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

3 JULIE QUESSADA^{1,*}, VINCENT RIVIERE², MARC CHEYLAN³, ALBAN GUILLAUMET⁴

4 ¹ *Observatoire des Sciences de l'Univers de Rennes, Université de Rennes, Campus de Beau-*
5 *lieu, 263 Avenue Général Leclerc, 35042 Rennes, France*

6 ² *AGIR écologique, 147 ancienne route d'Esparron, 83470 Saint Maximin la Sainte Baume,*
7 *France*

8 ³ *Ecole Pratique des Hautes Etudes, Paris Sciences Lettres University, 4-14 rue Ferrus, Paris,*
9 *France*

10 ⁴ *Department of Biological and Environmental Sciences, Troy University, Troy, AL 36082, USA.*

11 **Corresponding author. Email: juliequessada@gmail.com.*

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15

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17

18 **Abstract.** The European Leaf-toed Gecko, *Euleptes europaea*, a rock-dwelling nocturnal
19 gecko characteristic of Mediterranean Islands, is facing local extinctions and population de-
20 cline at the margins of its range. Population monitoring through artificial retreat-sites (ARS)
21 was implemented on French's Grand Rouveau and If islands to study the effects of management
22 measures. We used Generalized Linear Models to identify: (i) the environmental variables
23 (such as substrate, vegetation, and exposure to wind and sun) influencing the maximum number
24 of individuals observed in ARS (studied in both islands); and (ii) the factors influencing ARS

25 daily use (occupancy), including individual attributes such as age and weight, external temper-
26 ature, and disturbance (Grand Rouveau only). The maximum number of geckos appeared to be
27 determined by the thermal properties of ARS, as mediated by exposure to the dominant wind
28 and sunlight, rather than by the structure of the habitat and nearby vegetation. An individual
29 gecko's presence in an ARS was positively related to its presence in the same ARS on the
30 previous day and negatively related to its age, to the temperature of the previous night, and the
31 number of days of disturbance. These results provide insights into the factors governing the
32 selection and use of ARS by the European leaf-toed gecko and open perspectives on the use of
33 ARS for the monitoring and conservation of this and other elusive terrestrial reptiles.

34

35 **Keywords.** Anthropogenic disturbance, gecko, habitat selection, Mediterranean islands, re-
36 treat-site, thermoregulation.

37

38

INTRODUCTION

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

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

52 The European Leaf-toed Gecko *Euleptes europaea* (Gené, 1839), family Sphaerodac-
53 tylidae, is endemic to the Mediterranean region and characteristic of Mediterranean Islands.
54 Although its distribution has been described as a biogeographical enigma (Delaugerre and
55 Cheylan, 1992), it is thought to have regressed from the continents resulting in a fragmented
56 and mainly insular distribution (Delaugerre, 1981a, Delaugerre, 1981b, Renet et al., 2008,
57 Vacher and Geniez, 2010, Fig. 2). Indeed, apart from a few continental stations in Tuscany
58 (Italy), Liguria (Italy), Campania (Italy) and the Alpes-Maritimes (France), the species is only
59 present on the islands of the western Mediterranean region: Corsica and Sardinia and their
60 islets, the Galite archipelago (Tunisia), the Tuscan archipelago (Italy) and the islands of the
61 Provençal coast (France) (Delaugerre et al., 2011, Di Nicola et al., 2022). The European Leaf-
62 toed Gecko is the smallest species of gecko in Europe (on average 6-7 cm in length including
63 tail, Arnold and Oviden, 2014). It is an insectivorous and strictly nocturnal species avoiding
64 light, which is active from dusk to dawn. It is a rock-dwelling species that lives in cracks and
65 micro-cracks in rocks and buildings (Dardun, 2003). These natural shelters are of major im-
66 portance for this poikilothermic species, which takes advantage of the heat stored by the rock
67 to regulate its body temperature (Delaugerre, 1984). These cracks could also provide shelter
68 from adverse weather conditions and diurnal predators (Delaugerre and Corti, 2020).

69 Having been qualified as a species pre-adapted to the island environment because of its
70 low biomass and its ability to survive in very small populations, it is the vertebrate that is found
71 on islands with the most drastic conditions in the Mediterranean regions, including very small
72 area, reduced food web and low biomass (Delaugerre and Corti, 2020). However, this species
73 is declining at the margins of its range and facing local extinctions both on islands and the

74 continent (Dardun, 2003, Delaunay, 2003, Salvidio and Delaunay, 2003, Vacher and Geniez,
75 2010, Delaunay et al., 2011, Corti *et al.*, 2022). The exact causes of these declines are unknown
76 but could be due to a combination of factors, including predation by the Black Rat *Rattus rattus*
77 and the feral Cat *Felis catus* (Tranchant et al., 2003, Vacher and Geniez, 2010, Delaunay et
78 al., 2019), restoration of old buildings which serve as a refuge for the European Leaf-toed
79 Gecko (AGIR écologique, 2016, Renet and Monnet, 2021), competition with the Turkish
80 Gecko *Hemidactylus turcicus* and the Common Wall Gecko *Tarentola mauritanica* (Linnaeus,
81 1758) (Renet and Monnet, 2021), introduction of new pathogens brought by the Common Wall
82 Gecko (Delaunay and Cheylan, 1992), abandonment of pastoralism leading to the closure of
83 environments (Renet et al., 2013), urbanization (Renet et al., 2013), and increase in the fre-
84 quency of forest fires (Delaunay and Cheylan, 1992). For these different reasons, the species
85 is classified near threatened in the red list of Reptiles and Amphibians of the Mediterranean
86 Basin and endangered in the red list of the Provence-Alpes-Côte d'Azur region in France (Cox
87 et al., 2006, Marchand et al., 2017).

88 The European Leaf-Toad Gecko is an elusive species that is strictly nocturnal and can
89 inhabit remote islands. As a consequence, the research of the species in activity, aiming for a
90 better understanding of its ecology and conservation status, faces significant logistical chal-
91 lenges. A variety of monitoring techniques have been tested, including nighttime prospection
92 with flashlights of potentially favorable rocky microsites (Delaunay, 2002, Krebs et al., 2015,
93 Couturier et al., 2020). However, nighttime inspections typically resulted in a small number
94 of data points, insufficient for proper monitoring of the species (Vincent Rivière, pers. obs.).
95 Because terrestrial ectotherms often use retreat-sites to regulate their body temperature and
96 achieve their eco-physiological needs (Huey et al., 1989, Grillet et al., 2010), several studies
97 have used artificial retreat-sites (ARS) to monitor reptiles or attempt to restore their habitat
98 (Webb and Shine, 2000, Croak et al., 2010, Grillet et al., 2010, Moore et al., 2022). Monitoring

99 of the European Leaf-toed Gecko using artificial retreat-sites was thus set up on the island of
100 Grand Rouveau (Var, France) in 2014 and on the island of If (Bouches-du-Rhône, France) in
101 2016 (AGIR écologique, 2016, Cheylan et al., 2016) using three stacked roman roof tiles cov-
102 ered with stones (Fig. 1, Cheylan et al., 2016). These ARS were typically colonized rapidly (in
103 less than a month) and their occupancy reached up to 76% on If Island, making these ARS a
104 promising tool to monitor European Leaf-toed Gecko populations (AGIR écologique, 2016,
105 Cheylan et al., 2016). But, to the best of our knowledge, no study has investigated the individual
106 and environmental factors involved in the selection and daily use of ARS by the species.

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

114

115 MATERIAL AND METHODS

116 *Study sites*

117 The island of If (43.22729°N, 5.32584°E) is part of the Frioul archipelago, off the coast of
118 Marseille (Bouche-du-Rhône, France), in the heart of the Calanques National Park. In response
119 to the restoration of the ramparts of If's castle, measures were taken to reduce the damage
120 caused to the population of the European Leaf-toed Gecko on this island. Long-term monitor-
121 ing of this population via artificial retreat-sites (ARS) has been implemented on If since Sep-
122 tember 2016 (AGIR écologique, 2016) in order to monitor the impact of the restoration and the
123 effectiveness of the compensation measures. Twenty-seven ARS are currently positioned on If

124 Island. They have been empirically arranged so that at least one ARS is placed within each
125 main vegetation assemblage of the island (Fig. 2a). Since 2016, European Leaf-toed Geckos
126 are counted in every ARS 2 to 3 times a year.

127 The island of Grand Rouveau (43.08038°N, 5.76757°E) is part of the Embiez archipel-
128 ago off the town of Six-Fours-Les-Plages (Var, France). Most of the land is owned by the Con-
129 servatoire du Littoral and its management is entrusted to the city of Six-Fours-Les-Plages, in
130 association with the “Initiative pour les Petites Iles de Mediterranée” (PIM initiative) (AGIR
131 écologique, 2021). Monitoring of the European Leaf-toed Gecko population by ARS started in
132 2014 on Grand Rouveau (Cheylan et al., 2016). Thirty-three ARS are currently positioned on
133 the island, with at least one ARS within each main vegetation assemblage of the island (Fig.
134 2b). Since July 2014, European Leaf-toed Geckos are counted in every ARS 2 to 3 times a year,
135 with at least one survey in the spring and one in autumn.

136

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

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

146 We verified that our response variable *max_num* did not depend on the number of sam-
147 pling periods, used as a proxy for the time since installation of the ARS: Spearman’s rank cor-
148 relation coefficient, $\rho = -0.08$, $P = 0.56$. Our data set included candidate variables measured

149 within a radius of 5 or 10 meters around the site, variables describing the environmental con-
150 ditions at the ARS itself, including classes of exposure to the major winds of the region (vari-
151 ables *N_WNW* and *ENE_ESE*) as well as sun exposure in classes at different orientations (*E*,
152 *SE*, *S*, *SW*, and *W*) and cumulatively (*Sun_pc*), as well as the distance in meters from the retreat-
153 site to the sea (*Sea_d*) and to the nearest ARS (*Arti_g*), with the latter two measured in QGIS
154 3.16 (QGIS Development Team, 2022). Variables concerning wind and sun exposure are cate-
155 gorical (with 3 levels), whereas variables such as *Sun_pc*, *Sea_d* or *Arti_g* are numerical. For
156 a complete description of variables in our data set, refer to Table 1.

157

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

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

173 (at Cape Cépet, ~15 km from Grand Rouveau) using the website www.meteociel.fr. New arri-
174 vals during the protocol (n = 3 individuals) were processed in the same way and included in
175 the study.

176

177 *Statistical analyses for environmental variables and numbers within retreat-sites*

178 All statistical analyses were performed with R 4.0.4 (R Core Team, 2021). The relationship
179 between the maximum number of individuals observed in each ARS (our response variable
180 *max_num*, see Table 1) and our set of candidate environmental variables was modeled using
181 Generalized Linear Models and a negative binomial distribution (function *glm.nb* in R's MASS
182 package). This distribution is suitable for over-dispersed discrete variables including many low
183 count data and a few high counts that stretch the distribution (Zuur et al., 2009). To reduce the
184 risk of overfitting with our large, full set of 39 explanatory variables (for 60 data points), we
185 used a conservative forward model selection approach as follows. First, starting from the (con-
186 stant) null model, an explanatory variable was entered into the best model only if it resulted in
187 a drop in the second-order AIC criterion (Akaike Information Criterion: Akaike, 1974), calcu-
188 lated using the AICc function in R's MuMIn package, and if the corresponding regression co-
189 efficient was significant at the 5% level (in the case of a factor with multiple levels, at least one
190 contrast needed to be significant). In addition, to reduce the risk of detecting spurious correla-
191 tions due to increased type I error, we limited the number of interactions tested to seven poten-
192 tially meaningful pairwise interactions among the set of variables retained after forward selec-
193 tion, excluding interactions between sun or wind exposure and the presence of a particular grass
194 species. None of the seven tested interactions were significant (not shown) and thus none were
195 included in the best model.

196 To assess model validity, we first used the *qresid* function of R's statmod package to
197 obtain randomized quantile residuals which are normally distributed (Dunn and Smyth, 2018).

198 Next, normality of the residuals was tested using a Shapiro-Wilk test (Shapiro and Wilk, 1965),
199 the homogeneity assumption was tested using Levene's test (Levene, 1960) for each categorical
200 variable included in the best model, independence was assessed by looking at the spatial dis-
201 tribution of the residuals, and R's *density* function was used to compare the distribution of
202 observed *max_num* with those predicted by the model.

203

204 *Statistical analyses for CMR and retreat-site occupancy*

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

217 The selection of the optimal model explaining ARS daily use (occupancy) was per-
218 formed using the top-down strategy which is adapted to mixed models (Zuur et al., 2009). To
219 identify the random part of the model, we used REML estimators (REstricted Maximum Like-
220 lihood; see Bolker et al., 2009, Zuur et al., 2009) to compare four models with identical fixed
221 effect structure (an additive model including all possible fixed effects factors) but different

222 random effect structure, namely a different random intercept for each individual (1|Ind), a ran-
223 dom slope for each individual that depended on the number of days of ARS disturbance (0 +
224 D_site|Ind), as well as random intercepts and slopes that were either correlated (1 + D_site|Ind)
225 or uncorrelated (1|Ind) + (0 + D_site|Ind). The optimal structure of the random component was
226 selected using the AICc criterion (Akaike Information Criterion corrected for small numbers,
227 Bolker et al., 2009, Hervé, 2014). The optimal fixed structure was then determined using for-
228 ward model selection and Maximum Likelihood (ML) estimators, which are more relevant in
229 the case of model comparisons with different fixed effects (Pinheiro and Bates, 2004, Millar,
230 2011). Although forward model selection did not include any interaction, we tested *a posteriori*
231 whether the inclusion of potentially relevant pairwise interactions resulted in lower AICc; the
232 model without any interaction was retained as the best model (not shown). Finally, the best
233 model was fitted using REML estimators to get a more reliable estimate of the different param-
234 eters (Zuur et al., 2009).

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

245

246

RESULTS

247 *Environmental variables and numbers within retreat-sites*

248 The best model included the variables *N_WNW*, *S*, *SW*, *Atr.sp*, and *Hor.mur* (Table 1 for varia-
249 ble description, Table 3, Fig. 3). A site completely exposed to the wind from N to WNW (level
250 = '2' of *N_WNW*) held fewer individuals than a site partially or completely protected from the
251 wind for this orientation (levels = '1' and '0', respectively; both $P < 0.001$, not shown), while
252 moderate or partial exposure to N to WNW winds (level = '1') yielded higher values of
253 *max_num* than any other situation (although the difference between levels '1' and '0' was not
254 significant: Table 3). In addition, sites partially or completely exposed to the southern sun (lev-
255 els '1' and '2' of variable *S*) had significantly larger numbers of European Leaf-toed Geckos
256 than sites in the shade for this orientation (level = '0', both $P < 0.03$), while, moderate or partial
257 sun exposure to the SW (level = '1' of variable *SW*) yielded significantly higher values of
258 *max_num* than either a lack of or complete sun exposure for this orientation (levels '0' and '2'
259 of variable *SW*, both $P < 0.001$, not shown). Finally, retreat sites that were surrounded by veg-
260 etation dominated by the grass *Hordeum murinum* or small bushes of *Atriplex* sp. held signifi-
261 cantly larger numbers of European Leaf-toed Geckos than the sites which did not (Table 3).

262 The hypothesis that quantile residuals followed a normal distribution could not be re-
263 jected (Shapiro test, $W = 0.99$, $P = 0.79$). The null hypothesis that the variances did not differ
264 among the different levels of each explanatory variable could not be rejected for any of the five
265 explanatory variables in the best model (Levene's test: all $P > 0.05$). However, the existence
266 of spatial autocorrelation in the residuals, notably at Grand Rouveau Island, suggests that the
267 independence hypothesis is not respected (Fig. S2). We thus used the *glmmfields* function in
268 R's *glmmfields* package to run the same (best) model while accounting for spatial autocorrela-
269 tion (Anderson and Ward, 2019). The coefficients obtained were very similar to those obtained
270 previously (not shown), suggesting that our results are also robust to this violation, although it
271 should be noted that the contrast between the levels '0' and '2' of the variable *S* was no longer

272 significant at the 5% threshold in the spatial model (estimate = 0.70, 95 %, CI = [-0.06;1.47]).
273 Finally, although the distribution of y -values predicted by the model resembles reality, the best
274 model tends to underestimate the highest observed values (Fig. S3).

275

276 *CMR and retreat-site occupancy*

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

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

290 The hypothesis that the distribution of the scaled residuals was uniform could not be
291 rejected (one-sample Kolmogorov-Smirnov test: $D = 0.037$, $P = 0.80$) and no outlier was de-
292 tected (DHARMA bootstrapped outlier test, $P = 1$). However, the dispersion of the residuals
293 was lower than expected (dispersion = 0.728, $P < 0.001$), which resulted in a loss of statistical
294 power (as opposed to overdispersion which results in inflated type I error: Hartig, 2022). Such
295 reduced power could explain, at least in part, the fact that some of the variables included in the
296 final model (after selection by AICc) were not significant at the 5% level (see Table 4). For

297 each of the fixed effects but one, we could not reject the null hypotheses of (within-group)
298 uniform distribution and (between-group) homogeneity (one-sample Kolmogorov-Smirnov
299 and Levene's tests, respectively: all $P > 0.37$, except *Pres-I* for which all $P < 0.01$).

300 Because *Pres-I* was the least significant variable included in the best model (Table 4: z
301 = 1.29, $P = 0.20$), we investigated the influence of *Pres-I* by re-running all analyses after drop-
302 ping it, yielding an alternative 'best model' called bm2. The difference in AICc between the
303 best model and bm2 was less than 2 ($\Delta\text{AICc} = 1.9$, Akaike weight for bm2 = 0.28). After drop-
304 ping *Pres-I*, all explanatory variables retained the sign of their coefficient, but all became sig-
305 nificant at the 5% level (compare with Table 4; *Night_temp*: Est = -0.10, $z = -2.13$, $P = 0.03$;
306 *Age_class*: Est = 3.00, $z = 2.02$, $P = 0.04$; *D_site*: Est = -1.14, $z = -4.73$, $P < 0.001$), and none
307 of the hypotheses examining the validity of the model could be rejected anymore (not shown).
308 This suggested that our conclusions regarding the influence of fixed-effect variables are robust
309 to the violations found when *Pres-I* is included.

310

311 DISCUSSION

312 *Importance of the thermal properties of the retreat site*

313 The first objective of this study was to determine the environmental variables affecting the
314 number of European Leaf-toed Gecko present in the artificial retreat-sites. Consistent with
315 studies in other reptiles (e.g., Huey, 1982), we found that three of the variables included in the
316 best model relate to exposure to the wind or sun, suggesting a strong influence of the thermal
317 properties of the retreat-sites (Table 3; Discussion below). Indeed, for nocturnal poikilotherms
318 that do not engage in direct insolation and spend the day in their retreat-sites such as the Euro-
319 pean Leaf-toed Gecko, the Turkish Gecko *Hemidactylus turcicus* (Hitchcock and McBrayer,
320 2006), the Broad-headed Snake *Hoplocephalus bungaroides* (Webb and Shine, 1998a), and the

321 Marbled Southern Gecko *Christinus marmoratus* (Kearney and Predavec, 2000), thermoregu-
322 lation depends on the choice of a retreat-site and the position occupied within that site (Huey,
323 1982, Webb and Shine, 1998a, Kearney and Predavec, 2000). Within their retreat-site, Euro-
324 pean Leaf-toed Geckos manage to maintain their body temperature above the atmospheric tem-
325 perature even when inactive (Delaugerre, 1984).

326

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

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

340 Additional findings suggest that the sun and wind exposure act in combination to de-
341 termine ARS quality for European Leaf-toed Gecko, although future studies directly investi-
342 gating the thermal properties of ARS and the temperature of the geckos will be necessary to
343 fully address this question. In the present study, more geckos were found in ARS that were
344 partially exposed to the mistral and partially exposed to the southwestern sun, as compared to
345 ARS that were either sheltered from or completely exposed to the mistral and southwestern sun

346 (Results and Fig. 3). These results suggest that overheating is also a concern, and that only a
347 narrow fraction of all possible environmental conditions provide optimal ARS conditions. Be-
348 cause of thermal inertia of the rock and slow heat absorption, nocturnal reptiles in retreat-sites
349 tend to reach their optimal temperature in the afternoon (Webb and Shine, 1998a, Kearney,
350 2002). A complete absence of cooling provided by the mistral or a strong exposure to afternoon
351 and evening sunshine could thus lead to temperatures beyond those optimal or even tolerable
352 for the species (Walls, 1983, Kearney, 2002, Edgar et al., 2010). This may be particularly true
353 during hot weather, raising the possibility of seasonal variation in the thermal properties of
354 ARS. For instance, in summer the nocturnal gecko *Christinus marmoratus* prefers high-shaded
355 rocks to medium and low-shaded ones and better tolerates low-shaded rocks when they are
356 thick (Kearney, 2002). Anecdotal data suggest that more European Leaf-toed Geckos may be
357 found in spring and fall, as compared to summer, in ARS of both Grand Rouveau and If islands
358 (pers. obs), although future work will be needed to better understand possible seasonal varia-
359 tion in their patterns of activities.

360

361 *Additional effect of surrounding vegetation on retreat site selection*

362 In addition to variables related to sun and wind exposure, the best model also included the
363 presence or absence of two plant groups: the bushy species of the genus *Atriplex* and the grass
364 species *Hordeum murinum*. This result about *Atriplex sp.* is consistent with recent papers high-
365 lighting the importance of vegetated habitat, and especially woody habitat, for this gecko long
366 perceived as solely associated with rocky environment. Salvi *et al.* (2023) described observa-
367 tions and adaptations consistent with an agile arboreal locomotion and Deso *et al.* (2023) de-
368 scribed the arboreal behavior of *E. europaea* on the alien *Eucalyptus sp.* species on two islands.
369 It is worth noting, however, that *Atriplex sp.* were dominant (see table 1 for definition) in two
370 ARS only in our samples, suggesting that the inclusion of this variable in our best model might

371 be an artifact of such a small sample size. Conversely, we are not aware of any study establish-
372 ing a relationship between *E. europaea* and *Hordeum marinum* or any other grass species.
373 Patches of *Hordeum* might shelter arthropods and thus provide a food supply for the European
374 Leaf-toed Gecko, a hypothesis that requires further testing.

375

376 *Model limitation for retreat site selection*

377 The best model appears insufficient to precisely predict gecko numbers in the most favored
378 retreat-sites. First, the uncertainty around the estimates, as quantified by the amplitude of the
379 confidence intervals, strongly increases when the estimated densities exceed approximately 15
380 individuals (Fig. 3). Second, the best model appears to slightly underestimate the densities in
381 the best retreat-sites (Fig. S3). Although it is always possible that we missed an important en-
382 vironmental predictor (despite our large data set: Table 1), the small difference between ob-
383 served and predicted values could be related to the gregarious behavior of the European Leaf-
384 toed Gecko, whose individuals tend to group together within natural or artificial retreats (e.g.,
385 up to 35 individuals observed under the same ARS on If; see also Delaugerre and Cheylan,
386 1992, Delaugerre and Corti, 2020). If this is true, we may expect the difference between any
387 two suitable retreat-sites to reflect local population size, taken as a proxy of the number of
388 potential colonizers, rather than the thermal properties of the retreat-site itself. The fact that
389 three adjacent sites at Grand Rouveau held the highest number of geckos for this island together
390 with the presence of residual spatial autocorrelation (Fig. S2) may be consistent with that view,
391 although future work will be needed to explore this hypothesis.

392

393 *Effect of disturbance on retreat-site occupancy*

394 Our daily surveys required a complete dismantling (and rebuilding) of the retreat-sites as well
395 as the handling of individual geckos for identification. As may have been anticipated, such a

396 disturbance was associated with a reduced probability of presence on the following day that
397 was accounted for in the estimation of the other model parameters (Table 4; see also Fig. 4 for
398 a comparison of two versus five days of disturbance). Since the CMR protocol was localized
399 in space (3 artificial retreat-sites concerned out of 33 on the island) and time (5 days) and
400 geckos can also find many suitable natural retreat-sites in the surroundings habitats, we do not
401 expect any impact on the conservation status of the European Leaf-toed Gecko in Grand Rou-
402 veau Island.

403

404 *Lack of movement between retreat-sites*

405 We did not observe any movement between the three retreat-sites monitored. Every individual
406 that was captured in one of our three retreat-sites either went missing for the rest of the study
407 or was captured at least once more at the same site. Although the three sites are relatively far
408 apart (distance: 21-41 meters), dispersal events can occur over more than 50 meters of rocky
409 line in the European Leaf-toed Gecko (Delaugerre and Corti 2020). Similar dispersal distances
410 were estimated in a slightly larger species, the Turkish Gecko *Hemidactylus turcicus*. Paulissen
411 et al. (2013) found that some adults of Turkish Gecko exhibited movements up to 67m, alt-
412 hough the average movement when the individuals were recaptured after less than 30 days was
413 only 5 m. Accordingly, besides site fidelity, several factors may explain a lack of movement
414 between sites and future studies will be needed to assess their relative importance. First, the
415 duration of the study may have been too short to detect movements between retreat-sites (only
416 4 days after the first capture). Second, movements may have occurred towards additional adja-
417 cent retreat-sites that have not been surveyed (see Fig. 2). Third, such movements between
418 retreat-sites may be more likely in summer, as opposed to early in the season (in April), as
419 higher temperatures may permit the species to wander away from the rocky environment and
420 move through the vegetation (Delaugerre and Cheylan, 1992). To assess the possibility of

421 movements between ARS, a longer CMR protocol using photo-identification could be valuable
422 (see Monnet et al., 2022). This method, which is currently being tested for future studies, would
423 have the advantages of avoiding daily manipulation and reducing the disturbance and the un-
424 certainty due to shedding that can result in marking loss in long-term studies. Implementing it
425 across an entire island could also enable us to estimate abundance of the species on Grand
426 Rouveau or If islands.

427

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

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

440

441 *Influence of outdoor temperatures on retreat-site occupancy*

442 The presence within the retreat-sites was negatively related to the temperature of the previous
443 night (Fig. 4), which could be explained in several non-mutually exclusive ways. First, prey
444 activity may be reduced during cold nights, reducing the incentive to leave the ARS (e.g. Lei
445 and Booth, 2014 and references therein). Second, a decreased metabolic rate in response to

446 cold temperatures could also lessen the incentive to forage and feed. In the Asian House Gecko
447 *Hemidactylus frenatus*, the resting and post-feeding metabolic rates decreased with a decrease
448 in temperature, and even in laboratory conditions with available living food, *H. frenatus* all but
449 ceased its feeding activity below 17 °C, probably because their body temperature became too
450 low to capture and digest prey efficiently (Lei and Booth, 2014). Third, European Leaf-toed
451 Geckos may have a greater reliance on ARS for thermoregulation purposes when temperatures
452 are lower. In agreement with that view, active individuals of the nocturnal Cap Verde Wall
453 Gecko *Tarentola substituta* experienced significantly lower body temperature than inactive
454 ones, and the body temperature of active geckos was correlated to air and soil temperatures,
455 while the body temperature of inactive individuals was correlated to refuge temperature
456 (Vasconcelos et al., 2012). Hence, geckos staying inside the ARS at night may benefit from its
457 residual heat and conserve higher body temperatures. Fourth, individual geckos may be able to
458 cover larger distances when temperatures are higher, allowing individuals to wander further
459 away from their ARS; which, in turn, could give them the possibility, or force them, to identify
460 and use a distinct retreat-site. Supporting the view that warm night favor extended foraging
461 opportunities, the Tree Dtella *Gehyra variegata* and the Eastern Stone Gecko *Diplodactylus*
462 *vittatus* had longer spans of activity on hot nights (Bustard, 1967, Bustard, 1968), and the Tokay
463 gecko *Gekko gecko* as well as the Gold Dust Day Gecko *Phelsuma laticauda* were significantly
464 more mobile when temperatures were warmer (Ringenwald et al., 2021, Wehsener, 2019, re-
465 spectively).

466

467 *Difference between age classes on retreat-site occupancy*

468 Juveniles appear to be more faithful to, or dependent on, artificial retreat-sites than older indi-
469 viduals (Fig. 4). A greater use of artificial retreat-sites by juveniles has also been observed in
470 the gecko *Oedura lesueurii*, for which 82% of the individuals occupying artificial retreat-sites

471 were juveniles (Webb and Shine, 2000). Future studies will be needed to understand this dif-
472 ference. For instance, adult and juvenile geckos may differ in their social behavior (Webb and
473 Shine, 2000), in their thermoregulatory behavior or performance (but see Aparicio Ramirez et
474 al., 2021, for a counter example in Crested Gecko *Correlophus ciliatus*), and in their response
475 to predation risk by native or invasive predators such as the Black Rat *Rattus rattus*. In the
476 French Mediterranean Bagaud Island, a successful eradication of the Black Rat was followed
477 by an increase of observations of European Leaf-toed Geckos outside shelters for both juve-
478 niles and adults together with a significant increase in the overall number of juveniles (but not
479 adults), suggesting the former age class may be the one most impacted by predation (Krebs et
480 al., 2015). The impact of Black Rat on European Leaf-toed Gecko populations could be as-
481 sessed by contrasting age-specific survival rates and population trajectories in islands with and
482 without Black Rat while controlling for between-island differences in environmental condi-
483 tions and gecko density. Partial rat control on a single island, which is considered on the island
484 of Gargalo, could provide a suitable alternative.

485

486

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493

494

SUPPLEMENTARY MATERIAL

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

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TABLES

732 **Table 1.** Description for environmental variables and gecko numbers within artificial retreat-
 733 sites (ARS). Legend: *max_num* is the response variable; explanatory variables calculated
 734 within a radius of 5 or 10 meters from the retreat-sites are identified at the end of description
 735 with the notation '(5m)' and '(10m)', respectively; the variable *Gen_sp* is actually referring to
 736 a set of 12 variables based on 12 plant species for which we determined whether they were
 737 dominant within the 5 meter radius of the ARS (value = 1) or not (0), such as *Atr.sp* referring
 738 to small bushes of *Atriplex sp.*, and *Hor.mur* to the grass *Hordeum murinum*; for the variable
 739 *Stru* (soil structure): 0 = a single substrate; 1: heterogeneous, with large substrate patches; 2:
 740 heterogeneous, with a mosaic of small patches; for sun exposure at different orientations (var-
 741 iables *E* to *W*): 0 = entirely shaded for this orientation, 1 = partially shaded for this orientation,
 742 2 = entirely exposed for this orientation; for wind exposure of the retreat-site for the two major
 743 winds in this region (variables *N_WNW* and *ENE_ESE*): 0 = entirely protected from the wind;
 744 1 = partially protected from the wind, 2 = entirely exposed to the wind. For each variable, its
 745 type (numerical or categorical) and the values that it can take are presented as well. See text
 746 for details.

747

Variable	Description	Type	Values/Range
<i>max_num</i>	Maximum number of geckos observed in the ARS	Num	0 to x
Site	Island on which the ARS is located	Cat	If, Rouveau
<i>Sea_d</i>	Distance from the sea (in meters)	Num	0 to x
<i>v0_5</i>	Cover of the vegetation layer from 0 to 5 cm (5 m)	Num	0 to 100 %
<i>v5_15</i>	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 (<i>Larus michahellis</i>) nests (5 m)	Num	0 to x
Pod.sp	Known presence of <i>Podarcis lizards</i> (<i>P. siculus</i> on If, <i>P. muralis</i> 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

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750 **Table 2.** Variables description for Capture-Mark-Recapture and ARS occupancy. *Pres* was our
 751 response variable, *Ind* was used as a random factor, and all other variables were used as candi-
 752 date explanatory (fixed effect) variables. For each variable, its type (numerical or categorical)
 753 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 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

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756 **Table 3.** Coefficients and their Standard Error (SE) for the best model explaining the maximum
757 numbers of European Leaf-toed Gecko observed within the ARS. For each categorical variable
758 (*N-WNW*, *S*, and *SW*), the coefficients reflect the effect of a given level compared to the effect
759 of level '0' that is included in the intercept (e.g., 0.15 is the predicted difference, on the log
760 scale, between gecko number when the ARS is partially protected from the wind [*N-WNW* =
761 1] and when it is entirely protected from the wind [*N-WNW* = 0]); significance levels: '***': P
762 < 0.001 , '**': $P < 0.01$, '*': $P < 0.05$). See Table 1 for variable description.

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

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765 **Table 4.** Coefficients and their Standard Error (SE) on the logit scale for the best model explain-
766 ing the probability of presence within the artificial retreat-site for an individual of European
767 Leaf-toed Gecko; significance levels: '*': $P < 0.05$, '!' = $P < 0.1$. See Table 2 for variable des-
768 cription.

769

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	.

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771

772 CAPTIONS TO FIGURES

773 **Fig. 1.** A) Example of European Leaf-toed Gecko artificial retreat-site (ARS) left "open" to
774 visualize the structure. B) Functional ARS completely covered with stones.

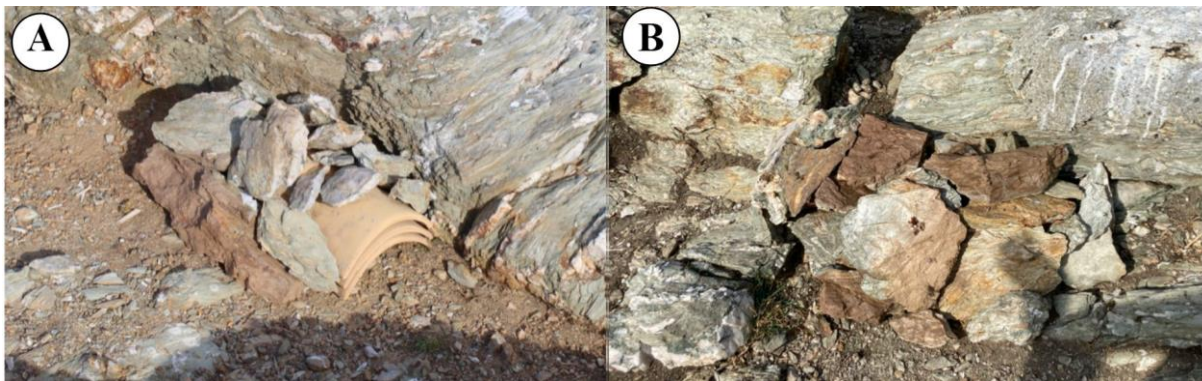
775 **Fig. 2.** Global distribution of the European Leaf-toed Gecko (in red) and locations of ARS on
776 the left: If Island, and on the right Grand Rouge Island. The three ARS used for the CMR
777 protocol are circled in red.

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

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

792

793 Figure 1.

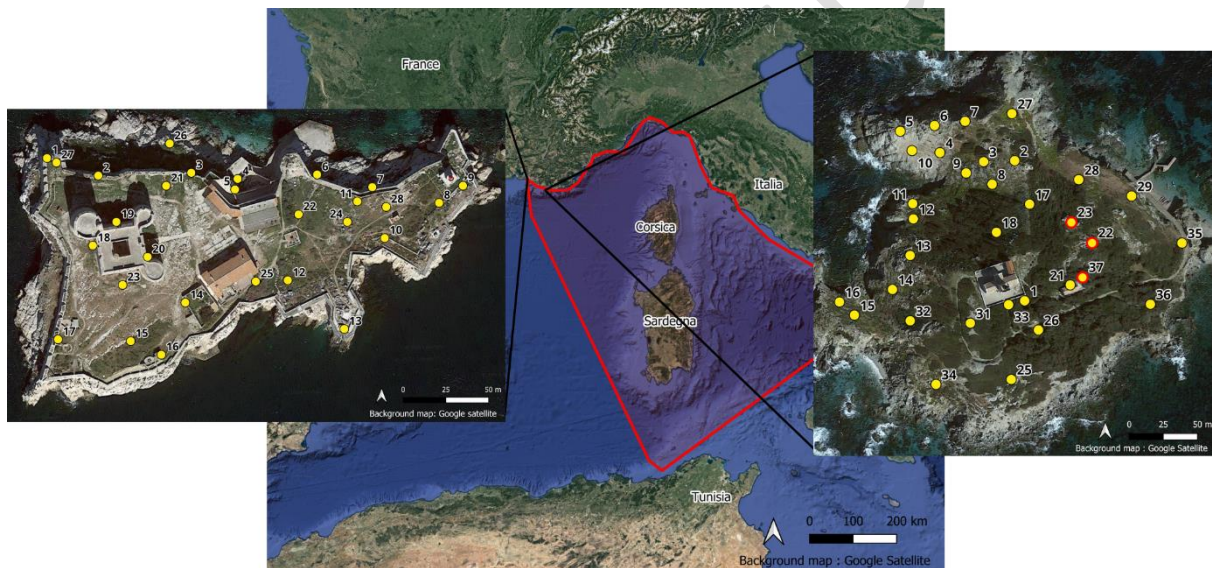


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797 Figure 2.



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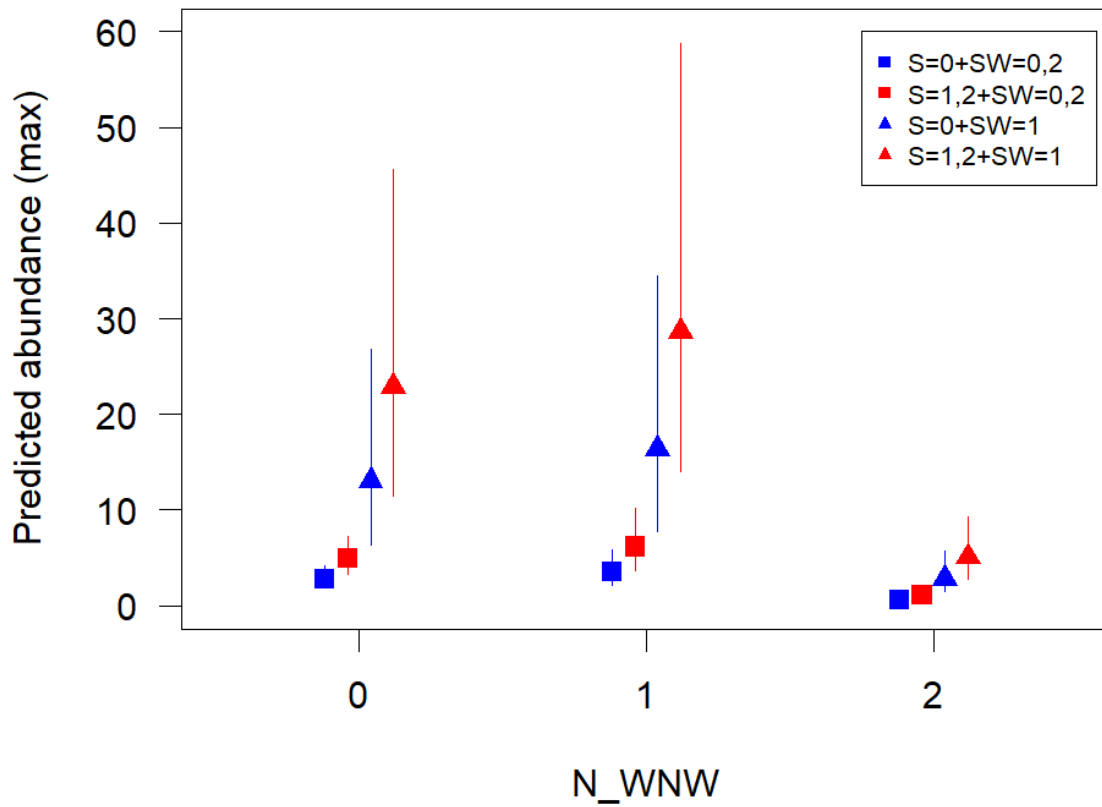
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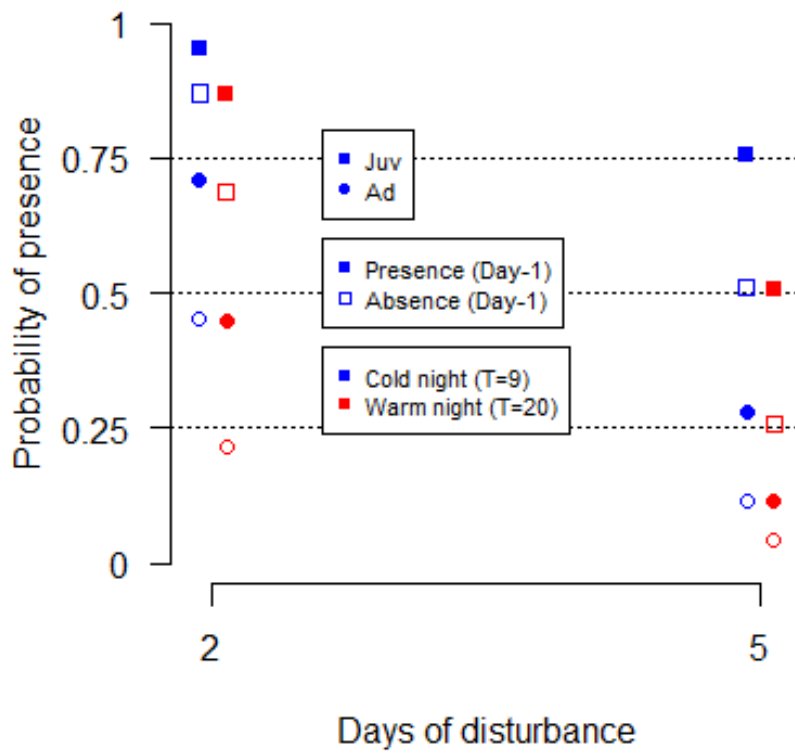
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803 Figure 3.



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805 Figure 4.



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