A., Carroll, S.P. (2006): Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecol. Lett.* **9**: 357-374.
- Stuart, Y.E., Campbell, T.S., Hohenlohe, P.A., Reynolds, R.G., Revell, L.J., Losos, J.B. (2014): Rapid evolution of a native species following invasion by a congener. *Science* **346**: 463-466.
- Thibault, J.C. (1992): Eradication of the Brown Rat from the Toro Islets (Corsica): remarks about an unwanted colonizer. *Avocetta* **16**: 114-117.
- Thibault, J.C., Delaunerie, M., Cheylan, G., Guyot, I., Miniconi, R. (1987): Les vertébrés terrestres non domestiques des îles Lavezzi (sud de la Corse). *Bulletin de La Société Linnéenne de Lyon* **56**: 73-103.
- Thibault, M., Brescia, F., Jourdan, H., Vidal, E. (2016): Invasive rodents, an overlooked threat for skinks in a tropical island hotspot of biodiversity. *New Zealand J. Ecol.* **41**: 74-83.
- Towns, D.R., Atkinson, I.A.E., Daugherty, C.H. (2006): Have the harmful effects of introduced rats on islands been exaggerated? *Biol. Inv.* **8**: 863-891.
- Traveset, A., Richardson, D. (2006): Biological invasions as disruptors of plant reproductive mutualisms. *Trends Ecol. Evol.* **21**: 208-216.

- Trompeter, W.P., Langkilde, T. (2011): Invader danger: Lizards faced with novel predators exhibit an altered behavioral response to stress. *Horm. Behav.* **60**: 152-158.
- Vigne, J.-D., Valladas, H. (1996): Small mammal fossil assemblages as indicators of environmental change in northern Corsica during the last 2500 years. *J. Archaeol. Sci.* **23**: 199-215.
- Whitaker, A.H. (1973): Lizard populations on islands with and without Polynesian rats, *Rattus exulans* (Peale). *Proc. New Zeal. Ecol.Soc.* **20**: 121-130.