Intra-annual variations of microhabitat use and movements of a critically endangered arboreal day gecko endemic to Reunion Island: implications for conservation

Arthur Choeur[1,2,*], Johanna Clémencet[3], Matthieu Le Corre[1], Markus A. Roesch[2], Mickaël Sanchez[2,3]

1 - UMR ENTROPIE, 15 Avenue René Cassin, 97400, Saint-Denis, La Réunion, France
2 - Nature Océan Indien, 46 rue des Mascarins, 97429 Petite-Île, La Réunion, France
3 - UMR PVBMT, 15 Avenue René Cassin, 97400, Saint-Denis, La Réunion, France
*Corresponding author; e-mail: choeurarthur.research@gmail.com
ORCID iD: Choeur: 0000-0002-1651-3797

Abstract. Habitat loss is the leading cause of reptile decline and therefore, habitat studies are crucial to implement conservation actions. We investigated the microhabitat use of the Manapany day gecko (*Phelsuma inexpectata*), a critically endangered species endemic to Reunion Island (Western Indian Ocean). Anthropogenic disturbances led to a severe fragmentation of the gecko population, and habitat requirements of this species are poorly known, impeding effective restoration work. We (i) investigated intra-annual variations in microhabitat use, (ii) investigated movement rate to better understand habitat use, and (iii) characterised egg-laying sites. We surveyed two gecko populations in remnant natural habitat annually during five years (2015-2019) and monthly in one of the populations during 18 consecutive months. A total of 2621 gecko detections were recorded and 25 egg-laying sites were characterised. Geckos used mainly native plant species, with a high preference for screw pine thickets. We observed seasonal variations in microhabitat preferences and movement rates. Geckos perched higher and thermoregulated motionless in the canopy during winter. In summer, geckos perched lower, spent less time thermoregulating and exhibited saxicolous behaviour, particularly in females. Egg-laying sites were mainly found in rock cavities surrounded by native plants and facing southwards. Our findings confirm the importance of native coastal vegetation for the conservation of this species. Seasonal shifts of microhabitat use indicate that *P. inexpectata* (i) need habitats with thermal heterogeneity to adapt to seasonal changes in their thermal environment, and (ii) adapt their microhabitat use according to their reproductive phenology, especially for egg-laying in rock cavities.

Keywords: activity, conservation, egg-laying site, Gekkonidae, habitat restoration, *Phelsuma inexpectata*, temporal variation, Western Indian Ocean.

Introduction

Habitat loss and degradation are considered to be the leading causes of reptile decline (Gardner, Barlow and Peres, 2007; Böhm et al., 2013). Reptiles are particularly threatened by habitat disturbances due to their low dispersal ability, specialisation in narrow ecological niches, and thermoregulatory constraints (Kearney, Shine and Porter, 2009; Böhm et al., 2013; Baguette, Stevens and Clobert, 2014). To address this threat, habitat studies are crucial to identify key habitat characteristics used by species to satisfy their requirements. Moreover, habitat studies help to identify threats, to understand factors determining species occurrence, and to guide conservation efforts (Manly et al., 2004).

Species-habitat associations are not necessarily static through time and can follow temporal dynamics related to changes in biotic and abiotic environmental characteristics, activities performed (e.g., mating, egg-laying, foraging), and age of individuals (Nemes et al., 2006;

Lunghi, Manenti and Ficetola, 2015; Rako-
tozafy, 2019). Small ectotherms, like geckos,
are particularly likely to adjust their micro-
habitat use through time because they are
highly dependent on optimal thermal condi-
tions for the maintenance of their body temper-
atures (Bartholomew, 1982; Vitt and Caldwell,
2013). For instance, geckos track optimal ther-
mal environments throughout the day (Hagey
et al., 2016) and stay near retreat sites dur-
ing cold weather (Bauer, 2013). Furthermore,
they use specific egg-laying sites for incubation
(Somaweera, 2009; Roesch, Hansen and Cole,
2021), which may explain changes in microhab-
itat use during reproductive season. Thus, it is
essential to introduce temporal variation in stud-
ies on microhabitat use of gecko species and
to characterise both breeding and non-breeding
habitats to gain a comprehensive view of their
ecological niche. In addition, putting into per-
spective the substrate used and the type of activ-
ity performed allow for a better understand-
ing of microhabitat use and ecological require-
ments of the species through time (Hagey et al.,
2016; Rakotozafy, 2019). Together, knowledge
on breeding habitat and temporal variations of
both habitat use and activities help to imple-
ment relevant conservation actions for arboreal
geckos (e.g., identify plant species to keep or
eliminate, identify alternative plant species to
restore suitable habitat conditions, create artifi-
cial egg-laying sites).

The genus *Phelsuma* comprises about fifty
species of mainly arboreal geckos found on
tropical islands in the Western Indian Ocean
(Rocha, Carretero and Harris, 2010). Some
species are more generalistic and are able to
exploit a wide range of habitats (Glaw and
Vences, 2007; Roberts and Daly, 2014; Sanchez
and Probst, 2017; Humphrey and Ward, 2018),
while others are more specialised and asso-
ciated with native plant species (Glaw and
Vences, 2007; Noble et al., 2011; Bungard et
al., 2014). Studies investigating the temporal
variation in microhabitat use of *Phelsuma* day
geckos suggest daily cycles (Hagey et al., 2016;

Rakotozafy, 2019), however, annual temporal
dynamics remained unstudied. Also, descrip-
tion of eggs-laying sites in *Phelsuma* species
are poorly documented (but see Roesch, Hansen
and Cole, 2021), whereas these breeding habi-
tats are a strong limiting factor for population
survival of most arboreal geckos (Ineich, 2010).

We studied the microhabitat use of the
Manapany day gecko (*Phelsuma inexpectata*
Mertens, 1966; hereafter referred to as MDG), a
critically endangered arboreal species endemic
to Reunion Island (Sanchez, 2021). Due to
habitat disturbances (urbanization, agriculture,
and invasive species), the population is today
fragmented into fifty small sub-populations
(Sanchez and Caceres, 2019) and is declining
rapidly (Choeur, 2021). Previous studies have
shown that populations are mainly associated
with remnant native coastal vegetation (Bour,
Probst and Ribes, 1995; Sanchez and Probst,
2011). However, there are no studies examin-
ing microhabitat use and intra-annual changes
in microhabitat use. In order to provide man-
agement guidance for the conservation of the
MDG, especially for the restoration of their
habitat, we jointly characterised (i) variation in
microhabitat use over the year, (ii) movement
rate (individuals in motion or not, defined here
to quantify movement activity of geckos; Stone
and Baird, 2002) over the year to better under-
stand variations in microhabitat use, and (iii)
egg-laying sites.

Materials and methods

Study area and study species

This study was carried out on the coastal cliffs of southern
Reunion Island (21°06′S, 55°36′E; Western Indian Ocean)
(fig. 1). The climate is tropical with a hot and humid season
from November to April (austral summer; mean monthly
temperature: 26°C, mean monthly precipitation: 146 mm),
and a dry and cooler season from May to October (austral
winter; mean monthly temperature: 22°C, mean monthly
precipitation: 96 mm) (Météo France, 2021). We studied
microhabitat use of the MDG in the two largest known
populations in remnant natural habitat; named "population
A" (0.84 Ha; approximately 60 adults in 2018, estimated
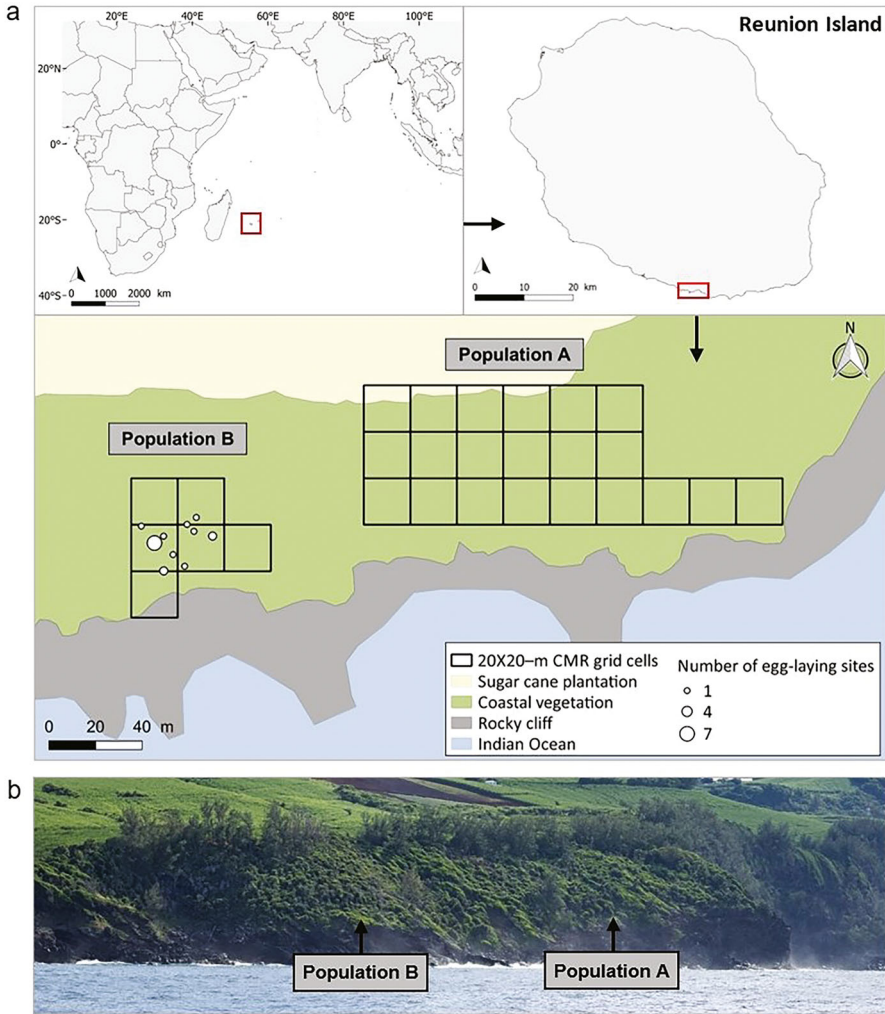from capture-mark-recapture studies) and "population B"

Figure 1. (a) Location of the study area, egg-laying sites, and populations A and B of *Phelsuma inexpectata* monitored between 2015 and 2019. (b) Habitat picture (taken by Debordes Laurent) of the study area (more pictures are available in the supplementary fig. S1).

(0.24 Ha, approximately 50 adults in 2018) (Choeur, 2021). For both populations, sex-ratio of adults is skewed and in favour of males (around 3:1) (Choeur, 2021). Both populations are distributed along a thin strip of coastal vegetation (<100 m) between sugarcane plantations and rocky cliffs (fig. 1). The vegetation consists of small patches of native plant species (screw pine thickets *Pandanus utilis*, and mixed thickets of *Scaevola taccada* and *Psiadia retusa*) surrounded by invasive plant species (*Casuarina equisetifolia* trees, thickets of *Schinus terebinthifolius*, *Flacourtia indica* and *Furcraea foetida*, the latter is only present in population A) (supplementary fig. S1). The soil is mainly covered by rocky outcrops and screw pine leaf litter. Due to the steep slope (approximately 40°) and orientation towards the south (193° N), both populations receive more sunlight in summer (on average 8 h/day) than in winter (on average

5 h/day) (Choeur et al., 2022a). Furthermore, this topography also results in south-facing locations receiving more direct sunlight in our study area and allowed detection of geckos in the whole canopy. Besides habitat degradation, the study area is also invaded by invasive mammal predators of reptiles, such as *Rattus rattus*, *Suncus murinus*, *Mus musculus*, and *Felis catus*, which further threaten the persistence of the MDG populations (Norbury et al., 2014; Palmas et al., 2017; Quiterie et al., 2019; Choeur et al., 2022b).

The MDG is a middle-sized gecko that can reach a total length of up to 13 cm (supplementary figure S2) and is insectivorous, nectarivore and frugivorous (Sanchez, Probst and Deso, 2009). It exhibits a seasonal reproductive pattern, lasting from the end of the austral winter to the end of the austral summer. Females use communal egg-laying sites and exhibit egg-laying site fidelity (Choeur et al., 2022a). Eggs

are glued on the substrate, where after hatching calcareous layers of the eggshells (known as 'egg scars') remain, which are detectable for many years (Roesch, Hansen and Cole, 2021; Choeur et al., 2022a). Age stage (juvenile or adult) and sex of adults can be determined visually according to a suite of morpho-anatomical features including body shape, body length, colour, and hemipenal bulges (supplementary fig. S2) (Sanchez, Probst and Deso, 2009). Adult MDG have individual head and dorsal markings (pattern of red spots on green background), which is highly polymorphic and can be used for individual identification (supplementary fig. S2).

Data collection

We defined microhabitat use as the substrate where the gecko was located upon detection, i.e., perch type, perch height, and sun exposure (Noble et al., 2011; Buckland et al., 2014; Delaney and Warner, 2016; Hagey et al., 2016; Augros et al., 2018). We collected data on microhabitat use and movement rate during capture-mark-recapture surveys (Choeur, 2021), following a robust design sampling method with each primary session comprising of three secondary sessions (Pollock, 1982; Lebreton et al., 1992). In brief, we divided the entire distribution of the populations A and B into 20 × 20 m grid cells (21 grid cells for population A and 6 for population B) (fig. 1). Over a 5-year period (2015-2019), we surveyed populations A and B annually between September and October. During each sampling occasion, one observer visually searched for geckos in each grid cell for 20 minutes. To maximise the probability of detection, geckos were searched for when weather conditions were favourable for their activity (absence of rain) and during activity periods (from 08:00 am to 05:00 pm). For each detection, we took several close-up photos of the gecko's unique colour pattern using a digital camera (Lumix DMC-FZ72, telephoto lens x60) to identify the gecko, and we recorded the sex and substrate used (e.g., plant species, dead wood, rock or ground). We only considered adult geckos in our study because there were not enough observations of juveniles to accurately characterise their habitats. Using the same protocol, we surveyed population B monthly from May 2018 to October 2019 (18 months). For this population, we also visually recorded perch height with an estimated accuracy of ±0.5 m, whether the gecko was moving (yes/no), and whether it had at least one part of its body in the sun (yes/no). For each survey in each grid cell, we recorded the percentage of sunshine over the 20 minutes of survey effort.

From February 2018 to August 2020, we searched for egg-laying sites inside leaf axes, tree cavities and rock cavities using a torch, for three hours per month in population B (see Choeur et al., 2022a). We defined an egg-laying site as a substrate with eggs and/or egg scars. We categorised egg-laying sites as active (with incubating eggs) or inactive (formerly used, with eggs hatched, egg scars or old eggs presumably dead covered with mould and brown spots). For active and inactive egg-laying sites, we recorded height above ground and the type of substrate (rock or plant; cavity or not; plant species and part of the plant). If eggs were in a cavity, we recorded entrance width and

height, cavity depth, and entrance aspect (orientation of egg-laying site entrance from 0° to 359°). For active egg-laying sites, we also recorded the orientation of eggs inside the cavity (side/overhang/bottom), and the cover of native and non-native plants in a 1 × 1 m grid cell surrounding the egg-laying site (defined as the vertical projection of all foliage into the horizontal surface). For active egg-laying sites on plants, we recorded species, plant height with a laser rangefinder (model Stanley TLM165, to the nearest 10 cm), and diameter at breast height (DBH). Percentages of plant cover was visually estimated with 10% accuracy. Metric measurements (except of plant height) were recorded using a measuring tape (to the nearest 1 mm). The aspects of the entrances were recorded using a digital compass (to the nearest 1°).

Data analysis

To characterise microhabitat use, we calculated the percentage of detections per substrate type during annual and monthly surveys for both populations. We performed multivariate analyses to investigate the variation in microhabitat use and movement rate over the year and between sexes during monthly surveys for population B. We used three distinct Generalized Linear Mixed Models (GLMMs) with a logit-binomial link distribution to test the effect of sex, period (month), and the interaction between sex and period on (i) the probability of geckos being in motion or not, (ii) the probability of geckos being in the sun or not (only sampling occasions carried out in sunny weather were considered for this analysis, representing 51% of total surveys), and (iii) the probability of geckos perching on rock or not. We also performed a Linear Mixed Model (LMM) to test the effect of sex, period (month), and the interaction between sex and period on perch height. To account for variation among individuals in our analyses, we identified photographed geckos based on their unique colour patterns. We included gecko ID as a random effect in our models (acting on the intercept of the regressions). We used the same approach for all models to test the respective effect of each explanatory variable in our study area using the R-package lme4 (Bates et al., 2015). First, for each variable, we calculated the difference of deviance between the full model and a model not including the target variable. Then, we built a complete model with all variables ordered from the variable that increased the deviance the most to the variable that increased the deviance the least when removed from the complete model. We used a stepwise backward elimination procedure of the least significant terms ($P > 0.05$) to determine the best minimal adequate model containing only significant terms (Burnham and Anderson, 2002; Crawley, 2007). We evaluated the ability of each best minimal adequate GLMM to predict modelled occurrence by estimating the area under the receiver operating characteristic (ROC) curve (Fielding and Bell, 1997) using the R-package pROC (Robin et al., 2021).

We used Rao's Spacing Test (R package circular; Agostinelli and Lund, 2017) to analyse the uniformity of egg-laying site aspect distribution (Roesch, Hansen and Cole, 2021). Throughout the text, descriptive results are given as means ± standard deviations (SD). All statistical

analyses were performed using R Version 3.6.0 (R Core Team, 2019) and with α value = 0.05 as the significance threshold.

Results

Microhabitat use, movement rate, and intra-annual variations

Total survey effort for population A (annual surveys) and population B (annual and monthly surveys) were 105 hours and 126 hours, respectively. We recorded 811 gecko detections in population A (243 females, 548 males, and 20 undetermined) and 1810 in population B (562 females, 1204 males, and 44 undetermined) of which 95.82% resulted in a matched photo-identification. In total during the five years of surveys, 289 adult geckos were photo-identified (population A: 59 females, 94 males, and 5 undetermined; population B: 63 females, 65 males, and 3 undetermined).

Based on the annual data, geckos were mainly observed on screw pine (*P. utilis*) in both populations (56.84% of detections for population A and 87.80% for population B) (fig. 2). In population A, 36.25% of detections were made on *F. foetida* and only occasionally on other substrates. In population B, 8.99% of detections were made on rock and only occasionally on other substrates (fig. 2).

During the 18 month-survey in population B (108 hours of survey effort), geckos used screw pine as a substrate throughout the year, whereas they used rocky substrates only between August and February (figs 3 and 4b). Females used rocky substrates significantly more often than males ($P < 0.05$) and rocky substrates were used significantly more in September ($P < 0.05$), October ($P < 0.001$), and December ($P < 0.01$) compared to August (defined as the reference month in this model) (figs 3, 4b, and supplementary table S1). The average perch height was 266.20 ± 171.58 cm (min.-max. = 0-1100 cm) and was significantly lower from August to April ($P < 0.001$ for all months except April where $P < 0.01$) compared to
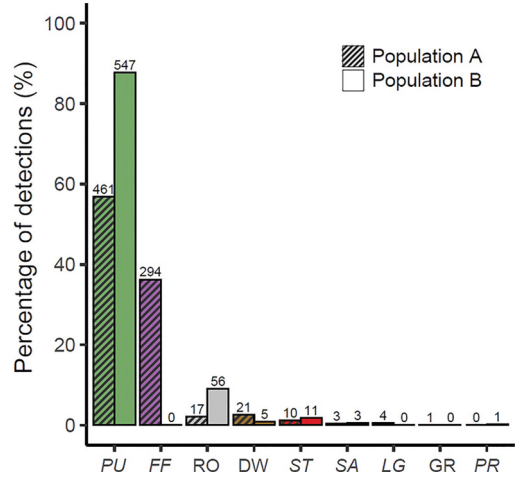

Figure 2. Percentage of *Phelsuma inexpectata* adult detections per substrate in population A and B during annual surveys between September and October on the coastal cliffs of southern Reunion Island (Western Indian Ocean) between 2015 and 2019. The text in italic indicates live plant substrates. *PU*: *Pandanus utilis*, *FF*: *Furcraea foetida*, RO: rock, DW: dead wood, *ST*: *Schinus terebinthifolius*, *SA*: *Scaevola taccada*, *LG*: *Litsea glutinosa*, GR: ground, and *PR*: *Psiadia retusa*. The numbers represent the number of gecko detections.

June (the reference month for this model and those presented below) (fig. 4a and supplementary table S2). We detected 56.97% of geckos with at least one body part in the sun and 27.51% of geckos in movement. On sunny days, geckos were significantly more often found in the sun in July ($P < 0.05$) and significantly less from December to March ($P < 0.05$ for December and February, and $P < 0.001$ for January and March) compared to June (fig. 4a and supplementary table S3). Geckos were observed in motion significantly more in August ($P < 0.05$) and October to February ($P < 0.01$ for October, $P < 0.001$ from November to February) and significantly less in April ($P < 0.05$) compared to June (fig. 4a and supplementary table S4). Throughout the year, percentages of geckos detected in the sun, in motion and their perch height were not significantly different between sexes. The area under the ROC curve for all three GLMM models were > 0.75, indicating a strong predictive capacity of the model (Fielding and Bell, 1997).
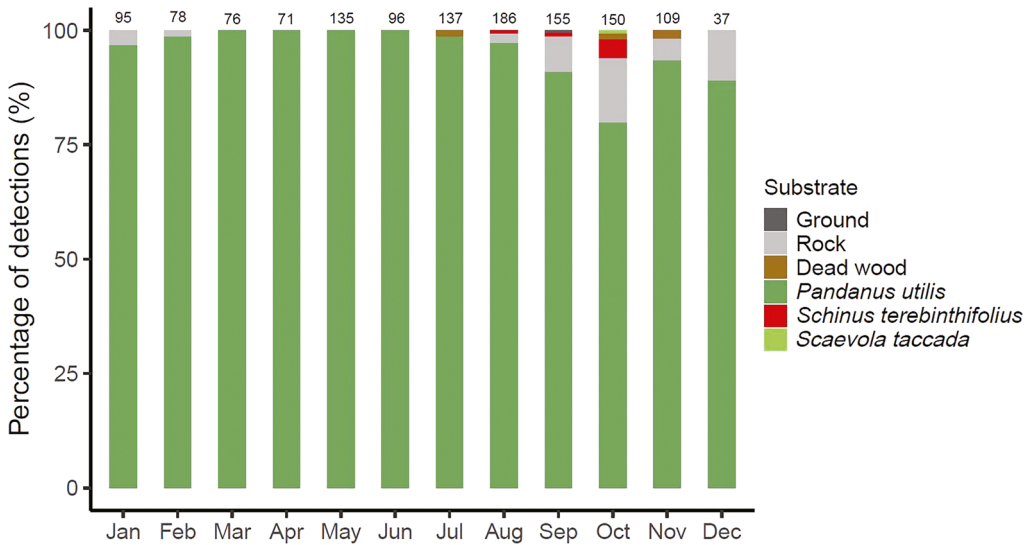
Figure 3. Percentage of *Phelsuma inexpectata* adult detections per substrate in population B during monthly surveys on the coastal cliffs of southern Reunion Island (Western Indian Ocean) between May 2018 and October 2019. The numbers represent the number of detections.

Egg-laying sites

Between February 2018 to August 2020 (covering 2.5 egg-laying seasons), we recorded 10 inactive and 15 active egg-laying sites containing a total of 67 eggs in population B. Egg-laying sites were mainly found in rock cavities (92%, $N = 23$) and to a lesser extent on screw pine leaves (4%, $N = 1$) and in screw pine trunk cavities (4%, $N = 1$) (see illustrations in Choeur et al., 2022a). Females glued their eggs to the side (58.57%) and overhang (41.43%) of the cavities. Mean height from the ground to the egg-laying sites was 133.25 ± 107.48 cm (min.-max. = 4.10-584.40 cm). For egg-laying sites in cavities (rock or trunk of *P. utilis*, $N = 24$), aspects of entrances were not uniformly distributed (Rao's Spacing Test: $U = 195$, $P < 0.001$) and predominantly oriented towards the south (87.50% of egg-laying sites were oriented between 130° and 240°) (fig. 5). Mean entrance height and width of egg-laying sites in cavities were 2.78 ± 2.75 cm (min.-max. = 0.50-10.90 cm) and 3.10 ± 3.08 cm (min.-max. = 0.60-11.00 cm), respectively, with a mean cavity depth of 5.57 ± 3.65 cm (min.-max. =

1.50-18.10 cm). Shapes of entrances of cavities were not round but generally ellipsoidal with either small height or width (supplementary table S5). For active egg-laying sites on screw pine ($N = 2$), mean DBH and tree height were 20.37 ± 2.25 cm (min.-max. = 18.78-21.96 cm) and 490.00 ± 268.70 cm (min.-max. = 300.00-680.00 cm), respectively. Plant cover surrounding active egg-laying sites (mean cover = $68.00 \pm 37.36\%$) was dominated by native plant species ($64.67 \pm 36.42\%$) and only occasionally by non-native plant species ($3.33 \pm 12.91\%$).

Discussion

The detailed description of egg-laying sites and temporal variations in microhabitat use and movement rates allowed us to gain an overview of MDG's ecological niche in a remnant natural habitat, and to better understand the ecological roles of microhabitats used through the prism of the physiological needs of day geckos. Our original results are essential for the habitat restoration of this critically endangered species
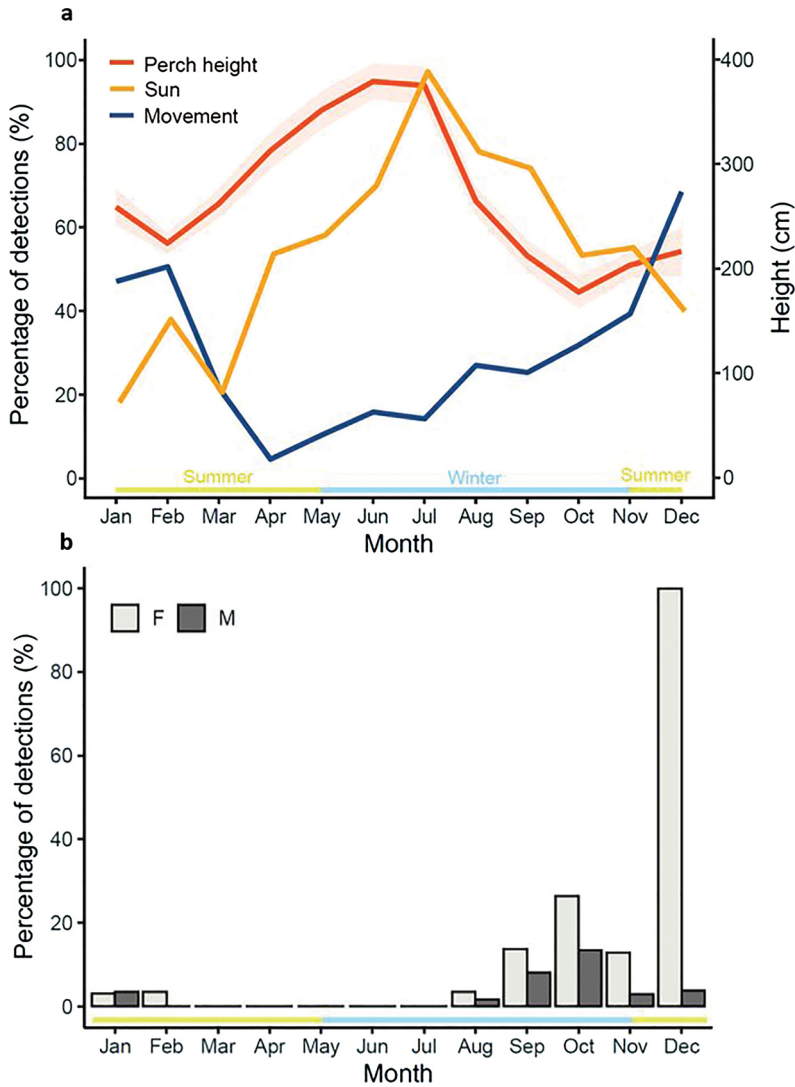
Figure 4. (a) Percentage of *Phelsuma inexpectata* adult detections in the sun (orange line), in movement (blue line) and perch height (red line with light red area representing standard errors), and (b) percentage of adult detections on a rocky substrate across the year in population B on the coastal cliffs of southern Reunion Island (Western Indian Ocean) monitored between May 2018 and October 2019. F = female and M = male.

and can also serve as a basis for further studies of other arboreal geckos.

Microhabitat use

Our study is the first to investigate the microhabitat use by the MDG. Our extensive sampling effort allowed us to describe microhabitat use of a large fraction of both studied populations. Based on estimates from previous capture-mark-recapture analysis (Choeur,

2021), we have detected each year 85.72 ± 3.51% of adults in population A and 89.97 ± 9.29% of adults in population B (100% over the 18 month-survey). We found a strong association with native screw pine thickets, the use of non-native *F. foetida*, and to a lesser extent the use of rocky substrates. The disproportionate use of screw pine was already reported for the MDG (Bour, Probst and Ribes, 1995; Sanchez and Probst, 2011), for other *Phelsuma* species
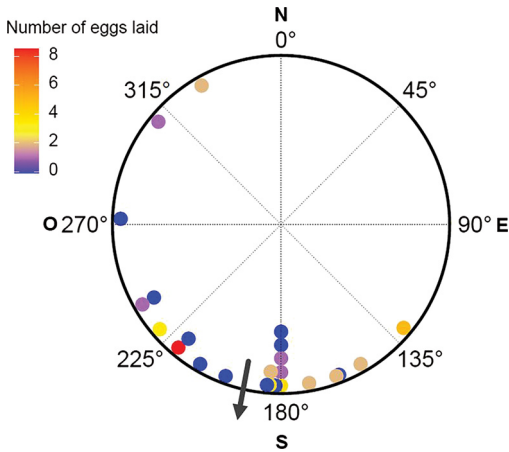
Figure 5. Aspect distribution of *Phelsuma inexpectata* egg-laying sites entrances (for egg-laying sites in cavities, $N = 24$) in population B on the coastal cliffs of southern Reunion Island (Western Indian Ocean) recorded between February 2018 and August 2020. Points represent individual egg-laying sites and the arrow indicates the topographical orientation of the study area. The colour gradient indicates the number of eggs laid for sites used over one breeding season or indicates the mean number of eggs laid for sites used over two breeding seasons. Egg-laying sites with 0 eggs (blue colour, $N = 10$) correspond to inactive sites and egg-laying sites with one or more eggs (purple to red colour, $N = 14$) correspond to active sites.

(Raxworthy and Nussbaum, 1993; Wanger et al., 2009; Noble et al., 2011; Bungard et al., 2014; Augros et al., 2018), and for many other tropical reptiles in Indian and Pacific Oceans (Lehtinen, 2002; Flecks et al., 2012). The non-native Agavaceae *F. foetida* is known to be used by several *Phelsuma* species (Sanchez and Probst, 2014; Sanchez and Caceres, 2019) and other tropical geckos (Sanchez et al., 2019). The use of rocky substrates has also been reported for *Phelsuma* species (Osadnik, 1984; Nussbaum et al., 2000; Roesch, Hansen and Cole, 2021), including the MDG (Deso and Probst, 2007). Our study focus was on adults and periods when the species is active (absence of rain and during the day) in a remnant natural habitat. To complete our work, further studies are needed to describe microhabitat use throughout their range (e.g., in semi-urban and urban areas), during inactive periods (e.g., at night), and for the juvenile stage.

Microhabitat use by the MDG can be explained by its thermal ecology, reproductive biology, and foraging behaviour. Microhabitat selection of diurnal arboreal lizards depends on several factors including the availability of shelters, basking sites, food, water, egg-laying sites, and optimal thermal conditions (Reagan, 1986; Ramírez-Bautista and Benabib, 2001; Cole, 2005; Furrer et al., 2006; Hansen et al., 2007; Buckland et al., 2014; Bungard et al., 2014). Screw pine and *Agavaceae* species are particularly attractive as they provide several resources: basking sites with high thermal heterogeneity (especially the complex network of branches and leaves of *P. utilis*; supplementary fig. S1) (Lehtinen, 2002), food resources (such as fruits, floral nectar, and insects attracted by fruits, flowers, and water retained in leaf axes), and egg-laying sites (Gardner, 1984; Lehtinen, 2002; Furrer et al., 2006; Choeur et al., 2022a). Rocky substrates accumulate heat from the sun and geckos gain heat from contact with this substrate (thigmothermy). Rocky substrates and screw pine trunks often provide cavities. Cavity availability is known to be an important habitat component for *Phelsuma* species (Buckland et al., 2014; Bungard et al., 2014) and other tropical arboreal geckos (Salvidio and Oneto, 2008; Ineich, 2010) because they are used as egg-laying sites, thermal shelters, and shelters from predators and weather (Crawford and Thorpe, 1979; Cole, 2005; Furrer et al., 2006). Apart from *F. foetida*, the MDG almost never used non-native plant species, although some are very abundant in the habitat (*S. terebinthifolius* and *F. indica*). These invasive plant species are unsuitable for geckos as they do not provide attractive basking sites (Fitzgerald, Shine and Lemckert, 2003; Pringle, Webb and Shine, 2003), trunk cavities (Bungard et al., 2014), and food resources (Valentine, Roberts and Schwarzkopf, 2007; Baider and Florens, 2011).

Intra-annual variations of microhabitat use and movement rate

MDG changed their microhabitat use and activity pattern throughout the year. In summer, geckos showed higher rates of movement, were less exposed to the sun and used rocky substrates more often, particularly in females. Towards the end of the summer, individuals progressively moved to higher perches. In winter, geckos were more often observed motionless on sun-exposed perches in the canopy. Towards the end of winter, individuals progressively moved to lower perches. Our study shows the great complexity of the microhabitat used by the MDG and the importance of microhabitat heterogeneity to meet the geckos' requirements.

Hagey et al. (2016) and Rakotozafy (2019) showed daily variation in microhabitat use of *Phelsuma* species, suggesting that thermal ecology can explain temporal patterns of microhabitat use. MDG have a small body size, which leads to high rate of heat loss or gain (Pough et al., 2003). For small ectotherms, the control of thermal interaction is very important to maintain the body temperature within the required range for vital physiological and behavioural processes (Vitt and Caldwell, 2013). Seasonal variations in thermal conditions (temperature and solar radiation) require MDG to adapt their microhabitat use to thermoregulate efficiently. Similarly, thermal conditions influence gecko activity rates because ectotherms must adapt their behaviours according to their body temperature (Vitt and Caldwell, 2013). Cooler temperatures and shorter periods of sunlight during winter constrain the MDG to thermoregulate for longer periods. During winter, geckos used perches high up in the canopy because they are the first to receive sunlight in the morning and ultimately received more sunlight throughout the day. Also, geckos which are in thermoregulation in the canopy have numerous shelters available to escape predators or to shelter during poor thermal conditions (especially spaces in the leaf axes of *P. utilis*). During summer

months, geckos have less need for thermoregulation and can be more active on perches below the canopy. Geckos may also use rocky substrates during these months to regulate their body temperature by thigmothermy while being in the shade to avoid overheating and desiccation.

The use of lower perches in summer is also linked to access to egg-laying sites, most of which are found in rock cavities. Geckos, particularly females, used rocky substrates only during the reproductive season (from August to February) and especially in September, October and December, during the main egg-laying period (Choeur et al., 2022a). Females used rocky substrates for reproductive purposes: searching for egg-laying sites, oviposition, eating shells of hatched eggs to replace their calcium stock, and cleaning the site for the next oviposition (Gardner, 1984; Osadnik, 1984; Caceres, Jasmin and Sanchez, 2010; Bauer, 2013). Males also used rocky substrates during the same season, probably to mate with females. Indeed, during the breeding period, we regularly observed males and females together near egg-laying sites, with males harassing females for mating.

In addition to thermoregulation and reproduction, food resources and predator presence influence microhabitat use and activity patterns of geckos (Bauer, 2013; Hagey et al., 2016). Seasonal changes in food availability (fruits, flowers, insects) are likely an important factor and requires further research. Indeed, MDG often forage within the stilt roots of screw pines when food resources (especially arthropods) are abundant, during humid austral summer, as it has also been observed for *Phelsuma borbonica* (M. Roesch personal observation).

Egg-laying sites

Egg-laying sites of MDG were mainly located in rock cavities and to a lesser extent on screw pines. Egg-laying sites were surrounded by native plant species and predominantly facing southwards. Inside of rock cavities,

females glued the eggs on the side and overhang. Knowing the abundance of adult females in population B (capture-mark-recapture estimates: $N_{2018} = 19$; $N_{2019} = 10$), their reproductive effort (around 3 eggs per year) (Choeur, 2021) and the number of eggs detected ($N = 67$; 77% of theoretical eggs laid), we consider that our sampling integrated the majority of the available egg-laying sites during the studied period. The remaining eggs are likely located in screw pines leaf axes, which are more difficult to detect.

Egg-laying site selection is an important component of fitness, particularly in animals without post-laying parental care, such as most geckos (Howard, 1978; Resetarits and Wilbur, 1989; Resetarits, 1996). Our results support previous studies indicating that *Phelsuma* species use rock and screw pine as egg-laying sites (Vinson and Vinson, 1969; Sanchez and Probst, 2017; Roesch, Hansen and Cole, 2021). Rock cavities provide stable environmental conditions and optimal temperatures due to the high thermal capacity of rock, which is important for egg incubation (Pough et al., 2003; Pike, Webb and Shine, 2010; Vitt and Caldwell, 2013). Furthermore, rock cavities protect eggs from intense weather events such as cyclones (Cole, 2005; Roesch, Hansen and Cole, 2021). Additionally, egg-laying sites in cavities with very small entrances can help avoid detection and predation by non-native mammal and bird predators. A camera-trap monitoring by one of the authors showed that black rats do not detect eggs inside small rock cavities in our study area (Choeur, 2021). Due to the study area's topography, cavities facing towards the south received more direct sunlight, which could explain why egg-laying sites were mainly oriented in this direction. Previous studies on *Phelsuma guentheri* and *P. borbonica* have shown preferences for cavity orientation towards optimal sun exposure (Sanchez and Vingadachetty, 2016; Roesch, Hansen and Cole, 2021), which could increase hatching success (Cole et al., 2013; Roesch, Hansen and Cole, 2021). The choice of

gluing eggs on the side and overhang in the cavities probably allows the protection of the eggs from flooding during heavy rain, which could occur if eggs were glued to the bottom of the cavity.

Because egg incubation depends on environmental conditions, such as temperature and humidity, nest site environment and cavity aspect influence incubation time, embryo survival and, consequently, hatching success (Packard, 1991; Elphick and Shine, 1999; Qualls and Andrews, 1999; Pough et al., 2003; Vitt and Caldwell, 2013). Based on our findings, the selection of egg-laying sites by the MDG could be a sum of adaptive strategies to increase hatching success and avoid egg predation. Predation pressure as selection force may also have led to the persistence of cavities that are inaccessible to predators. However, depending on the diversity of available habitat, the observed microhabitat use by the MDG for reproduction may be a default choice rather than a true preference. Further studies (e.g., comparison of habitat used and unused) are needed to confirm egg-laying habitat preferences for the MDG.

Conservation implications

Our findings show the importance of native coastal vegetation for the MDG, especially screw pines thickets. Other native coastal plants (like palm species, e.g., *Latania spp.*, absent from our study area) with similar characteristics (network of large leaves providing shelter and food) are probably also ideal host plants for the MDG. Invasive plant species are taking the place of native vegetation, leading to fragmentations of gecko populations and contributing to the decline of this threatened species. For example, the studied populations are separated by only 70 meters of invasive shrubs (*S. terebinthifolius* and *F. indica* thickets) that constitute a barrier to dispersal. Native coastal vegetation is one of the most endangered habitats of Reunion Island (Strasberg et al., 2005; Fenouillas et al., 2021). The protection and restoration of this vegetation should be regarded as a priority for

the MDG, but also for seabird colonies and for the suit of endemic plants which are restricted to this type of habitat (Choeur, 2021).

Our study is the first to provide a detailed description of the egg-laying sites of the MDG (aspect, substrate, height, depth, and width). Our results will be very useful to guide restoration work and to enrich habitats with artificial egg-laying sites that could help geckos to colonise restored habitats (Sanchez, 2012). Indeed, the availability of egg-laying sites is considered a main limiting factor for gecko populations because it is a major constrain on population growth (Castilla and Swallow, 1995; Salvidio and Oneto, 2008; Ineich, 2010; Augros et al., 2017; Roesch, Hansen and Cole, 2021).

Our results show that temporal variations of microhabitat use and movement rate are important aspects of the MDG ecological niche. We suggest that future studies on microhabitat use of arboreal tropical geckos need to take into account seasonal patterns. Seasonal shifts of microhabitat use by MDG suggest that thermal conditions are an important component of the ecological niche of *Phelsuma* species. Based on our results and those of other studies (Hagey et al., 2016; Rakotozafy, 2019), habitat restoration of native day geckos should focus on structural habitat components with high thermal heterogeneity.

Supplementary material. Supplementary material is available online at:
https://doi.org/10.6084/m9.figshare.21953420

References

Agostinelli, C., Lund, U. (2017): R package 'circular': Circular Statistics (version 0.4-93). URL https://r-forge.r-project.org/projects/circular/.

Augros, S., Faipoux, L., Bodin, M., Le Goff, A., Sanchez, M., Clémencet, J. (2017): Evidence of anthropogenic habitats colonization by the Réunion day gecko *Phelsuma borbonica* (Mertens, 1966) (Réunion Island, France): conservation implications. Herpetol. Notes **10**: 563-571.

Augros, S., Scherz, M.D., Wang-Claypool, C.Y., Montfort, L., Glaw, F., Hawlitschek, O. (2018): Comparative perch heights and habitat plant usage of day geckos (*Phelsuma*) in the Comoros Archipelago (Squamata: Gekkonidae). Salamandra **54**: 71-74.

Baguette, M., Stevens, V.M., Clobert, J. (2014): The pros and cons of applying the movement ecology paradigm for studying animal dispersal. Mov. Ecol. **2**: 1-13.

Baider, C., Florens, F.V. (2011): Control of invasive alien weeds averts imminent plant extinction. Biol. Invasions **13**: 2641-2646.

Bartholomew, G.A. (1982): Physiological control of body temperature. Biol. Reptilia **12**: 167-211.

Bates, D., Maechler, M., Bolker, B., Walker, S. (2015): Fitting linear mixed-effects models using lme4. J. Stat. Softw. **67**: 1-48.

Bauer, A.M. (2013): Geckos: the Animal Answer Guide. JHU Press, Baltimore.

Böhm, M., Collen, B., Baillie, J.E.M., Bowles, P., Chanson, J., Cox, N., Hammerson, G., Hoffmann, M., Livingstone, S.R., Ram, M., Rhodin, A.G.J., Stuart, S.N., Dijk, P.P. van, Young, B.E., Afuang, L.E., Aghasyan, A., García, A., Aguilar, C., Ajtic, R., Akarsu, F., Alencar, L.R.V., Allison, A., Ananjeva, N., Anderson, S., et al. (2013): The conservation status of the world's reptiles. Biol. Conserv. **157**: 372-385.

Bour, R., Probst, J.M., Ribes, S. (1995): *Phelsuma inexpectata* Mertens,1966, le lézard vert de Manapany-les-Bains (La Réunion): données chorologiques et écologiques (Reptilia, Gekkonidae). Dumerilia **2**: 99-124.

Buckland, S., Cole, N.C., Godsall, B., Rodríguez-Pérez, J., Gallagher, L.E., Henshaw, S.M., Harris, S. (2014): Habitat selection of the Mauritian lowland forest day gecko at multiple spatial scales: a baseline for translocation. Glob. Ecol. Conserv. **1**: 71-79.

Bungard, M.J., Jones, C., Tatayah, V., Bell, D.J. (2014): The habitat use of two species of day geckos (*Phelsuma ornata* and *Phelsuma guimbeaui*) and implications for conservation management in island ecosystems. Herpetol. Conserv. Biol. **9**: 551-562.

Burnham, K.P., Anderson, D.R. (2002): Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach, 2nd Edition. Springer, New-York.

Caceres, S., Jasmin, J.N., Sanchez, M. (2010): Observations comportementales chez le gecko vert des hauts, *Phelsuma borbonica* Mertens, 1942 (Squamata: Gekkonidae). Bull. Phaethon **30**: 10-19.

Castilla, A.M., Swallow, J.G. (1995): Artificial egg-laying sites for lizards: a conservation strategy. Biol. Conserv. **72**: 387-391.

Choeur, A. (2021): Conservation du gecko vert de Manapany (*Phelsuma inexpectata*) et du puffin du Pacifique (*Ardenna pacifica*). Approche multispécifique pour la conservation des falaises littorales du sud de l'île de La Réunion. Ph.D Dissertation, University of Reunion Island.

Choeur, A., Clémencet, J., Le Corre, M., Sanchez, M. (2022a): Evidence of seasonal reproduction, laying site fidelity, and oviposition synchronicity in the critically endangered endemic Manapany Day Gecko (*Phelsuma inexpectata*) from Reunion Island (western Indian Ocean). Salamandra **58**: 116-122.

Choeur, A., Faulquier, L., Orlowski, S., Dijoux, J., Potin, G., Bureau, S., Guilhaumon, F., Le Corre, M. (2022b): Impacts and management of unowned and owned cats at a seabird colony on Reunion Island (Western Indian Ocean). Biol. Invasions **24**: 2365-2382.

Cole, N.C. (2005): The ecological impact of the invasive house gecko *Hemidactylus frenatus* upon endemic Mauritian geckos. Ph.D Dissertation, University of Bristol.

Cole, N.C., Goder, M., Vencatasamy, D., Mootoocurpen, R., Havery, S., Gamble, F., Nundlaul, V. (2013): Restoration of Island Ecosystems in Mauritius: the Mauritius Reptile Recovery Programme Annual Report 2013. Unpublished report, Durrell Wildlife Conservation Trust, Jersey.

Crawford, C.M., Thorpe, R. (1979): Body temperatures of two geckos (*Phelsuma*) and a skink (*Mabuya*) in Praslin, Seychelles. Brit. J. Herpetol. **6**: 25-31.

Crawley, M.J. (2007): The R Book, 2nd Edition. John Wiley & Sons, Chichester.

Delaney, D.M., Warner, D.A. (2016): Age- and sex-specific variations in microhabitat and macrohabitat use in a territorial lizard. Behav. Ecol. Sociobiol. **70**: 981-991.

Deso, G., Probst, J.M. (2007): Observation d'un nouvel environnement chez le gecko vert de Manapany *Phelsuma inexpectata* Mertens, 1966 (Sauria: Gekkonidae). Bull. Phaethon **25**: 37-42.

Elphick, M.J., Shine, R. (1999): Sex differences in optimal incubation temperatures in a scincid lizard species. Oecologia **118**: 431-437.

Fenouillas, P., Ah-Peng, C., Amy, E., Bracco, I., Dafreville, S., Gosset, M., Ingrassia, F., Lavergne, C., Lequette, B., Notter, J.C., Pausé, J.M., Payet, G., Payet, N., Picot, F., Poungavanon, N., Strasberg, D., Thomas, H., Triolo, J., Turquet, V., Rouget, M. (2021): Quantifying invasion degree by alien plants species in Reunion Island. Austral Ecol. **46**: 1125-1137.

Fielding, A.H., Bell, J.F. (1997): A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. **24**: 38-49.

Fitzgerald, M., Shine, R., Lemckert, F. (2003): A reluctant heliotherm: thermal ecology of the arboreal snake *Hoplocephalus stephensii* (*Elapidae*) in dense forest. J. Therm. Biol. **28**: 515-524.

Flecks, M., Weinsheimer, F., Böhme, W., Chenga, J., Lötters, S., Rödder, D. (2012): Watching extinction happen: the dramatic population decline of the critically endangered Tanzanian Turquoise Dwarf Gecko, *Lygodactylus williamsi*. Salamandra **48**: 12-20.

Furrer, S.C., Jaag, K., von Stockar, S., Rübel, A. (2006): First experiences with free-ranging giant day geckos (*Phelsuma madagascariensis grandis*, Gray 1870) in the masoala rainforest exhibit in Zurich Zoo, Switzerland. Zoo Biol. **25**: 409-415.

Gardner, A.S. (1984): The evolutionary ecology and population systematics of day geckos (*Phelsuma*) in the Seychelles. Ph.D. Dissertation, University of Aberdeen.

Gardner, T.A., Barlow, J., Peres, C.A. (2007): Paradox, presumption and pitfalls in conservation biology: the importance of habitat change for amphibians and reptiles. Biol. Conserv. **138**: 166-179.

Glaw, F., Vences, M. (2007): A Field Guide to the Amphibians and Reptiles of Madagascar. Vences and Glaw Verlag, Cologne.

Hagey, T.J., Cole, N.C., Davidson, D., Henricks, A., Harmon, L.L., Harmon, L.J. (2016): Temporal variation in structural microhabitat use of *Phelsuma* geckos in Mauritius. J. Herpetol. **50**: 102-107.

Hansen, D.M., Kiesbüy, H.C., Jones, C.G., Müller, C.B. (2007): Positive indirect interactions between neighboring plant species via a lizard pollinator. Am. Nat. **169**: 534-542.

Howard, R.D. (1978): The influence of male-defended oviposition sites on early embryo mortality in bullfrogs. Ecology **59**: 789-798.

Humphrey, J.E., Ward, C.F.M. (2018): Madagascan Day Geckos (*Phelsuma spp.*) Exhibit Differing responses along a gradient of land-use change. Trop. Conserv. Sci. **11**: 1940082918760282.

Ineich, I. (2010): How habitat disturbance benefits geckos: conservation implications. C. R. Biol. **333**: 76-82.

Kearney, M., Shine, R., Porter, W.P. (2009): The potential for behavioural thermoregulation to buffer "cold-blooded" animals against climate warming. PNAS **106**: 3835-3840.

Lebreton, J.D., Burnham, K.P., Clobert, J., Anderson, D.R. (1992): Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol. Monogr. **62**: 67-118.

Lehtinen, R. (2002): The use of screw pines (*Pandanus spp.*) by amphibians and reptiles in Madagascar. Herpetol. Bull. **82**: 20-25.

Lunghi, E., Manenti, R., Ficetola, G.F. (2015): Seasonal variation in microhabitat of salamanders: environmental variation or shift of habitat selection? PeerJ **3**: e1122.

Manly, B.F., McDonald, L., Thomas, D.L., McDonald, T.L., Erickson, W.P. (2004): Resource Selection by Animals: Statistical Design and Analysis for Field Studies, 2nd Edition. Kluwer, London.

Météo France (2021): Temperatures and precipitions on Reunion Island. Données Publiques de Météo-France. URL https://donneespubliques.meteofrance.fr/.

Nemes, S., Vogrin, M., Hartel, T., Öllerer, K. (2006): Habitat selection at the sand lizard (*Lacerta agilis*): ontogenetic shifts. North-West. J. Zool. **2**: 17-26.

Noble, T., Bunbury, N., Kaiser-Bunbury, C.N., Bell, D.J. (2011): Ecology and co-existence of two endemic day gecko (*Phelsuma*) species in Seychelles native palm forest: *Phelsuma* niche partitioning in native habitat. J. Zool. **283**: 73-80.

Norbury, G., van den Munckhof, M., Neitzel, S., Hutcheon, A., Reardon, J., Ludwig, K. (2014): Impacts of invasive house mice on post-release survival of translocated lizards. N. Z. J. Ecol. **38**: 322-327.

Nussbaum, R.A., Raxworthy, C.J., Raselimanana, A.P., Ramanamanjato, J.B. (2000): New Species of Day Gecko, *Phelsuma* Gray (Reptilia: Squamata: Gekkonidae), from the Réserve Naturelle Intégrale d'Andohahela, Southern Madagascar. Copeia **2000**: 763-770.

Osadnik, G. (1984): An investigation of egg laying in *Phelsuma* (Reptilia: Sauria: Gekkonidae). Amphib.-Reptil. **5**: 125-134.

Packard, G.C. (1991): Physiological and ecological importance of water to embryos of oviparous reptiles. In: Egg Incubation, Its Effects on Embryonic Development in Birds and Reptiles, p. 213-228. Deeming, D.C., Ferguson, M.W.J., Eds, Cambridge University Press, Cambridge.

Palmas, P., Jourdan, H., Rigault, F., Debar, L., De Meringo, H., Bourguet, E., Mathivet, M., Lee, M., Adjouhgniope, R., Papillon, Y., Bonnaud, E., Vidal, E. (2017): Feral cats threaten the outstanding endemic fauna of the New Caledonia biodiversity hotspot. Biol. Conserv. **214**: 250-259.

Pike, D.A., Webb, J.K., Shine, R. (2010): Nesting in a thermally challenging environment: nest-site selection in a rock-dwelling gecko, *Oedura lesueurii* (Reptilia: Gekkonidae). Biol. J. Linn. Soc. **99**: 250-259.

Pollock, K.H. (1982): A capture-recapture design robust to unequal probability of capture. J. Wildl. Manag. **46**: 752-757.

Pough, F., Andrews, R., Cadle, J., Crump, M., Savitzky, A., Wells, K. (2003): Herpetology, 3rd Edition. Prentice Hall, New Jersey.

Pringle, R.M., Webb, J.K., Shine, R. (2003): Canopy structure, microclimate, and habitat selection by a nocturnal snake, *Hoplocephalus bungaroides*. Ecology **84**: 2668-2679.

Qualls, C.P., Andrews, R.M. (1999): Cold climates and the evolution of viviparity in reptiles: cold incubation temperatures produce poor-quality offspring in the lizard, *Sceloporus virgatus*. Biol. J. Linn. Soc. **67**: 353-376.

Quiterie, D., Martin, T., Sarah, S., Raphaël, G., Mathilde, M., Vidal, E. (2019): Sympatric invasive rats show different diets in a tropical rainforest of an island biodiversity Hotspot1. Pac. Sci. **73**: 199-214.

R Core Team (2019): R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rakotozafy, L.M. (2019): Population structure, activity pattern, and microhabitat use of *Phelsuma klemmeri* at Mandrozo, Madagascar. Malagasy Nature **13**: 88-96.

Ramírez-Bautista, A., Benabib, M. (2001): Perch height of the arboreal lizard *Anolis nebulosus* (Sauria: Polychrotidae) from a tropical dry forest of Mexico: effect of the reproductive season. Copeia **2001**: 187-193.

Raxworthy, C.J., Nussbaum, R.A. (1993): A New Madagascan *Phelsuma*, with a Review of *Phelsuma trilineata* and Comments on *Phelsuma cepediana* in Madagascar (Squamata: Gekkonidae). Herpetologica **49**: 342-349.

Reagan, D.P. (1986): Foraging behavior of *Anolis stratulus* in a Puerto Rican rain forest. Biotropica **18**: 157-160.

Resetarits, W.J. (1996): Oviposition site choice and life history evolution. Am. Zool. **36**: 205-215.

Resetarits, W.J., Wilbur, H.M. (1989): Choice of oviposition site by *Hyla chrysoscelis*: role of predators and competitors. Ecology **70**: 220-228.

Roberts, S.H., Daly, C. (2014): A rapid herpetofaunal assessment of Nosy Komba Island, northwestern Madagascar, with new locality records for seventeen species. Salamandra **50**: 18-26.

Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J.C., Müller, M., Siegert, S., Doering, M., Robin, M.X. (2021): pROC: an open-source package for R and S+ to analyze and compare ROC curves. BMC Bioinf. **12**: 1-8.

Rocha, S., Carretero, M.A., Harris, D.J. (2010): Genetic diversity and phylogenetic relationships of *Mabuya spp.* (Squamata: Scincidae) from western Indian Ocean islands. Amphib.-Reptil. **31**: 375-385.

Roesch, M.A., Hansen, D.M., Cole, N.C. (2021): Understanding demographic limiting factors to species recovery: nest-site suitability and breeding ecology of *Phelsuma guentheri* on Round Island, Mauritius. GECCO **30**: e01761.

Salvidio, S., Oneto, F. (2008): Density regulation in the Mediterranean leaf-toed gecko *Euleptes europaea*. Ecol. Res. **23**: 1051-1055.

Sanchez, M. (2012): Mitigating habitat loss by artificial egg laying sites for Reunion day gecko *Phelsuma borbonica*, Sainte Rose, Reunion Island. Conserv. Evid. **9**: 17-21.

Sanchez, M. (2021): *Phelsuma inexpectata*. The IUCN Red List of Threatened Species **2021**: e.T17450049A17450059. Downloaded on 05 September 2021.

Sanchez, M., Caceres, S. (2019): Plan national d'actions en faveur des Geckos verts de La Réunion *Phelsuma borbonica* et *Phelsuma inexpectata*. NOI/ONCFS pour la DEAL Réunion, Reunion Island.

Sanchez, M., Choeur, A., Bignon, F., Laubin, A. (2019): Reptiles of the Iles Eparses, Indian Ocean: inventory, distribution, and conservation status. Herpetol. Conserv. Biol. **14**: 481-502.

Sanchez, M., Probst, J.M. (2011): Distribution and conservation status of the Manapany day gecko, *Phelsuma inexpectata* MERTENS, 1966, an endemic threatened reptile from Réunion Island (Squamata: Gekkonidae). Cah. Sci. Océan Indien Occident. **2**: 13-28.

Sanchez, M., Probst, J.M. (2014): Distribution and habitat of the invasive giant day gecko *Phelsuma grandis* Gray 1870 (Sauria: Gekkonidae) in Reunion Island, and conservation implication. Phelsuma **22**: 13-28.

Sanchez, M., Probst, J.M. (2017): *Phelsuma borbonica* Mertens, 1966 (Sauria: Gekkonidae) sur l'île de La Réunion. Répartition et habitats naturels. Bull. Soc. Herp. Fr. **162**: 17-30.

Sanchez, M., Probst, J.M., Deso, G. (2009): *Phelsuma inexpectata* Mertens, 1966 (Squamata: Gekkonidae) sur l'île de La Réunion: écologie, répartition et menaces. Bull. Soc. Herp. Fr. **132**: 43-69.

Sanchez, M., Vingadachetty, J. (2016): Etude pour améliorer la conservation des populations de *Phelsuma borbonica* occupant les aménagements artificiels en milieu naturel du Parc national de La Réunion – Action 2: Taux d'éclosion des oeufs – Rapport Final n°2. Rapport Nature Océan Indien pour le Parc national de La Réunion, Reunion Island.

Somaweera, R. (2009): Reproductive ecology of the Kandyan Day Gecko, *Cnemaspis kandiana*, in Gannoruwa Forest Reserve. J. Natl. Sci. Found. **37**: 13-22.

Stone, P.A., Baird, T.A. (2002): Estimating lizard home range: the Rose model revisited. J. Herpetol. **36**: 427-436.

Strasberg, D., Rouget, M., Richardson, D.M., Baret, S., Dupont, J., Cowling, R.M. (2005): An Assessment of Habitat Diversity and Transformation on La Réunion Island (Mascarene Islands, Indian Ocean) as a Basis for Identifying Broad-scale Conservation Priorities. Biodivers. Conserv. **14**: 3015-3032.

Valentine, L.E., Roberts, B., Schwarzkopf, L. (2007): Mechanisms driving avoidance of non-native plants by lizards. J. Appl. Ecol. **44**: 228-237.

Vinson, J., Vinson, J.M. (1969): The saurian fauna of the Mascarene Islands. A revision of the fauna. The Maurit. Inst. Bull. **6**: 203-320.

Vitt, L.J., Caldwell, J.P. (2013): Herpetology: an Introductory Biology of Amphibians and Reptiles, 4th Edition. Academic Press, New-York.

Wanger, T.C., Motzke, I., Furrer, S.C., Brook, B.W., Gruber, B. (2009): How to monitor elusive lizards: comparison of capture-recapture methods on giant day geckos (Gekkonidae, *Phelsuma madagascariensis grandis*) in the Masoala rainforest exhibit, Zurich Zoo. Ecol. Res. **24**: 345-353.