Acta Herpetologica 19(2): 123-137, 2024
DOI: 10.36253/a_h-14527

Selection and daily occupancy of artificial retreat-sites by a declining Mediterranean island specialist, the European leaf-toed gecko *Euleptes europaea*

Julie Quessada[1,2,3,*], Vincent Riviere[3], Marc Cheylan[4], Alban Guillaumet[5]

[1] *Observatoire des Sciences de l'Univers de Rennes, Université de Rennes, Campus de Beaulieu, 263 Avenue Général Leclerc, 35042 Rennes, France*
[2] *Station d'Ecologie Théorique et Expérimentale (SETE), CNRS UAR2029, 2 route du CNRS, 09200 Moulis, France*
[3] *AGIR écologique, 147 ancienne route d'Esparron, 83470 Saint Maximin la Sainte Baume, France*
[4] *Ecole Pratique des Hautes Etudes, Paris Sciences Lettres University, 4-14 rue Ferrus, Paris, France*
[5] *Department of Biological and Environmental Sciences, Troy University, Troy, AL 36082, USA*
**Corresponding author.* Email: juliequessada@gmail.com / julie.quessada@agirecologique.fr

Submitted on: 2024, 13th March; revised on: 2024, 18th April; accepted on: 2024, 7th May
Editor: Enrico Lunghi

Abstract. The European Leaf-toed Gecko, *Euleptes europaea*, a rock-dwelling nocturnal gecko characteristic of Mediterranean Islands, is facing local extinctions and population decline at the margins of its range. Population monitoring through artificial retreat-sites (ARS) was implemented on French's Grand Rouveau and If islands to study the effects of management measures. We used Generalized Linear Models to identify: (i) the environmental variables (such as substrate, vegetation, and exposure to wind and sun) influencing the maximum number of individuals observed in ARS (studied in both islands); and (ii) the factors influencing ARS daily use (occupancy), including individual attributes such as age and weight, external temperature, and disturbance (Grand Rouveau only). The maximum number of geckos appeared to be determined by the thermal properties of ARS, as mediated by exposure to the dominant wind and sunlight, rather than by the structure of the habitat and nearby vegetation. An individual gecko's presence in an ARS was positively related to its presence in the same ARS on the previous day and negatively related to its age, the temperature of the previous night, and the number of days of disturbance. These results provide insights into the factors governing the selection and use of ARS by the European leaf-toed gecko and open perspectives on the use of ARS for the monitoring and conservation of this and other elusive terrestrial reptiles.

Keywords. Anthropogenic disturbance, gecko, habitat selection, Mediterranean islands, retreat-site, thermoregulation.

INTRODUCTION

Due to their isolation and unique environmental characteristics, including simplified food webs and small population sizes, islands are areas of high conservation value (Rodrigues et al., 2004, Gros-Désormeaux, 2012). They are often characterized by unique ecological assemblages, including many endemic and paleo-endemic species that have disappeared from the continent (Rodrigues et al., 2004, Blondel and Cheylan, 2008, Nias et al., 2010, Roberston et al., 2011, Gros-Désormeaux, 2012, Médail, 2017). With more than 10,000 islands and islets, about 5% of the world's total, the Mediterranean basin is a global hotspot for island environments (Blondel et al., 2010, Bellard et al., 2014, Médail, 2017) and one of 36 terrestrial biodiversity hotspots (Médail and Myers, 2004). Conservation challenges in the Mediterranean region include multiple forms of environmental exploitation and transformation, includ-

ISSN 1827-9635 (print)
ISSN 1827-9643 (online)

ing biological invasions, that are compounded by contemporaneous climate warming (e.g., Cheylan and Poitevin, 1994, Hulme et al., 2008, Underwood et al., 2009, Blondel et al., 2010, Médail, 2017, Lefebvre et al., 2019, Silva-Rocha et al., 2019, MedECC, 2020, Médail, 2022).

The European Leaf-toed Gecko *Euleptes europaea* (Gené, 1839), family Sphaerodactylidae, is endemic to the Mediterranean region and characteristic of Mediterranean Islands. Although its distribution has been described as a biogeographical enigma (Delaugerre and Cheylan, 1992), it is thought to have regressed from the continents resulting in a fragmented and mainly insular distribution (Delaugerre, 1981a, Delaugerre, 1981b, Renet et al., 2008, Vacher and Geniez, 2010, Fig. 1). Indeed, apart from a few continental stations in Tuscany (Italy), Liguria (Italy), Campania (Italy) and the Alpes-Maritimes (France), the species is only present on the islands of the western Mediterranean region: Corsica and Sardinia and their islets, the Galite archipelago (Tunisia), the Tuscan archipelago (Italy) and the islands of the Provencal coast (France) (Delaugerre et al., 2011, Di Nicola et al., 2022). The European Leaf-toed Gecko is the smallest species of gecko in Europe (on average 6-7 cm in length including tail, Arnold and Ovenden, 2014). It is an insectivorous and strictly nocturnal species avoiding light, which is active from dusk to dawn. It is a rock-dwelling species that lives in cracks and micro-cracks in rocks and buildings (Dardun, 2003). These natural shelters are of major importance for this poikilothermic species, which takes advantage of the heat stored by the rock to regulate its body temperature (Delaugerre, 1984). These cracks could also provide shelter from adverse weather conditions and diurnal predators (Delaugerre and Corti, 2020).

Having been qualified as a species pre-adapted to the island environment because of its low biomass and its ability to survive in very small populations, it is the vertebrate that is found on islands with the most drastic conditions in the Mediterranean regions, including very small area, reduced food web and low biomass (Delaugerre and Corti, 2020). However, this species is declining at the margins of its range and facing local extinctions both on islands and the continent (Dardun, 2003, Delaugerre, 2003, Salvidio and Delaugerre, 2003, Vacher and Geniez, 2010, Delaugerre et al., 2011, Corti *et al*, 2022). The exact causes of these declines are unknown but could be due to a combination of factors, including predation by the Black Rat *Rattus rattus* and the feral Cat *Felis catus* (Tranchant et al., 2003, Vacher and Geniez, 2010, Delaugerre et al., 2019), restoration of old buildings which serve as a refuge for the European Leaf-toed Gecko (AGIR écologique, 2016, Rennet and Monnet, 2021), competition with the Turkish Gecko *Hemidactylus turcicus* and the Common Wall Gecko *Tarentola mauritanica* (Linnaeus, 1758) (Renet and Monnet, 2021), introduction of new pathogens brought by the Common Wall Gecko (Delaugerre and Cheylan, 1992), abandonment of pastoralism leading to the closure of environments (Renet et al., 2013), urbanization (Renet et al., 2013), and

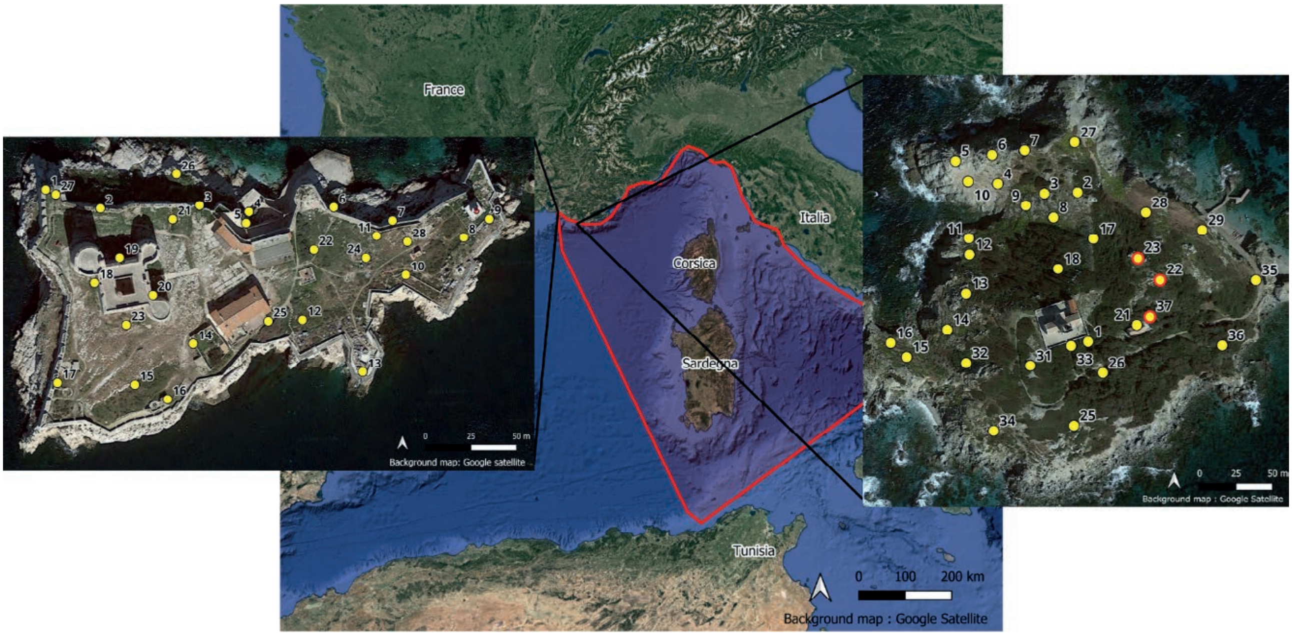

Fig. 1. Global distribution of the European Leaf-toed Gecko (in red) and locations of ARS on the left: If Island, and on the right Grand Rouveau Island. The three ARS used for the CMR protocol are circled in red.

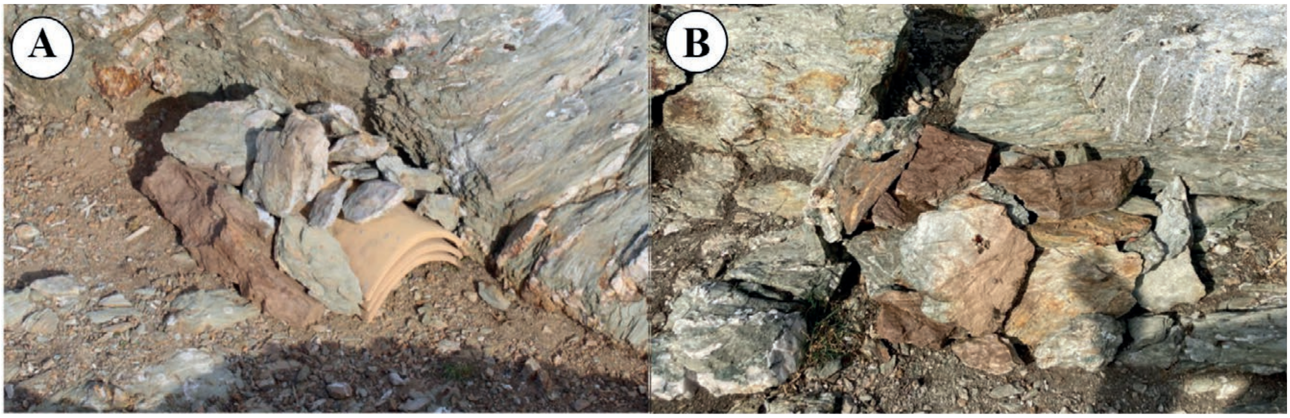

Fig. 2. A) Example of European Leaf-toed Gecko artificial retreat-site (ARS) left «open» to visualize the structure. B) Functional ARS completely covered with stones.

increase in the frequency of forest fires (Delaugerre and Cheylan, 1992). For these different reasons, the species is classified near threatened in the red list of Reptiles and Amphibians of the Mediterranean Basin and endangered in the red list of the Provence-Alpes-Côte d'Azur region in France (Cox et al., 2006, Marchand et al., 2017).

The European Leaf-Toad Gecko is an elusive species that is strictly nocturnal and can inhabit remote islands. As a consequence, the research on the species in activity, aiming for a better understanding of its ecology and conservation status, faces significant logistical challenges. A variety of monitoring techniques have been tested, including nighttime prospection with flashlights of potentially favorable rocky microsites (Delaugerre, 2002, Krebs et al., 2015, Couturier et al., 2020). However, nighttime prospections typically resulted in a small number of data points, insufficient for proper monitoring of the species (Vincent Rivière, pers. obs.). Because terrestrial ectotherms often use retreat-sites to regulate their body temperature and achieve their eco-physiological needs (Huey et al., 1989, Grillet et al., 2010), several studies have used artificial retreat-sites (ARS) to monitor reptiles or attempt to restore their habitat (Webb and Shine, 2000, Croak et al., 2010, Grillet et al., 2010, Moore et al., 2022). Monitoring of the European Leaf-toed Gecko using artificial retreat-sites was thus set up on the island of Grand Rouveau (Var, France) in 2014 and on the island of If (Bouches-du-Rhône, France) in 2016 (AGIR écologique, 2016, Cheylan et al., 2018) using three stacked roman roof tiles covered with stones (Fig. 2, Cheylan et al., 2018). These ARS were typically colonized rapidly (in less than a month) and their occupancy reached up to 76% on If Island, making these ARS a promising tool to monitor European Leaf-toed Gecko populations (AGIR écologique, 2016, Cheylan et al., 2018). But, to the best of our knowledge, no study has investigated the individual and environmental factors involved in the selection and daily use of ARS by the species.

Our overall objective is to provide important knowledge on the ecological preferences and life habits of the species that can be used to improve monitoring protocols and conservation measures targeted for the European Leaf-toad Gecko. Specifically, this study has two main objectives, namely identifying: (i) the environmental variables such as substrate, vegetation, and exposure to wind and sun influencing the maximum number of individuals observed in ARS; and (ii) the factors influencing ARS daily use (occupancy), including individual attributes such as age and weight, external temperature, and disturbance.

MATERIAL AND METHODS

Study sites

The island of If (43.279806°N, 5.325575°E) is part of the Frioul archipelago, off the coast of Marseille (Bouche-du-Rhône, France), in the heart of the Calanques National Park. In response to the restoration of the ramparts of If's castle, measures were taken to reduce the damage caused to the population of the European Leaf-toed Gecko on this island. Long-term monitoring of this population via artificial retreat-sites (ARS) has been implemented on If since September 2016 (AGIR écologique, 2016) in order to monitor the impact of the restoration and the effectiveness of the compensation measures. Twenty-seven ARS are currently positioned on If Island. They have been empirically arranged so that at least one ARS is placed within each main vegetation assemblage of the island (Fig. 1a). Since 2016, European Leaf-toed Geckos are counted in every ARS 2 to 3 times a year.

The island of Grand Rouveau (43.08038°N, 5.76757°E) is part of the Embiez archipelago off the town of Six-Fours-Les-Plages (Var, France). Most of the land is owned by the Conservatoire du Littoral and its management is entrusted to the city of Six-Fours-Les-Plages, in association with the "Initiative pour les Petites Iles de Mediterranée" (PIM initiative) (AGIR écologique, 2021). Monitoring of the European Leaf-toed Gecko population by ARS started in 2014 on Grand Rouveau (Cheylan et al., 2018). Thirty-three ARS are currently positioned on the island, with at least one ARS within each main vegetation assemblage of the island (Fig. 1b). Since July 2014, European Leaf-toed Geckos are counted in every ARS 2 to 3 times a year, with at least one survey in the spring and one in autumn.

Field protocol for environmental variables and gecko numbers within retreat-sites

The collection of environmental data occurred in April 2021 for If Island and April 2022 for Grand Rouveau Island. The complete list of variables collected is provided in Table 1. The number of geckos was characterized by our response variable called *max_num* (see Table 1) which corresponds to the maximum number of individuals observed in the retreat-site since the beginning of the monitoring (2014 for Grand Rouveau Island and 2016 for If Island). On average, each ARS was surveyed 14.6 times (SD = 3.4), out of a maximum possible number of 19 between July 2014 and April 2022. The survey of an ARS is done by moving the ARS inside a box before opening it, in such a way that no individual can be missed or escape.

We verified that our response variable *max_num* did not depend on the number of sampling periods, used as a proxy for the time since installation of the ARS: Spearman's rank correlation coefficient, rho = -0.08, P = 0.56. Our data set included candidate variables measured within a radius of 5 or 10 meters around the site, variables describing the environmental conditions at the ARS itself, including classes of exposure to the major winds of the region (variables *N_WNW* and *ENE_ESE*) as well as sun exposure in classes at different orientations (*E*, *SE*, *S*, *SW*, and *W*) and cumulatively (*Sun_pc*), as well as the distance in meters from the retreat-site to the sea (*Sea_d*) and to the nearest ARS (*Arti*_g), with the latter two measured in QGIS 3.16 (QGIS Development Team, 2022). Variables concerning wind and sun exposure are categorical (with 3 levels), whereas variables such as *Sun_pc*, *Sea_d* or *Arti_g* are numerical. For a complete description of variables in our data set, refer to Table 1.

Field protocol for Capture-Mark-Recapture and retreat-site occupancy

A protocol of Capture-Mark-Recapture (CMR) was carried out on the island of Grand Rouveau. All individuals of three ARS (#22, #23 and #37, see Fig. 1 for location) were captured during the daytime monitoring of April 14, 2022. These ARS were selected because they were adjacent to each other and held the highest number of geckos for the island. Each gecko was individually marked using water and pigment markers (edding 4040 CREATIVE marker) with a unique combination of leg marks (see Fig. S1 for an example of marked individuals). Because there is no known or suspected predator of the European Leaf-toad Gecko on either island, an increased predation risk due to colorful marking was not perceived as a significant issue for this study. For each marked individual, we recorded the site of capture as well as its weight and age class (see Table 2 for complete variable description). Sex was not recorded as it could not be safely determined for sub-adults and juveniles based on morphological features. All individuals were then returned to their ARS. These three ARS were surveyed daily for the next 4 days, allowing us to record the presence history of the marked individuals during these 4 recapture events. In addition, nighttime and daytime temperatures were obtained from the nearest weather station (at Cape Cépet, ~15 km from Grand Rouveau) using the website www.meteociel.fr. New arrivals during the protocol (n = 3 individuals) were processed in the same way and included in the study.

Statistical analyses for environmental variables and numbers within retreat-sites

All statistical analyses were performed with R 4.0.4 (R Core Team, 2021). The relationship between the maximum number of individuals observed in each ARS (our response variable *max_num*, see Table 1) and our set of candidate environmental variables was modeled using Generalized Linear Models and a negative binomial distribution (function *glm.nb* in R's MASS package). This distribution is suitable for over-dispersed discrete variables including many low-count data and a few high counts that stretch the distribution (Zuur et al., 2009). To reduce the risk of overfitting with our large, full set of 39 explanatory variables (for 60 data points), we used a conservative forward model selection approach as follows. First, starting from the (constant) null model, an explanatory variable was entered into the best model only if it resulted in a drop in the second-order AIC criterion (Akaike Information Criterion: Akaike, 1974),

Table 1. Description of environmental variables and gecko numbers within artificial retreat-sites (ARS). Legend: *max_num* is the response variable; explanatory variables calculated within a radius of 5 or 10 meters from the retreat-sites are identified at the end of the description with the notation '(5m)' and '(10m)', respectively; the variable G*en_sp* is actually referring to a set of 12 variables based on 12 plant species for which we determined whether they were dominant within the 5-meter radius of the ARS (value = 1) or not (0), such as *Atr.sp* referring to small bushes of *Atriplex sp.*, and *Hor.mur* to the grass *Hordeum murinum*; for the variable *Stru* (soil structure): 0 = a single substrate; 1: heterogeneous, with large substrate patches; 2: heterogeneous, with a mosaic of small patches; for sun exposure at different orientations (variables *E* to *W*): 0 = entirely shaded for this orientation, 1 = partially shaded for this orientation, 2 = entirely exposed for this orientation; for wind exposure of the retreat-site for the two major winds in this region (variables *N_WNW* and *ENE_ESE*): 0 = entirely protected from the wind; 1 = partially protected from the wind, 2 = entirely exposed to the wind. For each variable, its type (Num = numerical; Cat = categorical) and the values that it can take are presented as well. See text for details.

Variable	Description	Type	Values/Range
max_num	Maximum number of geckos observed in the ARS	Num	0 to x
Site	Island on which the ARS is located	Cat	If, Rouveau
Sea_d	Distance from the sea (in meters)	Num	0 to x
v0_5	Cover of the vegetation layer from 0 to 5 cm (5 m)	Num	0 to 100 %
v5_15	Cover of the vegetation layer from 5 to 15 cm (5 m)	Num	0 to 100 %
v15_40	Cover of the vegetation layer from 15 to 40 cm (5 m)	Num	0 to 100 %
v40	Cover of the vegetation layer above 40 cm (5 m)	Num	0 to 100 %
Goel	Number of yellow-legged gull (*Larus michahellis*) nests (5 m)	Num	0 to x
Pod.sp	Known presence of *Podarcis* lizards (*P. siculus* on If, *P. muralis* on Rouveau) on the ARS	Cat	0 / 1
Gen.sp	For 12 plant species, significant presence or not (5 m)	Cat	0/1
Rock	Cover of rocky substrate (5 m)	Num	0 to 100 %
Earth	Cover of other non-sandy and non-rocky natural substrate (5 m)	Num	0 to 100 %
Stone	Cover of construction stone (5 m)	Num	0 to 100 %
Sand	Cover of sandy substrate (5 m)	Num	0 to 100 %
Conc	Cover of concrete substrate (5 m)	Num	0 to 100 %
Stru	Soil structure (see legend for details)	Cat	0,1,2
Nat_g	Presence of natural (rocky) habitat for the species (10 m)	Cat	0 / 1
Arti_g	Distance from the nearest ARS (in meters)	Num	0 to x
Ant_g	Presence of anthropogenic habitat (10 m)	Cat	0 / 1
Mov	ARS moved since the beginning of the monitoring	Cat	0 / 1
Rep	ARS repaired since the beginning of the monitoring	Cat	0 / 1
E	Sun exposure of the ARS to the east	Cat	0,1,2
SE	Sun exposure of the ARS to the south-east	Cat	0,1,2
S	Sun exposure of the ARS to the south	Cat	0,1,2
SW	Sun exposure of the ARS to the south-west	Cat	0,1,2
W	Sun exposure of the ARS to the west	Cat	0,1,2
Sun_pc	Total sun exposure (sum of each direction of exposure)	Num	0 to 10
N_WNW	Wind exposure of the retreat-site to the 'Mistral' (dominant wind)	Cat	0,1,2
ENE_ESE	Wind exposure to the second major wind in the region	Cat	0,1,2

calculated using the AICc function in R's MuMIn package, and if the corresponding regression coefficient was significant at the 5% level (in the case of a factor with multiple levels, at least one contrast needed to be significant). In addition, to reduce the risk of detecting spurious correlations due to increased type I errors, we limited the number of interactions tested to seven potentially meaningful pairwise interactions among the set of variables retained after forward selection, excluding interactions between sun or wind exposure and the presence of a particular grass species. None of the seven tested interactions were significant (not shown) and thus none were included in the best model.

To assess model validity, we first used the *qresid* function of R's statmod package to obtain randomized quantile residuals which are normally distributed (Dunn and Smyth, 2018). Next, normality of the residuals was tested using a Shapiro-Wilk test (Shapiro and Wilk, 1965), the homogeneity assumption was tested using Levene's test (Levene, 1960) for each categorical variable included in the best model, independence was assessed by looking at the spatial distribution of the residuals, and

Table 2. Variables description for Capture-Mark-Recapture and ARS occupancy. *Pres* was our response variable, *Ind* was used as a random factor, and all other variables were used as candidate explanatory (fixed effect) variables. For each variable, its type (Num = numerical; Cat = categorical) and the values that it can take are presented.

Variable	Description	Type	Values / Range
Ind	Unique identifier of the individual	Cat	1 to 77
Pres	Presence or absence of the individual in the ARS	Cat	0/1
Pres-1	Presence or absence of the individual in the ARS on the previous day	Cat	0/1
Site	ARS where the individual was captured and returned	Cat	22, 23, 37
Weight	Weight (g) of the individual when first captured	Num	0.31 to 2.66
Age_class	Age class of the individual, based on morphological features. Adults and subadults could not be safely distinguished and thus they are grouped together.	Cat	Adult or juvenile
Night_temp	Temperature, in °C, of the night before the daily survey, as measured at 3 AM on the same day (data taken from www.meteociel.fr)	Num	9 to 20
Day_temp	Temperature, in °C, at 1 PM the day of the survey (www.meteociel.fr)	Num	17 to 22
D_site	Number of consecutive days of ARS disturbance	Num	1 to 5

R's *density* function was used to compare the distribution of observed *max_num* with those predicted by the model.

Statistical analyses for CMR and retreat-site occupancy

Because detection probability was always one (the survey method allows the detection of the total number of individuals present in an ARS) and we did not detect any movement between ARS, we did not attempt to estimate transition probabilities (using a multi-state CMR model), as initially planned; instead, we focused on individual occupancy, the probability for a gecko to be found at its shelter-site on any given night. To account for repeated measures of our binary response variable (*Pres*) over time, the influence of potential explanatory variables was assessed using Generalized Linear Mixed Models (GLMM) with the function *glmmTMB* in R's glmmTMB package, using a Bernoulli distribution and a logit transformation. The candidate variables included *Pres-1,* the presence or absence of the individual in the ARS on the previous day, to account for possible temporal autocorrelation. Only recapture data were analyzed in order to have *Pres-1* value available for every *Pres* value. The complete list of variables is provided in Table 2.

The selection of the optimal model explaining ARS daily use (occupancy) was performed using the top-down strategy which is adapted to mixed models (Zuur et al., 2009). To identify the random part of the model, we used REML estimators (REstricted Maximum Likelihood; see Bolker et al., 2009, *Zuur* et al., 2009) to compare four models with identical fixed effect structure (an additive model including all possible fixed effects factors) but different random effect structure, namely a different random intercept for each individual (1|Ind), a random slope for each individual that depended on the number of days of ARS disturbance (0 + D_site|Ind), as well as random intercepts and slopes that were either correlated (1 + D_site|Ind) or uncorrelated (1|Ind) + (0 + D_site|Ind). The optimal structure of the random component was selected using the AICc criterion (Akaike Information Criterion corrected for small numbers, Bolker et al., 2009, Hervé, 2014). The optimal fixed structure was then determined using forward model selection and Maximum Likelihood (ML) estimators, which are more relevant in the case of model comparisons with different fixed effects (Pinheiro and Bates, 2004, Millar, 2011). Although forward model selection did not include any interaction, we tested *a posteriori* whether the inclusion of potentially relevant pairwise interactions resulted in lower AICc; the model without any interaction was retained as the best model (not shown). Finally, the best model was fitted using REML estimators to get a more reliable estimate of the different parameters (Zuur et al., 2009).

To assess model validity, we used an approach adapted to GLMM models implemented in R's DHARMa package (Hartig, 2022). Instead of conventional residuals, the method uses simulated scaled residuals (obtained with the *simulateResiduals* function) that are bounded between 0 and 1. If the model has been specified correctly, a uniform (flat) distribution is expected for the scaled residuals (Hartig, 2022). We first tested whether the overall distribution, the number of outliers, and the dispersion of the scaled residuals conformed to expectations using the functions *testUniformity*, *testOutliers* and *testDispersion*, respectively. In addition, for all fixed-effect predictors included in the best model (after transforming numerical variables such as *Night_temp* into categorical predictors) we used the *testCategorical* function to check for within-group deviations from uniformity and between-group deviation from homogeneity.

RESULTS

Environmental variables and numbers within retreat-sites

The best model included the variables *N_WNW*, *S*, *SW*, *Atr.sp*, and *Hor.mur* (Table 1 for variable description, Table 3, Fig. 3). A site completely exposed to the wind from N to WNW (level = '2' of *N_WNW*) held fewer individuals than a site partially or completely protected from the wind for this orientation (levels = '1' and '0', respectively; both *P* < 0.001, not shown), while moderate or partial exposure to N to WNW winds (level = '1') yielded higher values of *max_num* than any other situation (although the difference between levels '1' and '0' was not significant: Table 3). In addition, sites partially or completely exposed to the southern sun (levels '1' and '2' of variable *S*) had significantly larger numbers of European Leaf-toed Geckos than sites in the shade for this orientation (level = '0', both *P* < 0.03), while, moderate or partial sun exposure to the SW (level = '1' of variable *SW*) yielded significantly higher values of *max_num* than either a lack of or complete sun exposure for this orientation (levels '0' and '2' of variable *SW*, both *P* < 0.001, not shown). Finally, retreat sites that were surrounded by vegetation dominated by the grass *Hordeum murinum* or small bushes of *Atriplex* sp. held significantly larger numbers of European Leaf-toed Geckos than the sites which did not (Table 3).

Table 3. Coefficients and their Standard Error (SE) for the best model explaining the maximum numbers of European Leaf-toed Gecko observed within the ARS. For each categorical variable (*N-WNW*, *S*, and *SW*), the coefficients reflect the effect of a given level compared to the effect of level '0' that is included in the intercept (e.g., 0.15 is the predicted difference, on the log scale, between gecko number when the ARS is partially protected from the wind [N-WNW = 1] and when it is entirely protected from the wind [N-WNW = 0]); significance levels: '***': P < 0.001, '**': P < 0.01, '*': P < 0.05). See Table 1 for variable description.

Variable / Level	Coefficient	SE	z	P-value	
(Intercept)	1.10	0.19	5.62	1.86e-08	***
N-WNW / 1	0.15	0.25	0.58	0.56	
N-WNW / 2	-1.52	0.27	-5.64	1.71e-08	***
S / 1	0.83	0.29	2.82	0.005	**
S / 2	0.71	0.32	2.20	0.028	*
SW / 1	1.37	0.33	4.11	3.88e-05	***
SW / 2	-0.39	0.31	-1.25	0.21	
Atr.sp / 1	1.89	0.48	3.93	8.58e-05	***
Hor.mur / 1	0.88	0.27	3.20	0.001	**

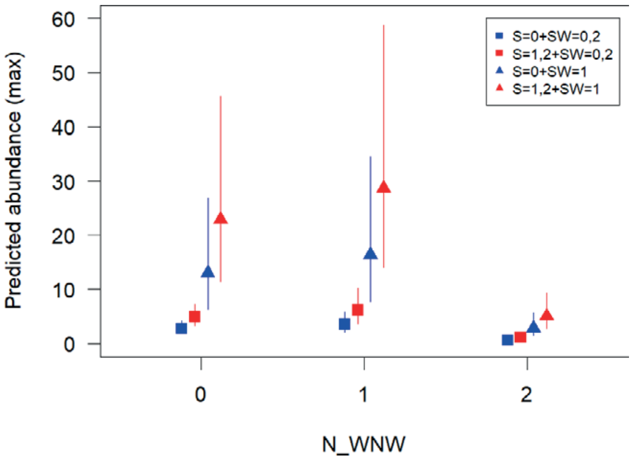

Fig. 3. Model-based predictions, including 95% confidence intervals, for the maximum number of geckos found in artificial retreat-sites (*max_num*) as a function of different parameter combinations; the predictions are based on the best model but after grouping modalities with similar effects to reduce the number of parameter combinations and provide greater clarity: S = 1,2 corresponds to S = 1 or S = 2, SW = 0,2 corresponds to SW=0 or SW=2. Atr.sp and Hor.mur were fixed to 0. See Table 1 for the description of variables.

The hypothesis that quantile residuals followed a normal distribution could not be rejected (Shapiro test, W = 0.99, P = 0.79). The null hypothesis that the variances did not differ among the different levels of each explanatory variable could not be rejected for any of the five explanatory variables in the best model (Levene's test: all *P* > 0.05). However, the existence of spatial autocorrelation in the residuals, notably at Grand Rouveau Island, suggests that the independence hypothesis is not respected (Fig. S2). We thus used the *glmmfields* function in R's glmmfields package to run the same (best) model while accounting for spatial autocorrelation (Anderson and Ward, 2019). The coefficients obtained were very similar to those obtained previously (not shown), suggesting that our results are also robust to this violation, although it should be noted that the contrast between the levels '0' and '2' of the variable *S* was no longer significant at the 5% threshold in the spatial model (estimate = 0.70, 95 %, CI = [-0.06; 1.47]). Finally, although the distribution of *y*-values predicted by the model resembles reality, the best model tends to underestimate the highest observed values (Fig. S3).

CMR and retreat-site occupancy

The total dataset of the CMR protocol consisted of 203 captures (first captures and recaptures) of 77 unique individuals, with only 3 individuals being new arrivals (not captured during the first day but captured during one of the four days of recapture); 19 individuals were captured only during the first day, and not during any of the four days of recapture. On the first day, the ARS #22, #23 and #37, selected for the CMR protocol, were respectively occupied by 17, 36 and 21 unique individuals.

The best model identified by the top-down approach suggested that the probability of presence of geckos in their ARS (occupancy) was greater when the individual was present the previous day as well as for juveniles as compared to adults and subadults but was negatively related to the temperature of the previous night and the number of days of disturbance (Table 4 and Fig. 4). In addition, the random effect structure selected by AICc (0 + D_site | Ind; Akaike weight = 0.466) suggested the existence of between-individual variation in the response to disturbance.

The hypothesis that the distribution of the scaled residuals was uniform could not be rejected (one-sample Kolmogorov-Smirnov test: D = 0.037, *P* = 0.80) and no outlier was detected (DHARMa bootstrapped outlier test, *P* = 1). However, the dispersion of the residuals was lower than expected (dispersion = 0.728, *P* < 0.001), which resulted in a loss of statistical power (as opposed to overdispersion which results in inflated type I errors: Hartig, 2022). Such reduced power could explain, at least in part, the fact that some of the variables included in the final model (after selection by AICc) were not significant at the 5% level (see Table 4). For each of the fixed effects but one, we could not reject the null hypotheses of (within-group) uniform distribution and (between-group) homogeneity (one-sample Kolmogorov-Smirnov and Levene's tests, respectively: all *P* > 0.37, except *Pres-1* for which all *P* < 0.01).

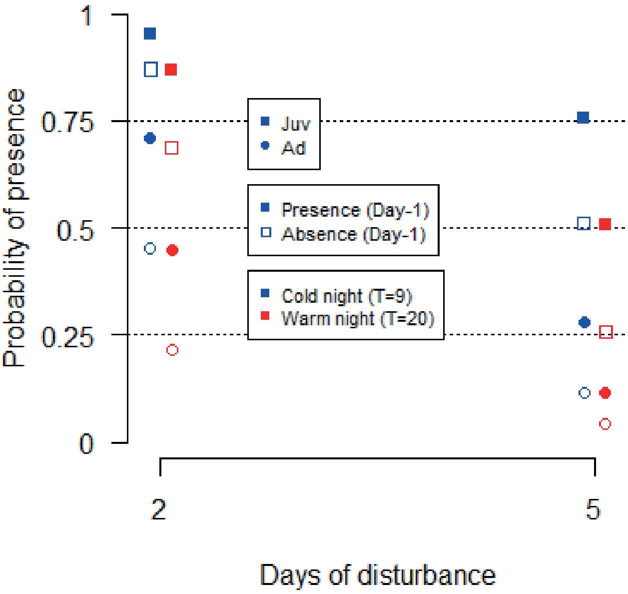

Fig. 4. Probability of presence (variable *Pres*) of a gecko in its ARS, as estimated from the best model's fixed effect coefficients and the inverse logit function, as a function of: (i) the number of days of disturbance (variable *D_site*; *x*-axis); we only show estimates for the two most extreme values, namely 2 and 5 days of disturbance; (ii) the individual's age class (Adult/Subadult or Juvenile, represented by circles or squares, resp.); (iii) presence or absence of the individual at the ARS on the previous day (filled or empty symbols, resp.); and (iv) the previous night's temperature; only the two most extremes temperatures in the data set are shown: T = 9 °C, shown in blue, and T = 20 °C, shown in red.

Because *Pres-1* was the least significant variable included in the best model (Table 4: z = 1.29, *P* = 0.20), we investigated the influence of *Pres-1* by re-running all analyses after dropping it, yielding an alternative 'best model' called bm2. The difference in AICc between the best model and bm2 was less than 2 (ΔAICc = 1.9, Akaike weight for bm2 = 0.28). After dropping *Pres-1*, all explanatory variables retained the sign of their coefficient, but all became significant at the 5% level (compare with Table 4; *Night_temp*: Est = -0.10, z = -2.13, *P* = 0.03; *Age_class*: Est = 3.00, z = 2.02, *P* = 0.04; *D_site*: Est = -1.14, z = -4.73, *P* < 0.001), and none of the hypotheses examining the validity of the model could be rejected anymore (not shown). This suggested that our conclusions regarding the influence of fixed-effect variables are robust to the violations found when *Pres-1* is included.

Table 4. Coefficients and their Standard Error (SE) on the logit scale for the best model explaining the probability of presence within the artificial retreat-site for an individual of European Leaf-toed Gecko; significance levels: '*': *P* <0.05, '.': = *P* <0.1. See Table 2 for variable description.

Variable / Level	Coefficient	SE	z	P-value	
(Intercept)	1.953	1.675	1.166	0.244	
Pres-1	1.090	0.847	1.287	0.198	
Night_temp	-0.101	0.044	-2.277	0.023	*
Age_class / Juvenile	2.088	1.153	1.811	0.070	.
D_site	-0.618	0.371	-1.665	0.096	.

DISCUSSION

Importance of the thermal properties of the retreat site

The first objective of this study was to determine the environmental variables affecting the number of European Leaf-toed Gecko present in the artificial retreat-sites. Consistent with studies in other reptiles (e.g., Huey, 1982), we found that three of the variables included in the best model relate to exposure to the wind or sun, suggesting a strong influence of the thermal properties of the retreat-sites (Table 3; Discussion below). Indeed, for nocturnal poikilotherms that do not engage in direct insolation and spend the day in their retreat-sites such as the European Leaf-toed Gecko, the Turkish Gecko *Hemidactylus turcicus* (Hitchcock and McBrayer, 2006), the Broad-headed Snake *Hoplocephalus bungaroides* (Webb and Shine, 1998a), and the Marbled Southern Gecko *Christinus marmoratus* (Kearney and Predavec, 2000), thermoregulation depends on the choice of a retreat-site and the position occupied within that site (Huey, 1982, Webb and Shine, 1998a, Kearney and Predavec, 2000). Within their retreat-site, European Leaf-toed Geckos manage to maintain their body temperature above the atmospheric temperature even when inactive (Delaugerre, 1984).

Complex combined effect of exposure to the sun and wind on retreat site selection

As may have been anticipated, sites partially or completely exposed to the southern sun had more European Leaf-toed Geckos than sites in the shade for this orientation (Fig. 3). Interestingly, however, such difference was minimal for retreat-sites that were completely exposed to north to west-northwest winds (Fig. 3), locally called the 'mistral', and characterized by strong, cold, and dry winds (Guenard et al., 2005). Overall, sites completely exposed to the mistral held fewer geckos than other sites (see Results and Fig. 3). This suggests the mistral is a limiting factor for the European Leaf-toed Gecko, likely because exposure to strong winds, especially in open habitats, leads to a reduction of temperature for the substrate and reptiles' body through convection (Logan et al., 2015, Ortega et al., 2017). While ARS made of rocks and tiles can provide shelter from desiccation, protecting European Leaf-toed Geckos from direct wind and maintaining some moisture (Edgar et al., 2010), ARS should not be immune to wind-induced cooling.

Additional findings suggest that the sun and wind exposure act in combination to determine ARS quality for European Leaf-toed Gecko, although future studies directly investigating the thermal properties of ARS and the temperature of the geckos will be necessary to fully address this question. In the present study, more geckos were found in ARS that were partially exposed to the mistral and partially exposed to the southwestern sun, as compared to ARS that were either sheltered from or completely exposed to the mistral and southwestern sun (Results and Fig. 3). These results suggest that overheating is also a concern, and that only a narrow fraction of all possible environmental conditions provide optimal ARS conditions. Because of thermal inertia of the rock and slow heat absorption, nocturnal reptiles in retreat-sites tend to reach their optimal temperature in the afternoon (Webb and Shine, 1998a, Kearney, 2002). A complete absence of cooling provided by the mistral or a strong exposure to afternoon and evening sunshine could thus lead to temperatures beyond those optimal or even tolerable for the species (Walls, 1983, Kearney, 2002, Edgar et al., 2010). This may be particularly true during hot weather, raising the possibility of seasonal variation in the thermal properties of ARS. For instance, in summer the nocturnal gecko *Christinus marmoratus* prefers high-shaded rocks to medium and low-shaded ones and better tolerates low-shaded rocks when they are thick (Kearney, 2002). Anecdotal data suggest that more European Leaf-toed Geckos may be found in spring and fall, as compared to summer, in ARS of both Grand Rouveau and If islands (pers. obs), although future work will be needed to better understand possible seasonal variation in their patterns of activities.

Additional effect of surrounding vegetation on retreat site selection

In addition to variables related to sun and wind exposure, the best model also included the presence or absence of two plant groups: the bushy species of the genus *Atriplex* and the grass species *Hordeum murinum.* This result about *Atriplex sp.* is consistent with recent papers highlighting the importance of vegetated habitats, and especially woody habitat, for this gecko long-perceived as solely associated with rocky environments. Salvi *et al.* (2023) described observations and adaptations consistent with an agile arboreal locomotion and Deso *et al.* (2023) described the arboreal behavior of *E. europaea* on the alien *Eucalyptus sp.* species on two islands. It is worth noting, however, that *Atriplex sp*. were dominant (see Table 1 for definition) in two ARS only in our samples, suggesting that the inclusion of this variable in our best model might be an artifact of such a small sample size. Conversely, we are not aware of any study establishing a relationship between *E. europaea* and *Hordeum marinum* or any other grass species. Patches of *Hordeum* might shelter arthropods and thus provide a food supply for the European Leaf-toed Gecko, a hypothesis that requires further testing.

Model limitation for retreat site selection

The best model appears insufficient to precisely predict gecko numbers in the most favored retreat-sites.

First, the uncertainty around the estimates, as quantified by the amplitude of the confidence intervals, strongly increases when the estimated densities exceed approximately 15 individuals (Fig. 3). Second, the best model appears to slightly underestimate the densities in the best retreat-sites (Fig. S3). Although it is always possible that we missed an important environmental predictor (despite our large data set: Table 1), the small difference between observed and predicted values could be related to the gregarious behavior of the European Leaf-toed Gecko, whose individuals tend to group together within natural or artificial retreats (e.g., up to 35 individuals observed under the same ARS on If; see also Delaugerre and Cheylan, 1992, Delaugerre and Corti, 2020). If this is true, we may expect the difference between any two suitable retreat-sites to reflect local population size, taken as a proxy of the number of potential colonizers, rather than the thermal properties of the retreat-site itself. The fact that three adjacent sites at Grand Rouveau held the highest number of geckos for this island together with the presence of residual spatial autocorrelation (Fig. S2) may be consistent with that view, although future work will be needed to explore this hypothesis.

Effect of disturbance on retreat-site occupancy

Our daily surveys required a complete dismantling (and rebuilding) of the retreat-sites as well as the handling of individual geckos for identification. As may have been anticipated, such a disturbance was associated with a reduced probability of presence on the following day that was accounted for in the estimation of the other model parameters (Table 4; see also Fig. 4 for a comparison of two versus five days of disturbance). Since the CMR protocol was localized in space (3 artificial retreat-sites concerned out of 33 on the island) and time (5 days) and geckos can also find many suitable natural retreat-sites in the surrounding habitats, we do not expect any impact on the conservation status of the European Leaf-toed Gecko in Grand Rouveau Island.

Lack of movement between retreat-sites

We did not observe any movement between the three retreat-sites monitored. Every individual that was captured in one of our three retreat-sites either went missing for the rest of the study or was captured at least once more at the same site. Although the three sites are relatively far apart (distance: 21-41 meters), dispersal events can occur over more than 50 meters of rocky line in the European Leaf-toed Gecko (Delaugerre and Corti 2020). Similar dispersal distances were estimated in a slightly larger species, the Turkish Gecko *Hemidactylus turcicus*. Paulissen et al. (2013) found that some adults of Turkish Gecko exhibited movements up to 67 m, although the average movement when the individuals were recaptured after less than 30 days was only 5 m. Accordingly, besides site fidelity, several factors may explain a lack of movement between sites and future studies will be needed to assess their relative importance. First, the duration of the study may have been too short to detect movements between retreat-sites (only 4 days after the first capture). Second, movements may have occurred towards additional adjacent retreat-sites that have not been surveyed (see Fig. 1). Third, such movements between retreat-sites may be more likely in summer, as opposed to early in the season (in April), as higher temperatures may permit the species to wander away from the rocky environment and move through the vegetation (Delaugerre and Cheylan, 1992). To assess the possibility of movements between ARS, a longer CMR protocol using photo-identification could be valuable (see Monnet et al., 2022). This method, which is currently being tested for future studies, would have the advantages of avoiding daily manipulation and reducing the disturbance and the uncertainty due to shedding that can result in marking loss in long-term studies. Implementing it across an entire island could also enable us to estimate the abundance of the species on Grand Rouveau or If islands.

Temporal autocorrelation on retreat-site occupancy: retreat-site fidelity or lack of nocturnal activity?

As expected, the probability of an individual being present in the ARS on any given day was greater when that individual was already present in this ARS the previous day (e.g., Fig. 4). This could be explained in two non-mutually exclusive ways. First, individuals may not be active every night and therefore can be present several days in a row. Testing this hypothesis may be possible via video recording of artificial retreat-sites in order to follow the exits and re-entries of previously marked individuals over several nights (Deso & Reynier, 2024). Second, active individuals may tend to return to the same retreat-site from one night to the next (site fidelity). Other species of geckos tend to be faithful to their retreat-site, as demonstrated in *Hoplodactylus chrysosireicus*, *H. duvaucelii* (Flannagan, 2000), and *Gonatodes vittatus* (Quesnel et al., 2002).

Influence of outdoor temperatures on retreat-site occupancy

The presence within the retreat-sites was negatively related to the temperature of the previous night (Fig. 4), which could be explained in several non-mutually exclusive ways. First, prey activity may be reduced during cold nights, reducing the incentive to leave the ARS (e.g., Lei and Booth, 2014 and references therein). Second, a decreased metabolic rate in response to cold temperatures could also lessen the incentive to forage and feed. In the Asian House Gecko *Hemidactylus frenatus*, the resting and post-feeding metabolic rates decreased with a decrease in temperature, and even in laboratory conditions with available living food, *H. frenatus* all but ceased its feeding activity below 17 °C, probably because their body temperature became too low to capture and digest prey efficiently (Lei and Booth, 2014). Third, European Leaf-toed Geckos may have a greater reliance on ARS for thermoregulation purposes when temperatures are lower. In agreement with that view, active individuals of the nocturnal Cap Verde Wall Gecko *Tarentola substituta* experienced significantly lower body temperature than inactive ones, and the body temperature of active geckos was correlated to air and soil temperatures, while the body temperature of inactive individuals was correlated to refuge temperature (Vasconcelos et al., 2012). Hence, geckos staying inside the ARS at night may benefit from its residual heat and conserve higher body temperatures. Fourth, individual geckos may be able to cover larger distances when temperatures are higher, allowing individuals to wander further away from their ARS; which, in turn, could give them the possibility, or force them, to identify and use a distinct retreat-site. Supporting the view that warm nights favor extended foraging opportunities, the Tree Dtella *Gehyra variegata* and the Eastern Stone Gecko *Diplodactylus vittatus* had longer spans of activity on hot nights (Bustard, 1967, Bustard, 1968), and the Tokay gecko *Gekko gecko* as well as the Gold Dust Day Gecko *Phelsuma laticauda* were significantly more mobile when temperatures were warmer (Ringenwald et al., 2021, Wehsener, 2019, respectively).

Difference between age classes on retreat-site occupancy

Juveniles appear to be more faithful to, or dependent on, artificial retreat-sites than older individuals (Fig. 4). A greater use of artificial retreat-sites by juveniles has also been observed in the gecko *Oedura lesueurii*, for which 82% of the individuals occupying artificial retreat-sites were juveniles (Webb and Shine, 2000). Future studies will be needed to understand this difference. For instance, adult and juvenile geckos may differ in their social behavior (Webb and Shine, 2000), in their thermoregulatory behavior or performance (but see Aparicio Ramirez et al., 2021, for a counter example in Crested Gecko *Correlophus ciliatus*), and in their response to predation risk by native or invasive predators such as the Black Rat *Rattus rattus*. In the French Mediterranean Bagaud Island, a successful eradication of the Black Rat was followed by an increase of observations of European Leaf-toed Geckos outside shelters for both juveniles and adults together with a significant increase in the overall number of juveniles (but not adults), suggesting the former age class may be the one most impacted by predation (Krebs et al., 2015). The impact of Black Rat on European Leaf-toed Gecko populations could be assessed by contrasting age-specific survival rates and population trajectories in islands with and without Black Rat while controlling for between-island differences in environmental conditions and gecko density. Partial rat control on a single island, which is considered on the island of Gargalo, could provide a suitable alternative.

ACKNOWLEDGEMENTS

The authors wish to thank the PIM Initiative (Initiative pour les Petites Îles de Méditerranée) for their constant support to this project via their program « îles sentinelles » and Michel-Jean Delaugerre for his feedback that helped improve an earlier version of this manuscript. The handling and the capture of the individuals were carried out under the permits DI-2018-130 and DI-2019-002 of the national park of the Calanques for the island of If and under the permit of May 13, 2020 granted by the prefect of the Var for the island of Grand Rouveau.

SUPPLEMENTARY MATERIAL

Supplementary material associated with this article can be found at <http://www-9.unipv.it/webshi/appendix/index.html> manuscript number 14527

REFERENCES

AGIR écologique (2016): Restauration du mur d'escarpe du Château d'If (Marseille, 13). Dossier scientifique accompagnant la demande de dérogation pour la capture, l'enlèvement, la destruction, la perturbation intentionnelle de spécimens de Phyllodactyle d'Europe, *Euleptes europaea* (Gené, 1839) (Rapport d'étude). Centre des Monuments Nationaux.

Akaike, H. (1974): A new look at the statistical model identification. IEEE Trans. Automat. Contr. **19**: 716-723.

Anderson, S. C., Ward, E. J. (2019): Black swans in space: modeling spatiotemporal processes with extremes. Ecology **100**: e02403.

Aparicio Ramirez, A., Perez, K., Telemeco, R. S. (2021): Thermoregulation and thermal performance of crested geckos (*Correlophus ciliatus*) suggest an extended optimality hypothesis for the evolution of thermoregulatory set-points. J. Exp. Zool. Part A **335**: 86-95.

Arnold, N., Ovenden, D. (2014): Le guide herpéto: 228 amphibiens et reptiles d'Europe. Delachaux et Niestlé.

Bellard, C., Leclerc, C., Courchamp, F. (2014): Impact of sea level rise on the 10 insular biodiversity hotspots: Sea level rise and insular hotspots. Global Ecol. Biogeog. **23**: 203-212.

Blondel, J., Cheylan, M. (2008): Lost species and animal survivors. In: Mediterranean Islands, pp. 41-45. Arnold, C., Ed, Survival Books, London

Blondel, J., Aronson, J., Bodiou, J. Y., Boeuf, G. (2010): The Mediterranean region: biological diversity in space and time. Oxford University Press Inc., New York

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.-S.S. (2009): Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol. Evol. **24**: 127-135.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M. (2017): glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal **9**: 378-400.

Bustard, H.R. (1967): Activity cycle and thermoregulation in the Australian gecko *Gehyra variegata*. Copeia **1967**: 753-758.

Bustard, H.R. (1968): Temperature dependent activity in the Australian gecko *Diplodactylus vittatus*. Copeia **1968**: 606-612.

Cheylan, M., Poitevin, F. (1994): Conservazione di rettili e anfibi. In: La gestione degli ambienti costieri e insulari del Mediterraneo, pp. 275-336. Monballiu,X., Torre, A., Eds, Edizioni del Sole, Alghero (IT).

Cheylan, M., Rivière, V., Cheylan, A. (2018): Évaluation d'une méthode de suivi à long terme du gecko Euleptes europaea sur l'île du Grand Rouveau (archipel des Embiez, Var, France). Revue d'Écologie, 2018, **73**: 526-536.

Corti, C., Cecchi, L., Thévenet, M., Delaugerre, M.J. (2022): Reptiles and micro-insular environments of the Tuscan Archipelago (Italy). Naturalista sicil. **46**: 111-116.

Couturier, T., Debize, E., Le Mire Pecheux, L., Geoffroy, D., Moussay, C., Jailloux, A., Besnard, A. (2020): Suivi des tendances de l'occupation de l'espace par une espèce rare et cryptique: l'Eulepte d'Europe *Euleptes europaea* dans les Parcs nationaux des Calanques et de Port-Cros. (Rapport méthodologique, protocole version 1). Coopération OFB-CEFE.

Cox, N., Chanson, J., Stuart, S. (2006): The Status and Distribution of Reptiles and Amphibians of the Mediterranean Basin. IUCN, Gland, Switzerland and Cambridge, UK.

Croak, B.M., Pike, D.A., Webb, J.K., Shine, R. (2010): Using artificial rocks to restore nonrenewable shelter sites in human-degraded systems: colonization by fauna. Restor. Ecol. **18**: 428-438.

Dardun, J.Y. (2003): Problématiques de conservation du Phyllodatyle d'Europe *Euleptes europaea* sur les iles de Marseille (archipel du Frioul et de Riou). Unpublished doctoral dissertation. Université de Corse, Faculté des sciences et techniques.

Delaugerre, M.J. (1981a): Le point sur la répartition géographique de *Phyllodactylus europaeus* Gené. Bull. Soc. Herp. Fr. **18:** 14-16.

Delaugerre, M.J. (1981b): Sur l'histoire naturelle de *Phyllodactylus europaeus* Gené, 1838 (Gekkonidae Sauria Reptiles). Port-Cros: Etude d'une population naturelle. Trav. Sci. Parc Nat. Port-Cros **6**: 147-175.

Delaugerre, M.J. (1984): Sur l'écologie thermique des geckos *Phyllodactylus europaeus*, *Hemidactylus turcicus* et *Tarentola mauritanica* : rythmes d'activité, températures et activité, répartition altitudinale. Trav. sci. Parc Nat. Reg. Port-Cros **3**: 96–127.

Delaugerre M.J. (2002): Le Phyllodactyle d'Europe *Euleptes europaea* sur l'île de Port- Cros réflexion pour la mise au point d'un protocole de suivi des populations. Rapport Parc National de Port-Cros.

Delaugerre, M.J. (2003): Le phyllodactyle d'Europe sur l'ile de Port-Cros. Synthèse et mise à jour des carnets de terrains des recherches conduites entre 1975 et 1985. Parc National de Port-cros 24.

Delaugerre, M.J., Cheylan, M. (1992): Atlas de répartition des batraciens et reptiles de Corse.

Delaugerre, M.J., Corti, C. (2020): Tiny but "strong": the European Leaf-toed gecko, *Euleptes europaea*, a terrestrial vertebrate able to survive on tiny islets. Israel J. Ecol. Evol. **66**: 223-230.

Delaugerre M.J., Ouni, R., Nouira, S. (2011): Is the European Leaf-toed gecko *Euleptes europaea* also an African? Its occurrence on the Western Mediterranean landbrige islets and its extinction rate. Herpetol. Notes **4**: 127-137.

Delaugerre, M.J., Sacchi, R., Biaggini, M., Lo Cascio, P., Ouni, R., Corti, C. (2019): Coping with aliens: how a native gecko manages to persist on Mediterranean islands despite the Black rat? Acta Herpetol. **19**: 89–100.

Deso, G., Priol, P., Reynier, T., Renet, J. (2023): High occupancy of European leaf-toed gecko *Euleptes europaea* in two island stands of *Eucalyptus sp.*: tree selection, co-occurrence and habitat effect. bioRxiv 2023.02.08.527781.

Deso, G., Reynier, T. (2024). Construction of a refuge wall with crevices to protect European leaf-toed geckos *Euleptes europaea* and young Turkish geckos *Hemidactylus turcicus* on the Ile du Levant, France. Herpetol. Bull. **167**: 20-24.

Di Nicola, M.R., Colombo, M., Russo, F. (2022): First record of european leaf-toed gecko *Euleptes europaea* (Gené, 1839)(Squamata, Sphaerodactylidae) in Campania (Italy). Rivista del Museo Civico di Scienze Naturali "Enrico Caffi" **35**: 79-82.

Dunn, P.K., Smyth, G.K. (2018): Generalized Linear Models With Examples in R, Springer Texts in Statistics. Springer New York, New York, NY.

Edgar, P., Baker, J., Foster, J. (2010): Reptile habitat management handbook. Amphibian and Reptile Conservation, Bournemouth.

Escofier, B. (1979): Traitement simultané de variables qualitatives et quantitatives en analyse factorielle. Cahiers de l'analyse des données **4**: 137-146.

Flannagan, H.J. (2000): Conservation Biology of the goldstripe gecko (*Hoplodactylus chrysosireticus*) and interactions with Duvaucel' s gecko (*Hoplodactylus duvaucelii*) on Mana Island, Cook Strait, New Zealand. Unpublished doctoral dissertation. Massey University, Palmerston North, New Zealand.

Grillet, P., Cheylan, M., Thirion, J.M., Doré, F., Bonnet, X., Dauge, C., Chollet, S., Marchand, M. A. (2010): Rabbit burrows or artificial refuges are a critical habitat component for the threatened lizard *Timon lepidus* (Sauria, Lacertidae). Biodivers. Conserv. **19**: 2039-2051.

Gros-Désormeaux, J.-R. (2012): La biodiversité dans des territoires insulaires, approche théorique et perspectives de développement. Developpement durable.

Guenard, V., Drobinski, P., Caccia, J.-L., Campistron, B., Bench, B. (2005): An Observational Study of the Mesoscale Mistral Dynamics. Boundary-Layer Meteorol. **115**: 263-288.

Hartig, F. (2022): DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. cran.r-project .https://cran.r-project.org/web/packages/DHARMa/vignettes/DHARMa.html [*accessed on 20 May 2022*]

Hervé, M. (2014): Aide-mémoire de statistique appliquée à la biologie. Construire son étude et analyser les résultats à l'aide du logiciel R.

Hitchcock, M.A., McBrayer, L.D. (2006): Thermoregulation in nocturnal ecthotherms: seasonal and intraspecific variation in the Mediterranean gecko (*Hemidactylus turcicus*). J. Herpetol. **40**: 185-195.

Huey, R.B. (1982): Temperature, physiology, and the ecology of reptiles. In: Biology of the Reptilia, Vol 12, Physiology (C), pp. 25-91. Gans, C., Pough, F.H., Eds, Academic Press, London.

Hulme, P.E., Brundu, G., Camarda, I., Dalias, P., Lambdon, P., Lloret, F., Medail, F., Moragues, E., Suehs, C., Traveset, A., Troumbis, A., Vilà, M. (2008): Assessing the risks to Mediterranean islands ecosystems from alien plant introductions. In: Plant Invasions: Human Perception, Ecological Impact and Management, pp. 39-56. Tokarska-Guzik, B., Brock, J.H., Brundu, G., Child, L., Daehler, C.C., Pyšek, P., Eds, Backhuys Publishers, Leiden, The Netherlands.

Kassambara, A. (2017): Practical Guide To Principal Component Methods in R: PCA, M (CA), FAMD, MFA, HCPC, factoextra (Vol. 2). Sthda.com.

Kearney, M. (2002): Hot rocks and much-too-hot rocks: seasonal patterns of retreat-site selection by a nocturnal ectotherm. J. Thermal Biol. **27**: 205-218.

Kearney, M., Predavec, M. (2000): Do nocturnal ectotherms thermoregulate ? A study of the temperate gecko *Christinus marmoratus*. Ecology **81**: 2984-2996.

Krebs, E., Abba, A., Gillet, P., Eudeline, R., Gauthier, J., Le Quilliec, P., Lorvelec, O., Martinerie, G., Vidal, E., Buisson, E. (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). Revue d'Ecologie, Terre et Vie **70**: 99-109.

Lefebvre, G., Redmond, L., Germain, C., Palazzi, E., Terzago, S., Willm, L., Poulin, B. (2019): Predicting the vulnerability of seasonally-flooded wetlands to climate change across the Mediterranean Basin. Sci. Total Environ. **692**: 546-555.

Lei, J., Booth, D.T. (2014): Temperature, field activity and post-feeding metabolic response in the Asian house gecko, *Hemidactylus frenatus*. J. Thermal Biol. **45**: 175-180.

Levene, H. (1960). Test of homogeneity of variances. In: Contributions to probability and statistics: Essays in honor of Harold Hotelling, pp. 278-292. Olkin, I., Ghurye, S.G., Hoeffding, W., Madow, W.G., Mann, H.B., Eds, Stanford University Press, Palo Alto (USA).

Logan, M.L., Fernandez, S.G., Calsbeek, R. (2015): Abiotic constraints on the activity of tropical lizards. Funct. Ecol. **29**: 694-700.

Marchand, M. A., Roy, C., Renet, J., Delauge, J., Meyer, D., Hayot, C. (2017): Liste rouge régionale des amphibiens et reptiles de Provence-Alpes-Côte d'Azur. Publication du Conservatoire des Espaces Naturels.

Médail, F. (2017): The specific vulnerability of plant biodiversity and vegetation on Mediterranean islands in the face of global change. Reg. Environ. Change. **17**: 1775-1790.

Médail, F. (2022): L'écosystème méditerranéen: états d'urgence. Pouvoirs **183**: 27-41.

Médail, F., Myers, N. (2004): Mediterranean Basin. In: Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions, pp 144-147. Mittermeier, R.A., Gil, P.R., Hoffman, M., Pilgrim, J., Brooks, T., Goettsch Mittermeier, C., Lamoreux, J., da Fonseca, G.A.B., Eds, Cemex Books on Nature. CEMEX, Mexico.

MedECC (2020): Climate and Environmental Change in the Mediterranean Basin – Current Situation and Risks for the Future. First Mediterranean Assessment Report [Cramer, W., Guiot, J., Marini, K. (eds.)] Union for the Mediterranean, Plan Bleu, UNEP/MAP, Marseille, France.

Millar, R.B. (2011): Maximum likelihood estimation and inference: with examples in R, SAS, and ADMB. Statistics in practice. John Wiley & Sons Ltd, Chichester, UK.

Monnet, C., Dokhelar, T., Renet, J. (2022): Rapid colour changes in a tiny threatened gecko do not impede computer-assisted individual recognition. bioRxiv 2022.03.16.484634.

Moore, E., Nimmo, D.G., Wassens, S., Michael, D.R. (2022): Use of artificial bark covers to investigate the distribution and abundance of arboreal lizards in a floodplain environment. Aust. J. Zool. **69**: 125-135.

Nias, R.C., Burbidge, A.A., Ball, D., Pressey, R.L. (2010): Island arks: the need for an Australian national island biosecurity initiative. Ecol. Manag. Restor. **11**: 166-167.

Ortega, Z., Mencía, A., Pérez-Mellado, V. (2017): Wind constraints on the thermoregulation of high mountain lizards. Int. J. Biometeor. **61**: 565-573.

Paulissen, M.A., Meyer, H.A., Hibbs, T.S. (2013): Movement patterns and sociality of the Mediterranean gecko, *Hemidactylus turcicus*, in southwestern Louisiana. Southwest. Nat. **58**: 344-350.

Pinheiro, J.C., Bates, D.M. (2004): Mixed-effects models in S and S-PLUS. Statistics and computing. Springer, New York, Berlin, Heidelberg.

QGIS Development Team (2022): QGIS Geographic Information System. QGIS Association.

Quesnel, V.C., Seifan, T., Werner, N., Werner, Y.L. (2002): Field and captivity observations of the lizard *Gonatodes vittatus* (Gekkonomorpha: Sphaerodactylini) in Trinidad and Tobago. Living World, Journal of the Trinidad and Tobago Field Naturalists' Club **2002**: 8-18.

R Core Team (2021): R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.

Renet, J., Gerriet, O., Jardin, M., Magne, D. (2008): Les populations de phyllodactyle d'Europe *Euleptes europaea* Gené, 1839 Reptilia Sauria Gekkonidae dans les Alpes Maritimes: premiers éléments sur leur répartition et leur écologie. Faune de Provence **24/25**: 117-126.

Renet, J., Gerriet, O., Kulesza, V., Delaugerre, M.J. (2013): Le Phyllodactyle d'Europe *Euleptes europaea* (Gené, 1839) (Reptilia, Squamata, Sphaerodactylidae) - Les populations continentales françaises ont-elles un avenir? Bull. Soc. Herp. Fr. **145/146:** 189-198.

Ringenwald, B.E., Bogacki, E.C., Narvaez, C.A., Stark, A.Y. (2021): The effect of variable temperature, humidity, and substrate wettability on Gecko (*Gekko gecko*) locomotor performance and behavior. J. Exp. Zool. Part A **335**: 454-463.

Roberston, P., Bainbridge, I., de Soye, Y. (2011): Priorities for conserving biodiversity on european islands. Presented at the Convention on the conservation of European wildlife and natural habitats, European Council, Strasbourg.

Rodrigues, A.S.L., Akçakaya, H.R., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Chanson, J.S., Fishpool, L.D.C., Da Fonseca, G.A.B., Gaston, K.J., Hoffmann, M., Marquet, P.A., Pilgrim, J.D., Pressey, R.L., Schipper, J., Sechrest, W., Stuart, S.N., Underhill, L.G., Waller, R.W., Watts, M.E.J., Yan, X. (2004): Global Gap Analysis: Priority Regions for Expanding the Global Protected-Area Network. BioScience **54**: 1092-1100.

Salvi, D., Berrilli, E., Bruni, G., Garzia, M., Gomes, V., Radi, G., Delaugerre, M.J. (2023): The secret life of a rock-dweller: arboreal acrobatics observed in the European leaf-toed gecko *Euleptes europaea*. Herpetozoa **36**: 135-141.

Salvidio, S., Delaugerre, M.J. (2003): Population dynamics of the european leaf-toed gecko (*Euleptes europaea*) in NW Italy: implications for conservation. Herpetol. J. **13**: 81–88.

Shapiro, S.S., Wilk, M.B. (1965): An analysis of variance test for normality (complete samples). Biometrika **52**: 591-611.

Silva-Rocha, I. R., Salvi, D., Carretero, M. A., Ficetola, G. F. (2019). Alien reptiles on Mediterranean Islands: A model for invasion biogeography. Divers. Distrib. **25**: 995-1005.

Tranchant, A., Vidal, E., Kayser, Y. (2003): Premières données sur le régime alimentaire du chat haret *Felis catus* en situation micro-insulaire méditerranéenne. Revue d'Ecologie, Terre et Vie, Société nationale de protection de la nature **58**: 411-418.

Underwood, E.C., Viers, J.H., Klausmeyer, K.R., Cox, R.L., Shaw, M.R. (2009): Threats and biodiversity in the mediterranean biome. Divers. Distrib. **15**: 188-197.

Vacher, J.-P., Geniez, M. (2010): Les reptiles de France, Belgique, Luxembourg et Suisse : Cahier d'identification. Cartes de distribution, Publications scientifiques du muséum. Biotope Éditions, Mèze.

Vasconcelos, R., Santos, X., Carretero, M.A. (2012): High temperatures constrain microhabitat selection and activity patterns of the insular Cape Verde wall gecko. J. Arid Environ. **81**: 18-25.

Walls, G.Y. (1983): Activity of the tuatara and its relationships to weather conditions on Stephens Island, Cook Strait, with observations on geckos and invertebrates. New Zeal. J. Zool. **10**: 309-317.

Webb, J.K., Shine, R. (1998a): Using thermal ecology to predict retreat-site selection by an endangered snake species. Biol. Conserv. **86**: 233-242.

Webb, J.K., Shine, R. (1998b): Thermoregulation by a Nocturnal Elapid Snake (*Hoplocephalus bungaroides)* in Southeastern Australia. Physiol. Zool. **71**: 680-692.

Webb, J.K., Shine, R. (2000): Paving the way for habitat restoration: can artificial rocks restore degraded habitats of endangered reptiles? Biol. Conserv. **92**: 93-99.

Wehsener, J.W. (2019): Foraging mode and the factors affecting foraging behavior in the diurnal arboreal gecko, *Phelsuma laticauda*. Unpublished Manuscript. Environmental Science Policy and Management, University of California, Berkeley, California 94720 USA.

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M. (2009): Mixed effects models and extensions in ecology with R, Statistics for Biology and Health. Springer New York, New York, NY, USA.