Social life or comfortable home? Factors involved in refuge selection in Cabo Verdean geckos

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Todas as correcções determinadas pelo júri, e só essas, foram efectuadas.

O Presidente do Júri,

MSc

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Resumo

Em pequenos sedentários ectotérmicos, a ecologia espacial resulta do jogo e múltiplos factores, às vezes conflituantes, como variáveis abióticas e interacções bióticas. Avaliar os custos e benefícios destas pressões é crucial para tomar decisões comportamentais correctas em termos de *fitness*. A osga endémica insular *Tarentola substituta* habita áreas rochosas e áridas onde os refúgios são limitados, a densidade de conspecíficos alta e os predadores escassos. Efectuaram-se duas experiências paralelas para testar o papel de factores ecológicos e sociais na selecção de refúgios por esta osga: no laboratório e numa área árida representativa da ilha de São Vicente, Cabo Verde, onde só ocorre esta espécie de réptil. A primeira realizou-se para analisar o papel dos factores ecológicos (temperatura, refúgio) e sociais (presença de conspecíficos) na escolha de refúgios. Efectuaram-se observações independentes num terrário de indivíduos isolados ou em combinações de dois de diferentes idades e sexos, permitindo-lhes escolher quatro tipos de refúgio: de alta/ baixa qualidade, perto/longe duma fonte de calor. Os resultados sugerem que as osgas seleccionam refúgios maiores em detrimento da presença de conspecíficos, mas nem sempre da qualidade térmica. Em termos sociais, o género, idade e diferenças de tamanho entre indivíduos moldaram os padrões de agregação, influenciando a frequência de ocorrência. Estes resultados estão de acordo com observações de campo, sugerindo a selecção de rochas como refúgios diurnos de acordo com as propriedades térmicas e agregações sociais sobretudo envolvendo machos e fêmeas adultos, mas não juvenis. Na experiência de campo, 10 estações foram amostradas relativamente à presença de osgas (considerando idade, sexo e tipo de agregação) e disponibilidade de refúgios de alta qualidade. Depois, a densidade desses refúgios foi manipulada para determinar quais os efeitos na escolha destes pelas osgas. Os resultados revelaram fidelidade em agregações macho/fêmea, mesmo depois da perturbação dos refúgios. Rochas maiores foram de novo o refúgio preferido, corroborando estudos anteriores. Por fim, notou-se um distúrbio menor nas estações onde refúgios de alta qualidade foram adicionados, provendo dados importantes para guiar a gestão da espécie. Em suma, estes resultados combinados fornecem informação sobre a ecologia espacial em ectotérmicos em condições de baixa predação, recursos limitados e alta competição intraespecífica, como as dos sistemas insulares.

Palavras-chave

Ilhas áridas; Cabo Verde; Comportamento social; Conservação; Ectotermos; Ecologia térmica; Gestão de habitat; Macaronésia; Répteis; *Trade-off* comportamental

Summary

In small sedentary ectotherms, spatial ecology results from the interplay between multiple, often conflicting factors, including abiotic environment and biotic interactions. Evaluating the costs and benefits of these pressures is crucial to make correct behavioural decisions in terms of fitness. The endemic island gecko *Tarentola substituta* inhabits arid rocky habitats where refuges are limited, density of conspecifics is high, and predators are almost absent. Two parallel experiments were conducted to determine the roles of ecological and social factors in refuge selection by this gecko: one in the lab, and another in a representative arid area of São Vicente Island, Cabo Verde, where only this reptile species is present. The first determined the roles of ecological (temperature, shelter size) and social (conspecifics' presence) factors in refuge selection. Independent observations of solo and pair combinations of different size and sex classes were set in a terrarium, allowing selecting four refuge options: cold small, hot small, cold large and hot large rock. Results suggest that geckos primarily select larger shelters trading-off the presence of conspecifics and, but not always, thermal quality. In social terms, the gender and age, and size disparity shaped the patterns of aggregation. These results reasonably match field observations, suggesting selection of rocks as diurnal retreats according to their thermal properties, and social aggregations mainly involving adult males and females but not juveniles. In the field experiment, 10 quadrats were surveyed for geckos (considering size, sex and aggregation) and high-quality refuge availability. Subsequently, the density of high-quality refuges was manipulated to determine its effects on refuge choice by geckos. Results showed aggregation fidelity in male/female, even after refuge disturbance, and bigger rocks as preferred refuges. After the addition of high quality refugia, the disturbance due to rock turning had less impact. This indicates future guidelines regarding the species management. Overall, this combined evidence provides insights on the spatial ecology of ectotherms under conditions of low predation, limited resources and high interspecific competition such as those prevailing on island systems.

Keywords

Arid islands; Behavioural trade-off; Cabo Verde; Conservation; Ectotherms; Habitat management; Macaronesia; Reptiles; Social behaviour; Thermal ecology

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General Introduction

Across all animal groups, different kinds of pressures are applied to each species, with each individual pressure being more or less impactful depending on which species are considered. Therefore, animal classes such as mammals, birds and reptiles will differ in the type of pressure which will influence their behaviour the most. As an example, the European robin *Erithacus rubecula* is characterized by having highly territorial males (Schwabl & Kriner, 1991). Therefore, at the conspecific level, this factor may greatly impact its behaviour. However, at the home range level, bird species are not so constrained due to their very large areas of coverage (Powell, 2000). Thus, it may have more ease in escaping a predator, seeking food or fleeing from an aggressive conspecific due to its mobility. This scenario contrasts with many terrestrial ectotherms with small body size, which are largely sedentary and hold small home ranges (Chown & Nicolson, 2004; Žagar *et al.*, 2018) when compared to mammals or birds, are largely exposed to local microhabitat changes having a greater impact in its fitness.

Ectotherms completely depend on the thermal environment to accommodate their thermal necessities (Huey, 1982), as opposed to endotherms such as birds or mammals. Because of that, they must select microhabitats according to their thermal properties. However, the spatial ecology at the microhabitat level is also constrained by other factors, which have to be balanced to optimiser fitness. As such, intra and interspecific competition (Downes & Shine, 1998; Langkilde & Shine, 2004; Vasconcelos *et al.*, 2012; Penado *et al.*, 2015), predator avoidance (Downes & Shine, 1998; Lapiedra *et al.*, 2018) and food availability (Stamps & Tanaka, 1981; Pafilis *et al.*, 2009) are elements that should be taken into consideration to evaluate habitat use by ectotherms. The neglection of these factors may lead to biased conclusions, since they may be the reason for the persistence of these individuals under sub-optimal conditions from any of these balancing factors. Furthermore, the comprehension of the microhabitat use, regarding biotic and abiotic variables (Carretero *et al.*, 2016), its crucial in order to understand their ecology and better direct conservation efforts.

Among ectotherms, reptiles are among the most studied classes regarding thermoregulation (Huey & Slatkin, 1976; Avery *et al.*, 1982; Huey & Kingsolver, 1989; Huey, 1982; Aguilar & Cruz, 2010; Seebacher & Franklin, 2005). More specifically, lizards and gecko species have been gathering a lot of attention in disentangling factors involved in their fitness and their relationship with behavioural thermoregulatory behaviour (Vasconcelos *et al.*, 2012; Vasconcelos *et al.*, 2017; Downes & Shine, 1998; Kearney & Prevadec, 2000; Kearney, 2002; Shah *et al.* 2004). Individuals inhabiting arid environments, especially islands, since these simple environments are rather useful for the study of the connecting factors between environmental temperature and microhabitat selection, in regards to gecko species (Vasconcelos *et al.*, 2012).

In this thesis, from the small ectotherms group a gecko species *Tarentola substituta* was chosen as a model species. More specifically, from an arid habitat within an island, due to the present conditions and their important ecological role in this type of environment (Cloudsley-Thompson, 1991). High diurnal temperatures present in arid islands lead these individuals to seek refuge during the day (Vasconcelos *et al.*, 2012), while cooler nocturnal temperatures allow for more proactive behaviour. This refuge selection behaviour may promote the occurrence of social interactions and agonistic behaviours (Penado *et al.*, 2015; Vasconcelos *et al.*, 2017), since the high conspecific density makes the number of optimal refuges quite limited. Therefore, the analysis of these biotic interactions, relation to their thermal environment and other microhabitat properties chosen by geckos, is facilitated, if arid habitats are chosen as research areas. Namely, the combination of factors such as the scarcity of predators, the absence of competitors and the low habitat complexity (Whittaker & Fernández-Palacios, 2007) and the biotic characteristics of this species (optimized food and water economy; sit-and-wait foraging and nocturnality) make this study subject and area makes it very attractive for the study of behavioural ecology study in geckos.

Thus, the aim of this thesis was to tackle two sets of questions addressing the refuge selection behaviour, its underlying aspects and impacts of human disturbance on the wild. The questions were the following: 1) In conditions of high temperature, low food and water availability, low predation pressure and high intraspecific competition, which are the relative contributions of temperatures, refuge traits and conspecific presence? Which takes precedence? 2) In these conditions, how refuge quality, density and disturbance impact on gecko populations? It is expected that the data obtained will be important to better allocate conservation measures and shed more light upon the understudied social behaviour in reptiles.

This thesis is divided into the following two chapters: an original article regarding a laboratory experiment for refuge selection in a endemic gecko, already submitted to the journal *Animal Behaviour*; and a report concerning the impacts of anthropogenic microhabitat disturbances in the same species, in the final stages of preparation before submission to the journal *Amphibian & Reptile Conservation*.

Original article: Insular geckos provide experimental evidence on refuge selection priorities by ectotherms

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Abstract

In small sedentary ectotherms, patterns of spatial use result from the interplay between multiple, often conflicting factors, including abiotic and biotic interactions. Evaluating the costs and benefits of these pressures is crucial to make correct behavioural decisions in terms of fitness. The insular São Vicente's wall gecko *Tarentola substituta* provides a relatively simple model system to study these questions as it inhabits arid rocky habitats where refuges are limited, density of conspecifics is high, and terrestrial predators are almost absent. In the field, adults tend to find diurnal shelter under mid-sized rocks, frequently in male-female couples, while juveniles occupy small rocks which are thermally suboptimal. A lab experiment was conducted to determine the roles of ecological (shelter size and temperature) and social (conspecifics) factors in refuge selection. Single and pair combinations of geckos of different age and sex classes were allowed to select among four refuges: cold small, hot small, cold large, or hot large rock. Based on previous studies, we hypothesized that larger and thermally buffered rocks would be the preferred refuges, and that adult male-female pairs under the same rock would be more frequent than other combinations.

Geckos primarily selected larger shelters, trading off the presence of conspecifics against thermal quality. In social terms, sex, adult condition and size-related disparity shaped the patterns of aggregation, resulting in lower aggregation frequencies between adults and juveniles and even between juveniles of different sizes. These results reasonably match field observations suggesting selection of rocks as diurnal retreats according to their thermal properties, and social aggregations mainly involving adult males and females but not juveniles. Overall, this combined evidence provides insights on the spatial ecology of geckos, and likely other ectotherms, under conditions of low predation, limited resources and high intraspecific competition, such as those prevailing on island systems.

Keywords: arid islands, behavioural trade-off, Macaronesia, reptiles, social behaviour, thermal ecology

Introduction

Refuge use by small sedentary ectotherms is influenced by several biotic and abiotic factors (Penado et al., 2015). Competition with conspecifics, or predator avoidance, and type and availability of refuges are some of the conditioning factors in small ectotherms fitness (Downes & Shine, 1998; Huey et al., 1989b). Among ectotherms, geckos stand out due to their key ecological role in food webs of arid habitats (Cloudsley-Thompson, 1991), especially on islands (Vitt & Caldwell, 2009). Furthermore, islands, especially arid ones, provide simplified systems of study, with scarcity of terrestrial predators, scarcity of competitors and low habitat complexity (Whittaker & Fernández-Palacios, 2007).

Use of refuges is crucial to prevent predation, but their selection is also constrained by abiotic factors. In particular, temperature is important for ectotherms since it can determine the rate of behaviours such as running, foraging, reproduction and survival (Angilletta, 2009; Huey, 1982). Active ectotherms aim to be close to their performance optimum (e.g. running), but when inactive they still need to prevent attaining critical temperatures while enabling digestion and possible behavioural interactions. Indeed, refuges play a role in aiding ectotherms to balance their thermal necessities with other biological functions in order to survive and thrive (Huey & Kingsolver, 1989). Diurnal reptiles select for basking sites and display postures enhancing heat gain or loss to keep body temperatures within a narrow range optimizing their biological functions (Huey, 1982). However, nocturnal geckos have limited possibilities for thermoregulation, attaining low body temperatures (Huey et al., 1989c; Kearney & Prevadec, 2000), although, conversely, they are more selective in their diurnal retreats to prevent overheating (Angilletta et al., 1999).

In addition, social and agonistic interactions may occur at the intraspecific level under refuges (Downes & Shine, 1998), which may influence the individual refuge selection. Geckos are frequently territorial sit-and-wait foragers, and hence prone to strong intraspecific interactions (Pianka & Vitt, 2003). Male lizards are much more aggressive than females towards other juveniles and adults (Cooper et al., 2015), and may actually hurt or display threating behaviour in cases of intraspecific male competition (Bohórquez-Alonso et al., 2014) or territorial defence (Marcellini, 1974). This suggests a prominent role of intraspecific competition for refuge in geckos, for determining individual fitness in these environments. Thus, refuge availability may pose social constrains among nocturnal geckos, since refuge choice becomes critical when gecko populations are close to carrying capacity, i.e, high gecko densities and limited refuges (Huey, 1982; Kearney, 2002; Shah et al., 2004). This scenario is particularly suited to arid islands (Vasconcelos et al., 2012a), contrary to continental or temperate areas. In the latter areas, factors such as thermal restriction or biotic interactions with other species usually keep populations at lower effective sizes and, hence, less limited by refuges, turning the refuge selection a multifactorial problem. Therefore, analysing the retreat-site features on islands may shed light upon the underlying social and ecological factors related to shelter choices that can then be applied to more complex systems. Beyond the intrinsic behavioural interest, this inference will be valuable in conservation terms considering the significance of microhabitat features for species distribution and abundance (Shah et al., 2004).

Summarizing, due to the high diurnal temperatures, adequate retreat-site choice of island geckos becomes crucial, since provides: (1) shelter from predators; (2) heat source for subsequent activity period (Huey et al., 1989a); (3) protection from over-heating (Kearney, 2002; Vasconcelos et al., 2012a); and (4) conditions within operative physiological ranges (Autumn & Nardo, 1995).

The present study follows an experimental approach, based on previous field and lab experience (Carretero et al. 2016, Vasconcelos et al. 2012, 2017), to infer the roles of ecological and social factors on the refuge selection by a sedentary ectotherm under a context of low predation pressure and high interspecific competition. As model organism we use the nocturnal wall gecko *Tarentola substituta* endemic of São Vicente Island, Cabo Verde. This rock-dwelling gecko spends the daylight hours inactive under refuges, with preference for medium to big-sized rocks (Vasconcelos et al., 2012a). Conspecifics have been observed aggregating predominantly in adult male and female couples, sharing mid-size rocks within and outside the reproductive season (Vasconcelos et al., 2012a, 2017). This suggests persistent competition for optimal refuges between adults (mainly males) and juveniles (Vasconcelos et al., 2012a).

Here, we address the following questions: 1) Does thermal environment influence refuge selection in *T. substituta*? 2) Does refuge quality affect aggregation behaviour? 3) Does the presence of conspecifics influence aggregation or agonistic behaviour? We predict that geckos will select retreat-sites in a non-random fashion according first to their sex and body size, second to the refuge size and only third to the thermal properties of the refuge. The high density of conspecifics leads us to believe that this will take precedent over other factors, while rock size will follow since it has already been shown its importance for this species (Vasconcelos et al. 2012). Results in this experimental simplified system are expected to contribute for the understanding of refuge selection, and will also shed light on the understudied social behaviour of geckos and other small sedentary ectotherms. In a more applied way, we aim to stablish a robust framework for the management and conservation of this endemic reptile and other species with similar requirements.

Methods

Study Species

Tarentola substituta (Squamata, Phyllodactylidae) is an endemic nocturnal, medium-sized (average snout-vent length, SVL, of 51.60 ± 3.64 mm) flattened gecko with a long tail, adhesive pads, and a large head with a pointed snout (Joger, 1984; Vasconcelos et al., 2012b). It is a rock-dwelling species which exclusively uses rocks as retreat-sites during high diurnal temperatures, with temperatures under refuges ranging between 22 and 41 ºC depending on the hour of the day and size of the rock (Vasconcelos et al., 2012a). The species remains active throughout the year (Schleich, 1987). It is locally very abundant and exclusively occurs across the vast arid areas of São Vicente Island, only avoiding the scarce sub-humid or sandy areas (Vasconcelos et al., 2013).

Experiment Description

A total of 45 individuals were collected from a single population in Calhau (16º 51’ 11.2” N, 24º 52’ 11.8” W), in equal number of males, females and juveniles (15 individuals each). The collection period (October 30, 2017) fell outside the reproductive season to prevent interaction with copulation and egg-laying. Habitat use and thermal ecology have already been assessed during the same period (Vasconcelos et al., 2012a; Carretero et al., 2016). Geckos were transported to the laboratory, where they were identified and placed in individually tagged cloth bags to reduce stress. The SVL of each individual (Ind) was measured to the nearest 1 mm with a ruler and its body mass weighted to the nearest 0.001 g (Table A1 in Appendixes), using a digital scale (Nahita Electric balance series 5153). Every individual was classified as adult or juvenile based on its SVL (juvenile ≤ 45 mm) and on the presence of evident secondary sexual characters (e.g. enlarged cloacal spurs in males) (Vasconcelos et al., 2012a). Adult individuals were sexed considering the presence of evident primary (e.g. hemipenises in males; eggs or follicles in females) and secondary sexual characters (Vasconcelos et al., 2012a). Additionally, males also presented higher body mass and larger body size in contrast to adult females (Schleich, 1987; see below). Individuals were consequently divided into three classes: males (M), females (F) or juveniles (J). All geckos were individually marked on the ventral side using a temporary marker pen and photographed (dorsal and ventral sides) on top of millimetre paper for additional identification.

The refuge selection experiment tests were conducted from October 31 to November 4, 2017. Experiments consisted of single individuals and pair combinations of geckos placed inside a terrarium (1x0.3x0.4 m), with two sets of refuge options: a high-quality refuge, a medium-sized rock following the definition by Vasconcelos et al., (2012a) – herein designated as big rock (20x10cm) – and a low-quality refuge – small rock (7x4cm) herein – placed close and far from a heat source produced by a 150 W infrared lamp (Fig. 1). The experiment was conducted in a laboratory at the University of Cabo Verde deprived of natural light and maintained at 21 °C, which was ensured by monitoring the air temperature with a digital thermometer (HIBKO 14, precision ±0.1ºC) before each round of 10 tests. A total of 520 refuge selection tests, randomized for time, terrarium, class or test type in R (code= function (n) sample (1:45, n, replace=T)), with n=10 in case of single tests and n=20 in case of pair tests). The initial test list was then manually corrected in order to avoid the same animal to perform consecutive tests. Tests were planned *a priori* to encompass a period of five days (October 31 to November 4, 2017), totalling 100-130 tests per day simultaneously using 10 terraria.

Tests were conducted from 8 a.m. to 8 p.m., with 20 tests performed per hour in total, using 10 terraria. Every day, at 7 a.m., 1h before removing the individuals from their individually marked bags, we turned on the lamps of each terrarium to create a gradient between 20 and 50°C (Carretero et al., 2016). Multiple randomized replications for all combinations of pairs of gecko classes (male–male, M/M; male–female, M/F; male–juvenile, M/J; female–female, F/F, female–juvenile, F/J; juvenile–juvenile, J/J), for individual geckos, terraria and time intervals were tested. Indices for size disparity in SVL (SVL_I) and mass (W_I) were calculated as (SVL Ind1-SVL Ind2)/ (SVL Ind1+SVL Ind2) and (W Ind1-W Ind2)/ (W Ind1+W Ind2), respectively.

Experimental tests were conducted by observers who were unaware of the experimental treatment. All individuals were initially placed inside an opaque plastic cup on standby for two minutes in the middle of the terrarium, before the beginning of the test. The test started as the cup was manually and blindly lifted lasting 45 min, during which geckos were left completely undisturbed. At the end of this time, every rock in each terrarium was lifted and the position of each individual was recorded (under refuge – big or small rocks – or outside refuge – on the walls, ground; on the hot or cold side of the terrarium). It was also registered if there was aggregation. After each test, individuals were placed back inside their bags and the following test would ensue. The test was considered not valid in the few cases when geckos escaped from the terrarium or a technical problem happened. In total, we performed 455 valid lab tests (of the 520 planned ones), which encompassed 89 single animal tests and 366 pair tests. The remaining 65 tests were removed from the analyses due to missing individuals (temporarily escaped from the terraria). Table A2 contains the details of the experiments and describes the variables used.

Four data-loggers (i-buttons Thermochron temperature loggers DS1923, Maxim Integrated Products) were placed beneath each rock of and rotated between randomly chosen terraria to monitor temperature (to the nearest 0.01ºC) and relative humidity (to the nearest 0.01 %) during the experiments, ensuring the differences between the four types of refuges (See Table A3).

Ethical Note

Individuals were kept in captivity for five days. While not tested, geckos were kept inside individually tagged cloth -bags to minimise stress. Geckos were released back in the collecting site after the experiments. Male/female individuals found together in the wild were retrieved to the respective original rocks. Collecting permit was provided by S. Araújo from 'Direcção Nacional do Ambiente' and experiments followed the ethical guidelines of Uni-CV, the ABS/ASAB guidelines for ethical treatment of animals and in Anonymous (2012).

Statistical Analysis

Biometric variables were log-transformed to ensure normality by means of Shapiro-Wilk tests and compared between classes using ANOVA (SVL and W) or ANCOVA (W with SVL as covariate). Temperature and humidity under the four refuges were compared by means of ANOVA for repeated measures with refuge size and refuge temperature as independent variables. The effect of the different factors (temperature, Temp; refuge type, Ref; presence of a conspecific, Agg; class of the individual and/or conspecific, Class/ Test; differences in SVL, SVL_I, and mass, W_I etcetera, see Table A2) shaping refuge selection of *T. substituta* in a controlled environment (constant air temperature and light conditions) were tested using Generalized Linear Mixed-Models (GLMM) using the glmer R-package from the lmer4 library with binomial as family. In single animal tests, the dependent variable was the presence or absence of an individual under a rock, Out, and rock size (big/small), class of the individual (M/F/J), and temperature (hot/cold) were classified as independent variables, even though other combinations were also tested (see Table A4). Also, SVL and W were used as continuous predictors. For the pair tests, the dependent variables were aggregation and presence outside the refuge. Rock size, temperature, SVL_I, W_I and test type (Table A2) were used as independent variables, while in the models using temperature as dependent variable, aggregation, SVL_I, W_I, refuge and test type were used as independent variables (see Table 1 and A4).In all tests, the variable Ind was used as random factor. Model evaluation were performed according Burnham & Anderson (2003) and Zuur et al. (2009). The models with the lowest AIC score, lower variable complexity and most explanatory significant results were selected among the multiple tested models. The significance level was set at P= 0.05 in all cases.

Results

Individual and Refuge Differences

Juveniles, females and males SVL measured 37.7±0.1, 51.1±0.1, and 53.3±0.1 mm, respectively; and weighted 1.51±0.01, 4.55±0.01, and 4.96±0.01 g, respectively (average±SD). These measurements did not deviate from normality (Shaphiro-Wilks, tests P >0.2). Beyond the obvious result that juveniles were smaller and lighter than adults, in our sample males were marginally longer than females (ANOVA $F_{1,28}$= 3.90, P= 0.05) but neither heavier in absolute terms (ANOVA $F_{1,28}$= 0.99, P= 0.33) nor heavier for the same length than them (ANCOVA $F_{1,26}$= 01.52, P= 0.23).

From the four data loggers, temperatures registered were (average±SD): small/ hot refuge (30.03±3.20 ºC); big/hot refuge (30.28±3.46 ºC); small/cold refuge (26.31±1.98 ºC); big/cold refuge (26.37±2.06 ºC). Hot rocks were consistently much hotter than cold rocks across tests regardless their size while small rocks were slightly hotter without no interaction between both factors (ANOVA hot/cold $F_{1,440}$= 706.53, P= 10^{-6}; big/small $F_{1,440}$ = 7.32, P= 0.007; hot/cold*big/small $F_{1,440}$= 2.82, P= 0.09). As for humidity, hot rocks were always less humid than cold rocks, big rocks were more humid than small rocks, but humidity differences were more contrasted between big hot and small hot rocks (ANOVA hot/cold $F_{1,440}$= 706.53, P= 10^{-6}; big/small $F_{1,440}$= 7.32, P= 0.007; hot/cold*big/small $F_{1,440}$= 2.82, P= 0.09).

Refuge Use

Most individuals were found under refuges, namely 692 times (Fig. 2). Individuals were registered outside refuge (in a wall or ground) 131 times (one case in single tests: F= 1; and 130 times in pair tests: F/F= 15, F/J= 31, J/J= 43, M/F= 12, M/J= 23, M/M= 6; Fig. 2).

On total, the big rocks were selected as refuge 646 times (Pairs: F/F= 104, F/J= 105, J/J= 86, M/F= 85, M/J= 81, M/M= 99; Fig.2). As for the smaller rocks, individuals used them as refuge 44 times in total, with only one occurrence (a juvenile) in the single animal tests.

Comparing the selection of hot versus cold side of the terraria (Temp), there were 387 geckos observations on the colder side of the terraria, of which 37 times in the single animal tests and 350 times for the pair tests. As for the hot side, it was chosen 350 times in total, 51 times in the single animals tests and 299 in the pair tests. Each diferent gecko class had a similar number of observations in the colder and in the hoter area of the terrarium.

Aggregation

During pair tests, individuals were found alone under a rock 560 times and aggregated under the same rock in 172 cases (F/F= 30, F/J = 32, J/J= 36, M/F = 24, M/J = 16, M/M= 34; see Fig. 2).

Interactions between Refuge Use, Temperature and Aggregation

GLMM models revealed complex relationships between rock size and temperature when geckos selected for refuges individually which added to the effect of aggregation when geckos were tested in pairs (Table 1). In some of the models there was evidence that sexual maturity and size disparity modulated the results.

Specifically, for the single animal tests, the results confirmed a clear pattern for seeking refuge under bigger rocks, with no clear preference of temperature (Fig. 2). Results also showed no significant differences in the GLMM models among gecko classes, sizes or weights, although juveniles seem to prefer hot rocks (model AS10 in Table A4 and raw data. In pair tests (Table 1), the GLMM showed that the percentage of individuals found outside refuges was significantly associated to juveniles (both in J/J and adult/juvenile tests), cold temperatures, to larger differences of SVL and weights between tested individuals, with a degree of interaction among these variables (Fig.2; Table 1 and raw data). However, no significant values were detected in the GLMM test for refuge types among gecko classes in pair tests (Fig. 2), although smaller rocks were significantly more used as refuges in the colder side of the terrarium (Table A4 and raw data).

Males and juveniles aggregated less than other pairs (Fig. 2). As expected, such trend was significantly mediated by SVL and/or weight disparities in GLMM models (Table 1).

In fact, low aggregation between both adult classes and juveniles and even between juveniles was mediated by disparities in SVL and/or body mass (Table 1). M/F tests seem to only interact significantly with SVL_I. The variable W_I *per se* was also significant for aggregation. Lastly, the combinations F/J and M/F differed from the remaining results for aggregation since when accounting for temperature, in the first case also when using W_I as covariant, the interaction was significant (Table 1). In both cases, geckos aggregated more when they were in the colder area of the terrarium.

Discussion

The results supported a clear refuge selection by *T. substituta*. As such, geckos selected refuges based on size, temperature and presence of conspecifics. However, these individuals seem to prioritize one factor (refuge size) above the others. Remarkably, lab results reasonably matched with our systematic observations in the field (Vasconcelos et al., 2012a), proving the realism or the experiment and providing insights on the organization of the spatial priorities for this species and for other sedentary ectotherms. In particular, our models suggest that geckos prioritize refuge size having their thermal properties a subsidiary role while social aggregations tend to be lower between males and juveniles, with size disparity between individuals having an important influence.

Under or Outside Refuge?

The study species seeks refuge during daytime in order to fulfil their thermal requirements as a nocturnal ectotherm and find protection from aerial predators (Vasconcelos et al., 2012a). As expected, most geckos tended to use the refuges provided in the experiment as diurnal retreat instead of keeping outside them in the terraria. Likely, this reflects the secretive behaviour and foraging strategy of *Tarentola* geckos (Lisičić et al., 2012; Penado et al., 2015; Vroonen et al., 2012) but also the resemblance between artificial refuges and those commonly used in the field (Vasconcelos et al., 2012a). In fact, in single tests, there is only one case registered of a female outside the refuge during the experiment. Furthermore, they tended to select big refuges regardless their sex and size. More importantly, this trend did not seem to be majorly affected by either the thermal properties of the rocks or the presence of conspecifics. This suggests that refuge size takes precedence on the other two factors. Geckos may find other resources under large-sized rocks (see below) that they cannot find under small ones, while ensuring a better thermal microhabitat even under similar radiation (Penado et al., 2015; Schlesinger & Shine, 1994a; Vasconcelos et al., 2012a).

Interactions between adults (of either sex) and juveniles are among the tests with higher number of cases with individuals found outside refuges, where juveniles are the ones found the most outside of the refuge. Indeed, larger individuals have been observed to dominate smaller conspecifics (Downes & Shine, 1998; Penado et al., 2015; Stamps, 1977b; Stamps & Tanaka, 1981, Williams & McBrayer, 2007), promoting the possibility of agonistic interactions and competition for optimal retreat-sites. Under laboratory conditions, larger male velvet geckos *Oedura lesueurii* forced smaller subordinate males to sub-optimal retreat-sites (Downes & Shine, 1998). The present experimental design only provided a single refuge of each type, which was expected to force the subordinate individual to use a suboptimal refuge. However, here, large rocks were apparently optimal in either cold or hot side of the terraria since the experimental design avoided temperatures close to critical maximum. Therefore, one of the apparent optimal refuges was available, which could have been selected instead of staying outside refuges. Nevertheless, in such a small area as a terrarium, the dominance effect might have led juveniles out of refuges. The findings of both Vasconcelos et al. (2012a) and our own field observations indicate a tendency for juveniles to be found under small rocks, which may suggest a competitive displacement to these sub-optimal refuges. Remarkably, in those tests between two adult males, the percentage of animals outside refuges was the lowest. This suggests that, in situations of balance between males similar in size and mass, staying under a refuge may represent a temporary state while geckos establish dominance. However, intriguingly juvenile–juvenile tests yielded the highest number of cases outside refuges. Apparently, intraspecific competition starting earlier than sexual maturity may have resulted in clear subordinate and dominant juveniles mediated by size differences (even though they were harder to detect by us due to the smaller SVL and weight differences between juveniles) or individual aggressive/ passive behaviour (Civantos, 2000; Stamps, 1977a; Stamps & Tanaka, 1981). All the above is well supported by the models regarding Out variable, where size and/or weight disparities significantly interacted with M/J, F/J and J/J tests.

Big or Small Rocks, Hot or Cold Refuges?

There was a clear preference, in all pair combinations, for the larger rock regardless the temperature, with no clear differences among test types. Also, in single tests, such preference stands, and only a juvenile was registered using a small rock. This may be attributed to the larger area of protection that a big rock offers, mainly shielding the animal from predators (Croak et al., 2008; Penado et al., 2015; Shah et al., 2004), but also due to its better thermal and hydric properties (buffered temperature variation and higher humidity values, see data-logger tests and Vasconcelos et al., 2012a).

Nonetheless, São Vicente’s wall gecko has few terrestrial predators and big rocks were chosen despite the temperature it yielded for most tests (both cold and hot sides of the terraria were chosen in roughly the same proportions; Fig. 2). Thus, preference for larger rocks may rely on other factors. Probably, large refuges harboured or attracted more potential prey beneath them (Hódar et al., 2006). Literature on nocturnal geckos and diurnal lizards frequently supports a preference for warmer refuges by day (Downes & Shine, 1998; Shah, 2002; Langkilde & Shine, 2004; Shah et al. 2004; Aguilar & Cruz, 2010), underlying its importance in aspects such improved locomotor and digestive performance. Notwithstanding, the environmental context is important to understand the thermoregulatory behaviour of this species. In such extreme conditions as those in São Vicente, low temperatures and humidity do not pose a constraint, as these individuals are mainly active at night, preferred temperatures are relatively low, and are quite resistant to dehydration (Carretero et al., 2016). In the study area, geckos have a clear need of refuge during high daily temperatures but avoided those attaining extreme temperatures risking overheating and possibly death (Vasconcelos et al., 2012a). This risk is higher when smaller rocks are chosen, and, in fact, dead juveniles have been occasionally found in the field (pers. obs.). Despite the data-loggers recording similar mean temperatures under each refuge (~30ºC), hot big rocks were preferred over the smaller hot ones and smaller rocks are significantly more used as refuges in the colder side of the terrarium. Due to its size, the smaller rock provides less heterogeneous temperatures (from centre to periphery) compared to the larger one, while offers a poorer shelter from the extreme heat from the infra-red lamp. It is also important to highlight that significant differences in temperature of the shared refuges were registered in females/juveniles, and males/females tests.

Aggregation

Although the overall levels of aggregation observed in the laboratory apparently approached those expected by chance (0.25%), some pair combinations clearly deviated from that pattern. In particular aggregation between males and juveniles was much lower than expected. This contrasts with juvenile-juvenile and male-male combinations whose aggregation percentage was higher than expected by chance. This pattern is expectable if agonistic interactions between males and juveniles occurred, and juveniles were expelled from the best available refuges, as observed in previous studies on this species (Vasconcelos et al., 2012a; Vasconcelos et al., 2017). In fact, the significant interactions of the aggregation events in male-juvenile, female-juvenile and juvenile-juvenile with size-related disparities (either SVL or weight) are a strong indication that differences in size may drive dominance for refuge use, suggesting the possibility of hierarchies even before sexual maturity, as suggested above. The high number of male-male aggregations was, however, unexpected since, in natural conditions, dominant male geckos do not tolerate other males under the same retreat-site (Downes & Shine, 1997; Schlesinger & Shine, 1994). A tentative explanation is that the short duration of test did not provide enough time for the adult males to establish dominance status, and therefore they were still interacting to determine which one would stay. It is also worth noting that the experiment was conducted out of the species reproduction period (Vasconcelos et al., 2012a), which could promote a less aggressive responses between males. Nevertheless, our results clearly evidence that territoriality and social interactions in this species extend beyond mating, likely involving other ecological aspects such as foraging, thermoregulation and defence (Mouton et al., 2000; Cooper et al., 2000).

In principle, male-female pairs should have yielded the highest aggregation frequency as a way to increase reproductive success and reduce agonistic interactions (Vasconcelos et al., 2017). However, during the sampling period, geckos were not reproducing. Moreover, one must consider that those pairs were randomly chosen and did not reflect the possibility of stable pairs in nature. Thus, males or females would not be necessarily prone to aggregate because they were unfamiliar. In fact, aggregation events were lower that observed in nature during the same period (32-38%, Vasconcelos et al., 2017). Remarkably, during a mark-capture-recapture census performed during the time of this experiment, two male-female pairs were found together under different rocks after four days (unpublished results) suggesting some degree of pair fidelity resilient to the interruption of reproduction and to perturbation. This aspect deserves further investigation since such stable social structure is uncommon among reptiles (Bull, 1988; Bull et al., 1998).

Conclusions

Overall, despite the simplicity of this laboratory setup, our results confirmed suggestions of previous field studies unravelling the complexity of behavioural decisions in refuge use by sedentary ectotherms. Decision-making abilities are needed to trade-off between multiple, often conflicting pressures encompassing social interactions, thermoregulation, predator avoidance and foraging. In this arid island system, geckos almost lack competitors and predators and are likely approaching carrying capacity of the system in terms of refuges and food. In these conditions, competition with conspecifics apparently plays a dominant role and ensuring a quality refuge has priority. Although the study we conducted was out of the reproductive season, results also suggest some stability on the social relations between adult males and females, which may carry non-reproductive benefits for both partners which deserves further attention.

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Data Accessibility

All data necessary for the replicability of this study is present in Appendixes and on-line files, including raw data sets, in figshare (available upon acceptance).

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Table 1. Most relevant models for single (S) and pair tests (P), with the respective AIC, and coefficients (Coef), standard deviation (SD) and *P*-values of significant outputs (* stands for *P*-values < 0.050, n.s. for non-significant outputs, and 1 | Ind stands for the variable used as random factor). Table A2 provides details on the variables used in the models.

Code	Variables	AIC	Output	*P*-		Coef	SD
S1	Ref ~ Temp + (1 | Ind)	9.2	Temp ‡	0.000	*	-334.1	15.5
S2	Ref ~ SVL * W + (1 | Ind)	12.8	All	n.s.			
S3	Ref ~ Temp * W + (1 | Ind)	13.2	Temp ‡	0.000	*	-2138.4	37.3
			W ‡	0.000	*	4935.5	123.6
			Temp W ‡	0.000	*	-4934.0	123.7
S4	Ref ~ W + (1 | Ind)	13.6	W	0.676			
S5	Ref ~ SVL + (1 | Ind)	13.9	SVL	0.781			
S6	Ref ~ Class + (1 | Ind)	16.7	All	n.s.			
S7	Ref ~ Class * Temp + (1 | Ind)	17.2	All	n.s.			
P1	Out ~ Temp * W_I + (1 | Ind1_2)	312.8	Temp W_I	0.033	*	-1.6	0.7
			W_I	0.021	*	1.8	0.8
			Temp W_I	0.663			
P2	Out ~ Temp * SVL_I + (1 | Ind1_2)	318.4	Temp	0.021	*	-1.6	0.7
			SVL_I	0.046	*	4.5	2.2
			Temp SVL_I	0.648			
P3	Out ~ Test * SVL_I * W_I + (1 | Ind1_2)	614.5	F/J	0.070			
			J/J	0.282			
			M/F	0.660			
			M/J	0.339			
			M/M	0.400			
			SVL_I	0.193			
			W_I	0.057			
			F/J SVL_I	0.048	*	-71.2	36.0
			J/J SVL_I	0.492			
			M/F SVL_I	0.458			
			M/J SVL_I	0.067			
			M/M SVL_I	0.349			
			F/J W_I	0.072			
			J/J W_I	0.284			
			M/F W_I	0.158			
			M/J W_I	0.124			
			M/M W_I	0.431			
			SVL_I W_I	0.061			
			F/J SVL_I W_I	0.039	*	383.6	185.8
			J/J SVL_I W_I	0.157			
			M/F SVL_I W_I	0.089			
			M/J SVL_I W_I	0.044	*	375.3	186.6
			M/M SVL_I W_I	0.716			
P4	Agg ~ Temp * W_I * SVL_I + (1 | Ind1_2)	646.9	All	n.s.			
P5	Out ~ Test + (1 | Ind1_2)	661.3	F/J	0.034	*	0.7	0.3
			J/J	0.000	*	1.2	0.3
			M/F	0.890			
			M/J	0.094			
			M/M	0.106			
P6	Agg ~ Test * Temp * SVL_I + (1 | Ind1_2)	661.4	F/J	0.008	*	3.0	1.1
			J/J	0.064			
			M/F	0.007	*	2.5	0.9
			M/J	0.950			
			M/M	0.023	*	2.5	1.1
			Temp	0.143			
			SVL_I	0.031	*	22.8	10.6
			F/J Temp	0.750			
			J/J Temp	0.538			
			M/F Temp	0.200			
			M/J Temp	0.725			
			M/M Temp	0.108			
			F/J SVL_I	0.014	*	-28.7	11.7
			J/J SVL_I	0.024	*	-34.7	15.4
			M/F SVL_I	0.016	*	-35.5	14.7
			M/J SVL_I	0.103			
			M/M SVL_I	0.091			
			Temp SVL_I	0.277			
			F/J Temp SVL_I	0.433			
			J/J Temp SVL_I	0.442			
			M/F Temp SVL_I	0.969			
			M/J Temp SVL_I	0.531			
			M/M Temp SVL_I	0.099			
		703.3	F/J	0.540			

P7	Agg ~ Test * W_I * SVL_I + (1 | Ind1_2)		J/J	0.243			
			M/F	0.577			
			M/J	0.044	*	-18.2	9.1
			M/M	0.395			
			SVL_I	0.716			
			W_I	0.007	*	-16.6	6.2
			F/J SVL_I	0.704			
			J/J SVL_I	0.635			
			M/F SVL_I	0.330			
			M/J SVL_I	0.028	*	136.4	62.2
			M/M SVL_I	0.594			
			F/J W_I	0.162			
			J/J W_I	0.001	*	25.4	7.9
			M/F W_I	0.065			
			M/J W_I	0.014	*	45.0	18.3
			M/M W_I	0.095			
			SVL_I W_I	0.017	*	195.4	81.5
			F/J SVL_I W_I	0.024	*	-189.8	84.3
			J/J SVL_I W_I	0.004	*	-286.6	100.5
			M/F SVL_I W_I	0.289			
			M/J SVL_I W_I	0.002	*	-411.3	134.0
			M/M SVL_I W_I	0.365			
P8	Agg ~ W_I * SVL_I + (1 | Ind1_2)	707.0	All	n.s.			
P9	Agg ~ Test * Temp + (1 | Ind1_2)	724.5	F/J	0.081			
			J/J	0.859			
			M/F	0.191			
			M/J	0.078			
			M/M	0.150			
			Temp	0.093			
			F/J Temp	0.010	*	-1.7	0.6
			J/J Temp	0.628			
			M/F Temp	0.024	*	-1.5	0.7
			M/J Temp	0.410			
			M/M Temp	0.448			
P10	Temp ~ Ref * SVL_I * W_I + (1 | Ind1_2)	750.4	All	n.s.			
P11	Temp ~ Ref * SVL_I + (1 | Ind1_2)	777.8	All	n.s.			
P12	Temp ~ Ref * W_I + (1 | Ind1_2)	784.2	All	n.s.			
P13	Temp ~Test * SVL_I+ (1 | Ind1_2)	838.8	F/J	0.012	*	1.7	0.7
			J/J	0.258			
			M/F	0.315			
			M/J	0.320			
			M/M	0.962			
			SVL_I	0.987			
			F/J SVL_I	0.075			
			J/J SVL_I	0.554			
			M/F SVL_I	0.172			
			M/J SVL_I	0.472			
			M/M SVL_I	0.516			
P14	Temp ~ Agg* SVL_I + (1 | Ind1_2)	842.7	All	n.s.			
P15	Temp ~ Agg* W_I + (1 | Ind1_2)	848.6	All	n.s.			
P16	Temp ~Test * Agg+ (1 | Ind1_2)	901.9	F/J	0.626			
			J/J	0.446			
			M/F	0.486			
			M/J	0.812			
			M/M	0.600			
			Agg	0.092			
			F/J Agg	0.009	*	-1.7	0.6
			J/J Agg	0.629			
			M/F Agg	0.023	*	-1.5	0.7
			M/J Agg	0.409			
			M/M Agg	0.446			
P17	Temp ~Test + (1 | Ind1_2)	906.4	All	n.s.			

‡ significance due to the single observation: a juvenile using the hot and small refuge.

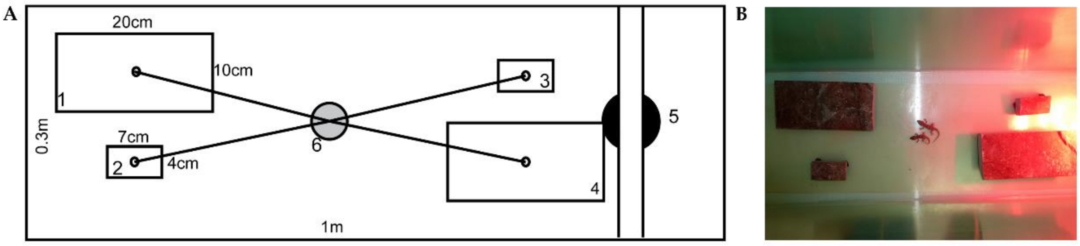

Figure 1. Layout of the terraria used in the experiment. A) The available refuge centroids are equidistant to the opaque cup where the tested animals were placed: 1. cold medium-sized rock; 2, cold small-sized rock; 3, heated small-sized rock; 4, heated medium-sized rock; 5, 150 W infrared lamp; 6, opaque plastic cup. B) Photography of a F/J test after removing the cup.

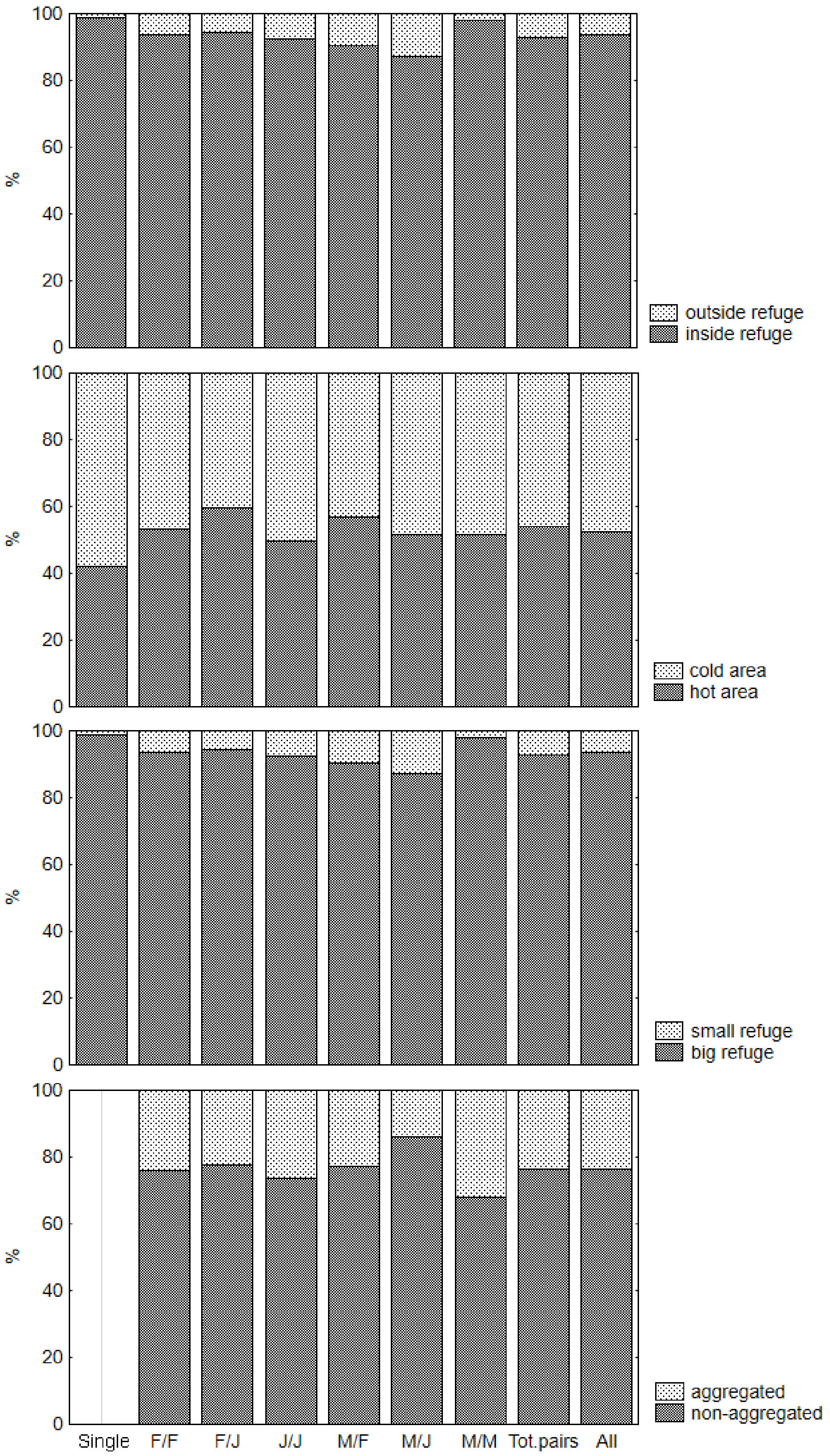

Figure 2. Test results. Percentage of individuals found under or outside refuges, on the hot or cold side of the terraria, using small or big refuges, and aggregated or not, considering the type of test (single, pairs, and in all tests).

Appendixes

Table A1 - Values of snout-vent length (SVL) and weight (W) of the *Tarentola substituta* individuals (Ind.) used in the lab experiments (M, Males; F, Females; J, Juveniles).

Ind.	SVL	W
M01	54	no data
M02	54	4.741
M03	52	5.021
M04	53	6.488
M05	51	4.047
M06	57	6.596
M07	52	4.461
M08	58	7.176
M09	54	5.373
M10	50	4.112
M11	54	5.239
M12	54	4.478
M13	48	2.817
M14	54	4.758
M15	55	4.236
F01	50	4.157
F02	56	6.37
F03	49	3.895
F04	57	7.197
F05	55	5.198
F06	54	4.596
F07	44	2.585
F08	48	3.049
F09	48	3.948
F10	47	3.608
F11	50	4.533
F12	53	4.412
F13	55	5.586
F14	50	4.785
F15	50	4.392
J01	35	1.367
J02	30	0.498
J03	39	1.631
J04	38	1.571
J05	41	2.281
J06	38	1.611
J07	41	2.059
J08	41	1.192
J09	40	2.092
J10	34	1.112
J11	48	2.151
J12	39	1.691
J13	36	1.383
J14	33	0.977
J15	33	0.998

Table A2 - Description of the variables of the refuge selection tests, their classes and respective codes.

Variable	Class	Code	Description
Ind.	Male	M01–M015	Individuals with enlarged spurs and developed cloacal pouches
	Female	F01–F15	Individuals with transparent ovarian follicles and/or no cloacal pouches
	Juvenile	J01–J15	Individuals smaller than 45 mm SVL and with no evident secondary sexual characters
		Ind.1	Focal individual
		Ind.2	Individual interacting with the focal individual
Snout-vent length		SVL	Measured from the tip of the snout to the cloaca
SVL Index		SVL_I	Formula used to measure the differences between the focal and the non-focal individual: (SVL(Ind1) -SVL(Ind2)) / (SVL(Ind1)+SVL(Ind2))
Weight		W	Measured using a digital scale
W Index		W_I	Formula used to measure the differences between the focal and the non-focal individual: (W(Ind1)-W(Ind2)) / (W(Ind1)+W(Ind2))
Test	Alone	M	One male was submitted to a test of refuge choice
		F	One female was submitted to a test of refuge choice
		J	One juvenile was submitted to a test of refuge choice
	Pairs	M/M	Two males were submitted to a test of refuge choice
		M/F	One male and one female were submitted to a test of refuge choice
		M/J	One male and one juvenile were submitted to a test of refuge choice
		F/F	Two females were submitted to a test of refuge choice
		F/J	One female and one juvenile were submitted to a test of refuge choice
		J/J	Two juveniles were submitted to a test of refuge choice
Aggregation (Agg)		Y	Individuals choose the same refuge and were found in contact with or within the distance of their own body length from at least one other individual
		N	Individuals found using different refuges or when were submitted to the test alone
Refuge (Ref)		B	Big rock chosen as refuge
		S	Small rock chosen as refuge
Outside refuge (Out)		Y	If the individual was found in a wall or ground of the terrarium
		N	If the individual was found under a rock
Temperature (Temp)		H	If the individual was found in the hottest half of the terrarium close to the heat source
		C	If the individual was found in the coldest half of the terrarium far from the heat source

Table A3 - Refuge type (BH, big hot rock; SH, small hot rock; BC, big cold rock; SC, small cold rock) where each data logger was set in the lab experiments. Their respective codes, average (Av.) and standard (STD) deviations temperature and humidity values are also given.

Code	Refuge type	Temperature		Humidity	
		Av.	STD	Av.	STD
DL01	SH	30.03	± 3.20	43.72	± 14.69
DL02	BH	30.28	± 3.46	40.57	± 14.02
DL03	BC	26.37	± 2.06	51.36	± 9.92
DL04	SC	26.31	± 1.98	52.40	± 9.87

Table A4 - Other GLMM models performed on single (S) and paired (P) animal tests with the respective AIC, and coefficients (Coef), standard deviation (SD) and *P*-values of significant outputs (* stands for *P*-values < 0.050, n.s. for non-significant outputs, and 1 | Ind stands for the variable used as random factor). Table A2 provides details on the variables used in the models.

Code	**Variables**	**AIC**	**Output**	***P*-value**		**Coef**	**SD**
A.S1	Out ~ Class + (1 | Ind)	11.2	All	n.s.			
A.S2	Out ~ Class * W + (1 | Ind)	17.2	All	n.s.			
A.S3	Ref ~ SVL * Class + (1 | Ind)	21.8	All	n.s.			
A.S4	Temp ~ Ref * W + (1 | Ind)	120.2	W	0.037	*	-0.3	0.1
			Ref	0.997			
A.S5	Temp ~ SVL * W + (1 | Ind)	121.8	All	n.s.			
A.S6	Temp ~ SVL + (1 | Ind)	121.9	All	n.s.			
A.S7	Temp ~ Ref * SVL + (1 | Ind)	122.9	All	n.s.			
A.S8	Temp ~ Ref * SVL * W + (1 | Ind)	123.2	All	n.s.			
A.S9	Temp ~ Class * W + (1 | Ind)	123.8	All	n.s.			
A.S10	Temp ~ Ref + (1 | Ind)	124.3	All	n.s.			
A.S11	Temp ~ Class * SVL + (1 | Ind)	124.9	J	0.039	*	-16.6	8.0
			M	0.276			
			SVL	0.030	*	-0.3	0.1
			J SVL	0.042	*	0.4	0.2
			M SVL	0.261			
A.S12	Temp ~ Class + (1 | Ind)	125.3	All	n.s.			
A.S13	Temp ~ Class * SVL * W + (1 | Ind)	126.4	J	0.002	*	-85.7	27.9
			M	0.000	*	-116.1	31.3
			SVL	0.000	*	-1.8	0.5
			W	0.000	*	-21.6	5.8
			J SVL	0.020	*	1.4	0.6
			M SVL	0.000	*	2.2	0.6
			J W	0.414			
			M W	0.001	*	21.2	6.5
			W SVL	0.000	*	0.4	0.1
			J W SVL	0.818			
			M W SVL	0.000	*	-0.4	0.1
A.S14	Temp ~ Class * Ref + (1 | Ind)	126.4	All	n.s.			
A.S15	Temp ~ Class * Ref * SVL * W + (1 | Ind)	126.7	J	0.164			
			M	0.057			
			Ref	0.996			
			SVL	0.058			
			W	0.137			
			J SVL	0.269			
			M SVL	0.043	*	2.2	1.1
			J W	0.549			
			M W	0.175			
			W SVL	0.123			
			J W SVL	0.916			
			M W SVL	0.140			
A.S13	Out ~ Class * Temp + (1 | Ind)	-	-	-			
A.S14	Out ~ Class * SVL * W + (1 | Ind)	-	-	-			
A.S15	Out ~ Class * SVL + (1 | Ind)	-	-	-			
A.S16	Out ~ Temp * SVL * W + (1 | Ind)	-	-	-			
A.S17	Out ~ Temp * SVL + (1 | Ind)	-	-	-			
A.S18	Out ~ Temp * W + (1 | Ind)	-	-	-			
A.S19	Out ~ SVL * W + (1 | Ind)	-	-	-			
A.S20	Out ~ Class * Temp * SVL * W + (1 | Ind)	-	-	-			
A.S21	Ref ~ Class * SVL * W + (1 | Ind)	-	-	-			
A.S22	Ref ~ Class * W + (1 | Ind)	-	-	-			
A.S23	Ref ~ Temp * SVL * W + (1 | Ind)	-	-	-			
A.S24	Ref ~ Temp * SVL + (1 | Ind)	-	-	-			

A.S25	Ref ~ Temp * Class * SVL * W + (1 | Ind)	-	-	-			
A.P1	Ref ~ Agg * W_I + (1 | Ind1_2)	273.8	All	n.s.			
A.P2	Ref ~ Agg * SVL_I * W_I + (1 | Ind1_2)	274.4	Agg	1.000			
			SVL_I	0.899			
			W_I	0.040	*	-4.2	2.1
			Agg SVL_I	1.000			
			Agg W_I	1.000			
			SVL_I W_I	0.175			
			Agg SVL_I W_I	1.000			
A.P3	Ref ~ Agg * SVL_I + (1 | Ind1_2)	283.1	All	n.s.			
A.P3	Ref ~ Temp * Agg + (1 | Ind1_2)	285.4	Temp	0.013	*	0.9	0.4
			Agg	1.000			
			Temp Agg	1.000			
A.P4	Ref ~ Temp * SVL_I * W_I + (1 | Ind1_2)	289.9	Temp	0.584			
			SVL_I	0.849			
			W_I	0.012	*	-6.0	2.4
			Temp SVL_I	0.923			
			Temp W_I	0.108			
			SVL_I W_I	0.163			
			Temp SVL_I W_I	0.291			
A.P5	Ref ~ Temp * W_I + (1 | Ind1_2)	290.8	All	n.s.			
A.P6	Ref ~ SVL_I * W_I + (1 | Ind1_2)	291.1	SVL_I	0.957			
			W_I	0.047	*	-4.0	2.0
			SVL_I W_I	0.243			
A.P7	Ref ~ Test * Agg + (1 | Ind1_2)	300.4	All	n.s.			
A.P8	Ref ~ Test * SVL_I * W_I + (1 | Ind1_2)	301.2	All	n.s.			
A.P9	Ref ~ Test * W_I + (1 | Ind1_2)	301.2	All	n.s.			
A.P10	Ref ~ Temp * SVL_I + (1 | Ind1_2)	302.5	All	n.s.			
A.P11	Out ~ Temp * SVL_I * W I + (1 | Ind1_2)	305.2	Temp	0.049	*	-2.5	1.2
			SVL_I	0.362			
			W_I	0.467			
			Temp SVL_I	0.286			
			Temp W_I	0.679			
			SVL_I W_I	0.282			
			Temp SVL_I W_I	0.225			
A.P12	Ref ~ Test * SVL_I + (1 | Ind1_2)	307.5	F/J	0.603			
			J/J	0.685			
			M/F	0.891			
			M/J	0.013	*	-3.0	1.2
			M/M	0.573			
			SVL_I	0.593			
			F/J SVL_I	0.466			
			J/J SVL_I	0.783			
			M/F SVL_I	0.689			
			M/J SVL_I	0.166			
			M/M SVL_I	0.916			
A.P13	Ref ~ Test * Temp + (1 | Ind1_2)	310.7	All	n.s.			
A.P14	Ref ~ Test * Temp * Agg + (1 | Ind1_2)	311.2	All	n.s.			
A.P15	Ref ~ Test + (1 | Ind1_2)	313.1	All	n.s.			
A.P16	Out ~ Test * Temp * SVL_I * W I + (1 | Ind1_2)	342.6	All	n.s.			
A.P17	Out ~ Test * Temp + (1 | Ind1_2)	345.8	All	n.s.			
A.P18	Agg ~ Ref * SVL_I * W_I + (1 | Ind1_2)	597.6	All	n.s.			
A.P19	Out ~ SVL_I * W I + (1 | Ind1_2)	631.1	All	n.s.			
A.P20	Out ~ Test * W_I + (1 | Ind1_2)	633.2	All	n.s.			
A.P21	Out ~ Test * SVL_I + (1 | Ind1_2)	640.2	All	n.s.			
A.P22	Agg ~ Test * Temp * W_I + (1 | Ind1_2)	667.8	All	n.s.			
A.P23	Agg ~ Temp * SVL_I + (1 | Ind1_2)	668.1	All	n.s.			
A.P24	Agg ~ Ref * Temp + (1 | Ind1_2)	673.9	All	n.s.			
A.P25	Agg ~ Temp * W I + (1 | Ind1_2)	680.2	All	n.s.			
A.P26	Agg ~ Test * Ref + (1 | Ind1_2)	684.1	All	n.s.			
A.P27	Agg ~ Test * SVL_I + (1 | Ind1_2)	739.5	F/J	0.006	*	1.9	0.7
			J/J	0.011	*	1.5	0.6
			M/F	0.020	*	1.5	0.6
			M/J	0.559			
			M/M	0.158			
			SVL_I	0.042	*	14.6	7.2
			F/J SVL_I	0.006	*	-21.9	7.9
			J/J SVL_I	0.015	*	-22.1	9.1
			M/F SVL_I	0.015	*	-28.6	11.8
			M/J SVL_I	0.052			
			M/M SVL_I	0.694			
A.P28	Agg ~ Test * W I + (1 | Ind1_2)		F/J	0.017	*	1.9	0.8
			J/J	0.418			
			M/F	0.494			

		756.5	M/J	0.316			
			M/M	0.997			
			W_I	0.628			
			F/J W_I	0.049	*	-4.8	2.4
			J/J W_I	0.503			
			M/F W_I	0.453			
			M/J W_I	0.154			
			M/M W_I	0.616			
A.P29	Agg ~ Test + (1 | Ind1_2)	800.5	All	n.s.			
A.P30	Temp ~ SVL_I * W_I + (1 | Ind1_2)	809.2	All	n.s.			
A.P31	Temp ~ Agg * SVL_I * W_I + (1 | Ind1_2)	813.7	All	n.s.			
A.P32	Temp ~ Test * Agg* SVL_I + (1 | Ind1_2)	831.8	F/J	0.014	*	2.0	0.8
			J/J	0.294			
			M/F	0.070			
			M/J	0.372			
			M/M	0.498			
			Agg	0.175			
			SVL_I	0.701			
			F/J Agg	0.475			
			J/J Agg	0.703			
			M/F Agg	0.060			
			M/J Agg	0.700			
			M/M Agg	0.159			
			F/J SVL_I	0.109			
			J/J SVL_I	0.494			
			M/F SVL_I	0.097			
			M/J SVL_I	0.788			
			M/M SVL_I	0.763			
			Agg SVL_I	0.350			
			F/J Agg SVL_I	0.261			
			J/J Agg SVL_I	0.648			
			M/F Agg SVL_I	0.494			
			M/J Agg SVL_I	0.446			
			M/M Agg SVL_I	0.154			
A.P33	Temp ~ Test * Agg * W_I + (1 | Ind1_2)		All	n.s.			
A.P34	Temp ~Test * W_I+ (1 | Ind1_2)	853.8	F/J	0.025	*	1.7	0.8
			J/J	0.948			
			M/F	0.605			
			M/J	0.410			
			M/M	0.914			
			W_I	0.656			
			F/J W_I	0.103			
			J/J W_I	0.728			
			M/F W_I	0.395			
			M/J W_I	0.379			
			M/M W_I	0.830			
A.P18	Agg ~ Ref * SVL_I + (1 | Ind1_2)	-	-	-			
A.P19	Agg ~ Ref * W_I + (1 | Ind1_2)	-	-	-			
A.P20	Ref ~ Test * SVL_I * W_I * Temp *Agg + (1 |	-	-	-			
A.P21	Temp ~ Test * SVL_I * W_I + (1 | Ind1_2)	-	-	-			
A.P22	Temp ~ Test * Ref * Agg + (1 | Ind1_2)	-	-	-			
A.P23	Temp ~ SVL_I * W_I * Test * Ref * Agg+ (1 |	-	-	-			
A.P24	Temp ~ SVL_I * Test * Ref + (1 | Ind1_2)	-	-	-			
A.P25	Temp ~ W_I * Test * Ref + (1 | Ind1_2)	-	-	-			
A.P26	Temp ~ Test * Ref + (1 | Ind1_2)	-	-	-			

Abstract in Portuguese

Os padrões do uso do espaço em pequenos ectotermos sedentários resultam do jogo entre múltiplos factores, frequentemente conflituantes, incluindo abióticos e interacções bióticas. Avaliar os custos e os benefícios dessas pressões é crucial para fazer as decisões comportamentais correctas em termos de aptidão biológica. A osga insular de São Vicente *Tarentola substituta* constitui um modelo relativamente simples para estudar estas questões, uma vez que habita locais áridos e rochosos onde os refúgios são escassos, a densidade de conspecíficos é elevada e os predadores terrestres são quase ausentes. No campo, os adultos tendem a refugiar-se durante o dia em rochas de tamanho médio, eventualmente em pares macho-fêmea, enquanto os juvenis ocupam rochas mais pequenas termicamente sub-óptimas. Foi realizada uma experiência laboratorial para determinar os papéis dos factores ecológicos (tamanho de refúgio e temperatura) e sociais (presença de conspecíficos) na selecção de refúgios. Indivíduos sozinhos e em combinações a pares de diferentes classes etárias e sexos puderam escolher entre quatro refúgios: pequeno e frio, pequeno e quente, grande e frio ou grande e quente. Baseados em estudos anteriores, prevemos que as pedras grandes e menos variáveis termicamente sejam os refúgios preferidos e que os pares macho-fêmea debaixo da mesma pedra sejam mais frequentes do que as outras combinações.

As osgas escolheram preferencialmente refúgios maiores em detrimento da presença de conspecíficos e da qualidade térmica. Em termos sociais, o sexo, a condição de adulto e disparidades de tamanho moldaram os padrões de agregação, resultando em menores frequências desta entre adultos e juvenis e até juvenis de diferentes tamanhos. Estes resultados corresponderam razoavelmente com as observações de campo, sugerindo que a selecção das rochas como refúgios diurnos é feita de acordo com as propriedades térmicas das mesmas e que as agregações sociais envolvem maioritariamente machos e fêmeas adultas, mas não juvenis. No geral, este conjunto de resultados proporciona mais evidências quanto à ecologia espacial das osgas, e possivelmente de outros ectotermos sob condições de baixa predação, recursos limitados e elevada competição interespecífica, tais como as que são observadas em sistemas insulares.

REPORT: If you move rocks, at least pile them: effect of habitat disturbance on an endemic gecko

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Abstract

Habitat changes are one of the leading factors for biodiversity loss. This impact has impacted considerably reptile populations across the globe. Endemic species facing these sorts of pressures should be managed with additional care, due to their higher vulnerability to extinction. The São Vicente wall gecko *Tarentola* substituta is a rock dwelling ectotherm, which is endemic to that island in the Cabo Verde Archipelago. However, despite its large distribution, the construction of a windmill farm has caused habitat disturbances with the construction of roads and consequential removal of rocks which serve as their diurnal refuges. In a field experiment, ten stations were surveyed for geckos (considering age, sex and aggregation type) and high-quality refuge availability. Then, the density of high-quality refuges was manipulated in the quadrates to determine its effects on refuge choice by geckos. The results obtained corroborated previous studies, as larger shelters were preferred as optimal refuges. In the field, it translates into non-reproductive intersex aggregations (male-female) which may have conservation repercussions in case of habitat disturbance. Furthermore, results indicated that in case of perturbation, it can be minimized with the addition of more optimal refuges despite the slow recovery of habitat balance by the individuals. In conclusion, this study sheds more light into the still understudied impacts of habitat disturbance on geckos in general and on this species in particular, and it suggests that long-term studies are done before any disturbances occur involving the refuges used by this species, so that the full extent of the perturbation impact is understood.

Keywords: arid islands, Cabo Verde, conservation, ectotherms, habitat management, refuges, reptiles,

Introduction

Anthropogenic changes to the habitat are among the greatest factors responsible for worldwide biodiversity loss (Haddad *et al.* 2015) having synergic effects with other global factors such as climate change and invasive species (Ducatez & Shine_2017). Habitat loss, degradation and fragmentation are of great concern for sedentary ectotherms such as reptiles, due to their low dispersal abilities and high dependence on the local environment (Böhm *et al.* 2013). However, the drivers of extinction risk for reptiles are severely understudied in comparison with those of other terrestrial vertebrates (Ducatez & Shine_2017). This lack of knowledge is especially important in nocturnal, small-sized, oviparous and occurring on arid regions species (Meiri and Chapple 2016). In this context, island reptiles are optimal model species for these studies due to their frequent endemic status, the simplicity of the landscape they inhabit, high densities of individuals and reduced interspecific interactions (Whittaker and Fernández-Palácios 2007; Penado *et al.* 2015) that could confound the results. As such, the knowledge acquired in these priority species and areas may be extrapolated to species inhabiting more complex systems, where it is far more difficult to isolate disturbance factors.

This experimental study was conducted in São Vicente Island, which is part of the Cabo Verde Archipelago, 825 km off the NW African coast. The most common reptile species present on the island is the endemic wall gecko *Tarentola substituta*. This small-to-medium-sized species spends the day under rocks which provide shelter from high temperatures, only becoming more active during the cooler night hours (Vasconcelos *et al.* 2012). Adults depend on mid and large rocks preferably closer one to each other, which use them for retreating by day, for thermoregulation and for foraging; juveniles can occupy small rocks but it is because they are displaced by adults and they cannot omplete the biological cycle if one these racks area available (Vasconcelos *et al.* 2012; Carretero *et al.* 2016; Vasconcelos *et al.* 2017)

Within the natural range of occurrence of *T. substituta*, a windmill farm was built to provide cleaner energy to the island. However, as in other public works, this involved considerable habitat disturbance by road construction and rocks movement during construction (Vasconcelos *et al.* 2011). As an exclusive rock-dwelling reptile found in high densities (Vasconcelos *et al.* 2013), this species is expected to be sensitive to those habitat changes and, hence, provides a good model for the response of reptile populations to similar conditions. Also, further research on the ecology of this species was suggested for guiding conservations actions (Vasconcelos 2013). This, together with a systematic monitoring of these geckos and their habitat since 2008, led us to use this system to address some questions regarding the impact of habitat disturbance on sedentary ectotherms and the effectiveness of management efforts. More specifically, we investigated to what extent disturbance and modification of refuge quality and density promote shifts in habitat preferences and social behaviours of the geckos. We predict that individuals will still select medium-sized and big rocks as refuge despite the disturbance. Additionally, we hypothesize that individuals will favour environments where high-quality refuge density is increased, with adults monopolizing the best refuges. These outcomes of this work are expected to serve as a conservation tool providing clear guidelines on how to minimize anthropogenic disturbance when this is unavoidable.

Material and Methods

A manipulation experiment from 02 to 08th of November 2017 was performed in an area nearby windmills, circa 3 km southeast of the mid-way between Mindelo and São Pedro road, São Vicente Island, Cabo Verde Archipelago. This area is characterized by its very dry conditions, with very sparse vegetation and abundant rocks of all sizes. In the framework of the works we managed to establish two sets (A and B) of five lined 10x10m quadrates, 10m apart, which were marked, georeferenced (Latitude and Longitude coordinates measured in its centroid using a GPS; Table 1) and surveyed for geckos. The surveys were conducted during the non-breeding season by day between 9.30 am and 6:00 p.m. Rocks were systematically turned, and rock crevices searched by the same three observers, with same search effort being devoted to all quadrates. The two lines of five quadrates each were within the same habitat but 250 m apart, and separated by a small valley, to reduce the possibility of animals to move from one set to another during the night. Animals found within quadrates were assigned to a sex and size class (adult/immature) according to Vasconcelos *et al.* (2012), photographed and individually marked with a marker pen in the belly for possible re-capture identification. In addition, 16 data-loggers (Embedded Data Systems, model DS1923) were placed under medium-sized and small rocks in eight of the ten quadrates to monitor the diel variations in temperature to the nearest 0.001ºC and humidity the nearest 0.001%.

On a first phase (three days), alongside with individual marking, several variables (high-quality refuge availability, gecko density, and aggregation) were noted as control data. The number of available rock refuges in each quadrate was counted and classified into three categories: small (less than one hand span), medium-sized (between one and three hand spans) and big (more than three hand spans) following Vasconcelos *et al.* (2012). High-quality refuge availability was measured as the number of big/ medium-sized rocks present in each station. Gecko density was measured as the number of total males, females and juveniles found within each quadrate. Individuals found under the same rock would be considered as aggregated. The number of pairs was counted as the number of male and female geckos found aggregating. In the second phase (two days), refuge manipulation was performed. Half of optimal rock refuges (i.e, medium-sized rocks, Vasconcelos *et al.* 2012, 2017) were hand removed from one of the line of quadrates, set B, while in the other line, set A, the number of quality refuges was duplicated by randomly placing medium-size rocks, extracted either from the first line or from a separate area and transported with the help of a wheelbarrow. As a result, five quadrates had the number of optimal refuges duplicated (set A) with the other five had them decreased to half (set B). After the refuge manipulation, quadrates were left for a resting day. In a third phase (three days) geckos were again surveyed following the same procedure in the manipulated quadrates.

Comparisons of the number of recorded geckos by quadrate with the standardised effort were conducted considering paired data (regarding the same quadrate) while the five quadrates within the same set of conditions (refuge increased or decreased) as sampling replicas. linear mixed models for paired data with high-quality refuge availability and test type (with no refuge manipulation, or increased/decreased refuges) or time (before or after the manipulation) as fixed factors, and quadrate number as random factors were used to detect significant differences between habitat treatments on gecko density. These models were tested for significance using ANOVA tests. For these calculations we used the R Package 'lmerTest' and *p*-values computed via the Satterthwaite approximation (Kuznetsova *et al.* 2017).

Results

The mean values of temperature and humidity in the quadrates was similar in small rocks (average=28.93ºC, range: 28.17–30.11ºC; average=65.34%, range: 57.06–74.86%) and medium-size rocks (average=28.26ºC, range: 27.56–29.56ºC; average=69.13%, range: 62.61–75.73%). Consistently higher average, maximum and minimum values of temperature and lower values of average, maximum and minimum values of humidity were found under small rocks than big rocks (t-test temperature: *P*= 2,51E-42; humidity: *P*= 8,0658E-154). Field surveys showed a higher number of cases of geckos found under big rocks across the whole experiment, with 29 cases, than under smaller rocks, with three cases for a total of 32 events.

Out of the total 32 registered individuals, 16 were found in pairs of two, of which seven of them were adult male/female pairs and only one male/juvenile aggregation, including 10 recaptured individuals (Table 1). In two cases, the same couple was recaptured under a different refuge in two sampling days. The latter couple was recaptured after the manipulation test. The total number of geckos per quadrate ranged from 0 to 11 individuals (B5; see Table 1) and the total average density per station was 3.2 animals (standard error = 1.245). Before and after the habitat manipulation test, the total density of geckos ranged from 0–5 and 0–6 individuals per quadrate, respectively (Table 1; Fig. 1). The average values of males, females, juveniles, pairs, and total number of geckos were lower after than before the test (Table 1; Fig. 1). Mean total values of geckos per quadrate decreased 0.60 in set A, and 1.00 in set B in comparison to mean values before manipulation.

Table 1. Number of male (M), female (F), juvenile (J), M-F pairs (P) and total (T) geckos present on each quadrate (Q) before and after the refuge manipulation test. The latitude (Lat) and longitude (Long) were registered in each quadrate. The number (Nr) and type of rocks (small, medium, Med or big) and the total (T) and average (Avg) values for all stations are also given. The stations A (A1–A5) had the number of optimal refuges increased after the test, and stations B (B1–B5) had it decreased.

			Before test								**After test**							
Q	**Lat**	**Long**	**Nr geckos**					**Nr of Rocks**			**Nr geckos**					**Nr of Rocks**		
			M	F	J	P	T	Small	Med	Big	M	F	J	P	T	Small	Med	Big
A1	16,83101	-25,02110	1	1	0	1	2	>100	50	12	0	0	0	0	0	>100	100	12
A2	16,83113	-25,02092	1	1	1	1	3	>100	53	2	1	0	0	0	1	>100	106	2
A3	16,83122	-25,02079	0	0	0	0	0	>100	43	4	0	0	0	0	0	>100	86	4
A4	16,83135	-25,02067	0	0	0	0	0	>200	7	3	0	0	1	0	1	>200	14	3
A5	16,83151	-25,02055	0	0	0	0	0	50-100	43	3	0	0	0	0	0	50-100	86	3
T			2	2	1	2	5		196		1	0	1	0	2		392	
B1	16,83314	-25,02153	0	0	0	0	0	>100	37	2	0	0	0	0	0	>100	20	2
B2	16,83129	-25,02140	0	0	0	0	0	>100	32	7	0	0	0	0	0	>100	16	7
B3	16,83148	-25,02131	2	0	3	1	5	>100	56	25	1	0	2	0	3	>100	28	25
B4	16,83160	-25,02120	2	2	1	2	5	±70	35	11	0	0	1	0	1	±70	18	11
B5	16,83174	-25,02106	2	2	1	2	5	50-75	38	6	1	5	0	1	6	50-75	20	6
T			6	4	5	5	15		198		2	5	3	1	10		102	
T_{all}			8	6	6	7	20				3	5	4	1	12			
Avg			0.8	0.6	0.6	0.7	2.0				0.3	0.5	0.4	0.1	1.2			

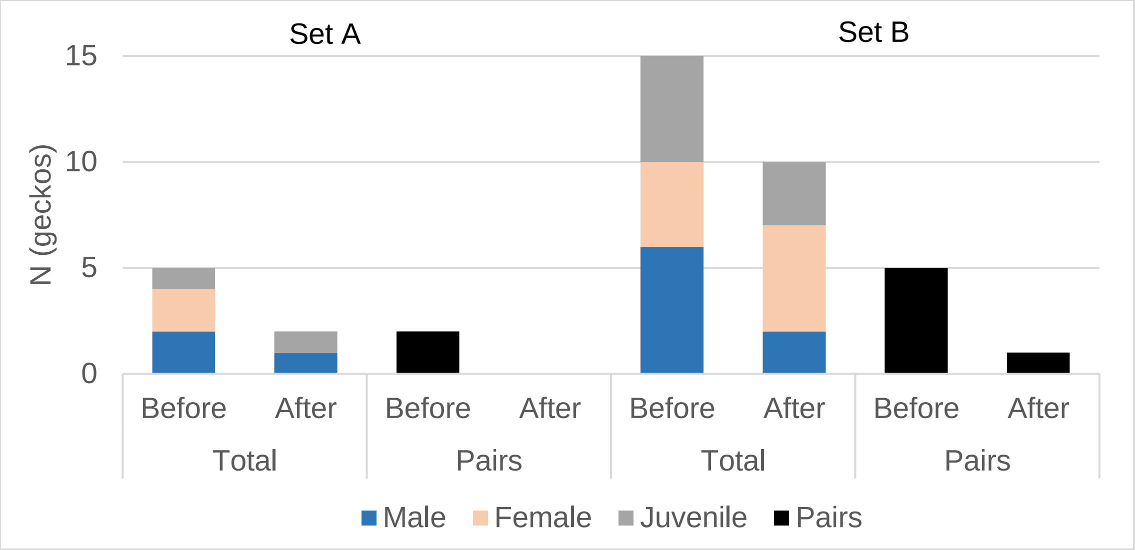

Fig.1 - A- Number of individuals and pairs (N) registered in the set A (quadrates on which the number of refuges was artificially increased; A1–A5) or B (quadrates on which the number of refuges was artificially decreased; B1–B5), before and after the disturbance.

Regardless the type of treatment, the manipulation of the habitat significantly decreased the number of geckos observed (Fig. 1) when number of high-quality rocks or the interaction between those and the time were considered, either in total (F=4.65; *p*=0.05 and F=5.04; *p*=0.05, respectively) or in pairs, just considering the first factor (F=7.36; *p*=0.02). Remarkably, there was a significant difference the total number of geckos found per quadrate when considering the interaction between the number of geckos found and the test type and the number of high-quality rocks (F=3.90; *p*=0.04), and quadrates as a random factor.

Discussion

The fact that the majority observed individuals during the whole experiment were found under medium-size and big rocks corroborates previous finding pointing these refuges as optimal and constraining for this species (Vasconcelos *et al.* 2012). However, it is unexpected that habitat manipulation led to a decrease in the number of individuals of every class, in total, and also of paired individuals either is such manipulation decreased or increased the number available quality refuges. This may indicate that the perturbation in the microhabitat structure itself, by the displacement of refuges and new position regarding other rocks, had an immediate negative impact on the apparent density of individuals found across quadrates. Logistic constraints did not allow continuing the gecko monitoring for a longer period. However, results suggest that rock movements by machinery as those executed during the building of the wind farm, have strong negative impacts even on highly abundant and non-threatened reptile species. If such perturbations are continuing during the breeding season, repercussions in the reproductive output and recruitment are also expected.

Previous studies have demonstrated that alteration of the physical environment by roads negatively impacts factors such as gene flow and fitness, as well as abundance (Delgado García *et al.* 2007; Tanner and Perry 2007). Furthermore, it is important to consider highly philopatric tendencies to a refuge have been reported for other *Tarentola* species, such as *T. mauritanica* which has a home range of 3.5 to 30 m^2 (Martínez-Rica, 1974). If this was also the case of *T. substituta*, mid-term consequences of habitat disturbance are expected. Mccoy *et al.* (2014) points that the potential impact of a disturbance is magnified and becomes more difficult to re-establish habitat balance, the more philopatric a species is to a site or refuge, which emphasizes the importance of understanding disturbances in the species range (Boudjemadi *et al.* 1999; Read 1999). Pike *et al.* (2010) showed that rock displacement which serve as refuge for velvet geckos *Oedura lesueurii*, may impact negatively this species if not replaced to their original positions where rocks fit closely to substrate forming an optimal refuge, highlighting the importance of re-establishing the original conditions as much as possible in case of disturbance. Despite these results, it can be inferred that the effect of the perturbation was less evident in the stations where the number of good rocks was increased, as opposed to the ones where it was decreased (Figure 1). Since there is a significant correlation between the total number of geckos and number of high-quality refuges available, stations were the rocks were added attained higher number of individuals found despite the perturbances. These results indicate that indeed this gecko species considers bigger rocks as optimal refuges (Huey *et al.* 1989; Penado *et al.* 2015), and while perturbations at the microhabitat may have an impact, the habitat quality may be increased by manipulation through the creation of novel natural or artificial refuges (Arida and Bull 2008), despite a slow response of the animals.

Remarkably, 16 out of the 22 individuals inside the quadrates were found in pairs, mostly heterosexual couples. This is in accordance with other systematic observations during the non-breeding season (Vasconcelos *et al.* 2017). It is noteworthy that are least two of the couples were found twice together, under a different rock on each occasion and one of them persisted after habitat manipulation. This suggests long-term mate fidelity in *T. substituta*, which can contribute to minimize the disturbance of social structure after the habitat perturbation. Nevertheless, the number of pairs significantly decreased after habitat disturbance, so this may affect not only isolated individuals but also negatively influencing this aggregation behaviour or other social behaviours. Even when adding seemingly harmless components to the microhabitat, considerable negative effects were felt from an anthropogenic influence at the microhabitat level in desert lizards, for instance (Hawlena *et al.* 2010) . Therefore, *T. substituta* may be sensitive to changes in the habitat at very fine scales, influencing behavioural choices (Carretero *et al.* 2016)

Conclusion

Habitat manipulation of optimal shelters does have a negative impact, which can be minimized through the increase of their density. Management efforts should aim to prevent the displacement of rocks while the impact of these perturbations is not fully understood, regarding their extent and time necessary for habitat balance restoration. However, in case of necessary disturbance, we recommend the creation of artificial shelters with piles of medium and large rocks in areas where rocks are already present, as there is a proven ability of some animals to occupy distant refuges along the time. We also recommend to and leave such areas untouched during subsequent works. This will likely minimize short-term perturbation in the social structure of populations and will allow developing high gecko densities in the log-term. Repeated rock movement in the same areas or leaving isolated, unconnected rock outcrops should be avoided. Lastly, it is recommended long-term studies to check the behavioural evolution of these changes, since cases with Australian geckos demonstrate their highly philopatric tendencies in short-time scales which can change as long-term scales are considered (Read 1999), and possible solutions for those impacts.

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Appendixes

José J. M. Pereira has a bachelor's degree in biology from the Faculty of Sciences of the University of Porto. He is currently finishing his MSc, and this paper will be a part of it. His interests include, animal behaviour, behavioural ecology and conservation.

Evandro P. Lopes is a researcher at the Cabo Verde University and CIBIO-InBIO as well as a Ph.D. student in Genetic Biodiversity and Evolution (BIODIV) at the Faculty of Sciences of the University of Porto. His research focuses on the use of molecular and ecological tools to study the native and non-native biodiversity from Cabo Verde Islands.

Miguel A. Carretero is an integrative biologist using reptiles as main (but not exclusive) model organisms. His interests embrace ecology, physiology, behaviour, morphology, life history, biogeography, interspecific relationships and conservation focusing on functional aspects, using experimental procedures and working under an evolutionary framework. Since 2001, he works as researcher and lecturer at CIBIO-InBIO, University of Porto.

Raquel Vasconcelos is a post-doc researcher at CIBIO-InBIO since 2012. Her main focus is combining molecular techniques with morphological data and ecological modelling for assisting conservation planning using island vertebrates (especially reptiles) as privileged models.

Concluding Remarks

In this study, it was possible to disentangle some of the factor's contributions to the refuge selection behaviour in a nocturnal small ectotherm. This was possible because we chose a simple model organism and ecosystem, from which we already had a substantial ecological knowledge, and because we adopted an experimental approach combining lab and field experiments which allow experimental manipulation of some of these factors systematic monitoring of the biological responses. The experimental results obtained not only reasonably match with previous results on thermal ecology, microhabitat selection and spatial use by *Tarentola substituta* (Vasconcelos et., 2012, 2017) but also allowed inferring on the prioritization of subjacent environmental forces for such biological responses. As such, this insular gecko provides an excellent model system for interpreting other more complex situations where multiple ectotherm species interact between them and with multiple endotherm predators in more complex environments as those found in temperate continental areas (Valverde, 1967).

To summarize the findings, in conditions of extreme habitat simplification and restriction, small individuals were frequently expelled from the refuges. This is likely mediated by body size and resource shortage in terms of shelter and probably food. Essentially bigger individuals could have not tolerated smaller ones, similar to what is found in the literature (Downes & Shine, 1998). This suggests that in conditions of insularity and aridity a life-history strategy based on survival rather than on offspring number (K versus r or slow versus fast, (Pianka, 1970; Stearns, 1983) is more likely to be successful and may explain why geckos laying small clutches from which hatch relatively large new-borns prevail in such conditions (Meiri *et al.*, 2012; Novosolov *et al.*, 2013; Schwarz & Meiri, 2017). Accordingly, in the field individuals sharing a refuge were almost exclusively adults with no smaller juvenile present. In terms of refuge size, a proxy for refuge quality, both laboratory and field results showed a clear preference of all geckos for larger rocks. Indeed, these bigger rocks proved to be thermally less variable, hence exposing geckos less overheating are optimal refuges (Vasconcelos *et al.*, 2012; our results), and likely would provide them with more potential prey (as sources of nutrients and water) regardless of their age class and sex. Therefore, body size and size differences among interacting individuals appear as a main driver of shelter occupation and social interactions in these geckos. Optimal refuges will fulfil intrinsic ectotherm requirements (better thermal and hydric properties as observed from the data loggers) but also, defend from aerial predation (no native terrestrial predators): larger area for protection and more room to accommodate a partner. Furthermore, laboratory tests showed despite the apparent critical important of refuge temperature in the field (juveniles were relegated to the small stones attained higher temperatures in midday, Vasconcelos *et al.*, 2012) all geckos roughly selected similar frequencies of cold and hot refuges. Considering that in the lab rock temperatures were maintained constant and far from lethal values, this suggests that extreme rather than mean temperatures may be the limiting factor. In fact, geckos demonstrated to have a wide range of preferred temperatures (Carretero et. al., 2016). Nonetheless, under controlled conditions, adult-juveniles aggregation frequency was influenced by temperature. In other gecko species, the importance of temperature in refuge selection is variable. Downes & Shine (1998) show a warmer preference in refuge selection in velvet geckos *Oedura lesueurii*, with smaller individuals being relegated to colder refuges. In contrast, shelter thermal properties were observed to not influence aggregation behaviour in Duvaucel's geckos, despite year around fluctuations in aggregation patterns (Barry *et al.*, 2014). Therefore, further tests are needed to determine temperature influence in this species.

Individuals were observed more frequently alone, as this will may have promoted species dispersion but also competition reduction in a sit-and-wait predator living in an environment with low prey availability (Hódar *et al.*, 2006). Nonetheless, aggregation frequency was lower in M/J, likely to have occurred dominance of bigger individuals over smaller ones. This finding in the lab contrasts with the lack of field observations of male/ juveniles aggregated under the same rock (Vasconcelos *et al.*, 2017) and suggest the short- and mid-term social responses may differ. On the other hand, several male/female pairs were registered in the field experiment, with two couples being recaptured in different sampling days despite the disturbance provoked. It is noteworthy that the whole study was conducted out of the reproductive season, which suggests that sociality in this species goes beyond reproduction. These results aligned with what was found in Vasconcelos *et al.* 2017 for these species, but this tendency of male-female aggregation can be found in other gecko species (Barry *et al.*, 2014). This was not observed in the lab, with male/females attaining a lower aggregation frequency than expected. These results differ from what was observed in the field, due to the likelihood that these pairs were artificial and thus, did not have the fidelity necessary to show higher aggregation frequency. Both, time variation and resilience of sociality during the non-breeding season would deserve further investigation in this model species.

Remarkably, the frequency of overall individuals and pairs registered in the field, which were almost exclusively male/females, did diminish after the disturbance provoked through the decrease/increase of optimal refuges between stations. This field evidence complements what was tested in the laboratory so that results obtained in the wild are better understood and corroborated with experiments which isolate desirable variables to be tested. Thus, with the important knowledge obtained through this project, we can conclude that geckos primarily select larger shelters, trading-off the presence of conspecifics and thermal quality. In social terms, gender, adult condition and size-related disparity shaped the patterns of aggregation. Furthermore, shelter manipulation provoked massive disturbances in demography and social structure of gecko populations. In a management context, such impacts should be avoided or, if unavoidable minimized by paling rock removed together with those untouched. The field experiment clearly demonstrates that microhabitat changes will significantly affect these small ectotherms, providing further guidelines for the reduction of anthropogenic impacts.

Lastly, future work to be followed posteriorly to the end of this project in order to further help to better understand the ecology of this endemic species are: 1) replica of the laboratory experiments during the mating season, since behavioural changes may be detected such as more aggressive juveniles in order to compete for females 2) tests for real-couple from the wild in the lab, in order to infer the aggregation rate differences between them and the artificial counterparts used in this study, and 3) long-term monitoring of social structure of gecko populations.

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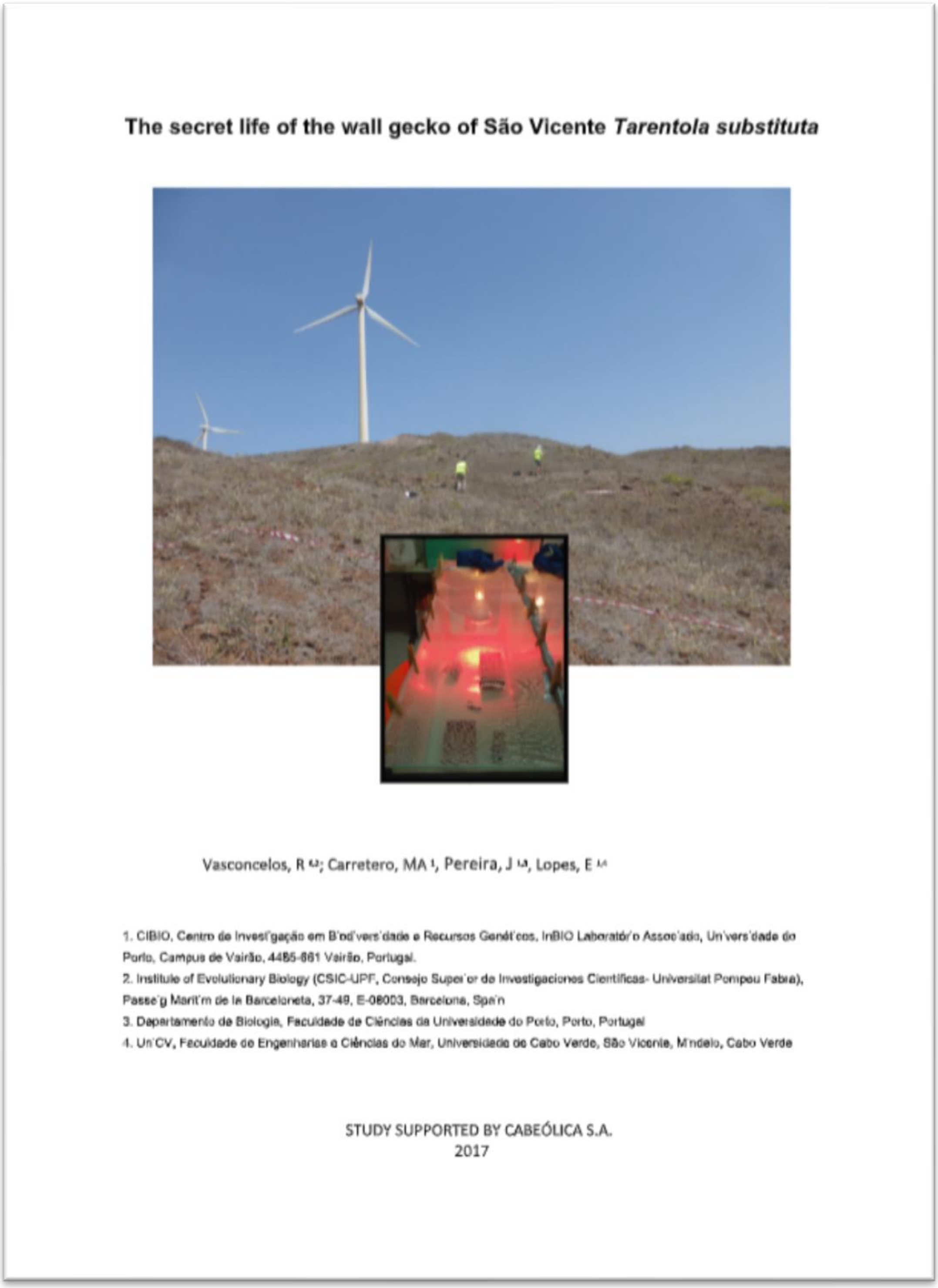
Suplementary Material

Appendix I – Unpublished reports

Vasconcelos R, Carretero M, Pereira J, Lopes E (2017). The secret life of the wall gecko of São Vicente *Tarentola substituta.* Report for Cabeólica, SA, 18 pp.



The secret life of the wall gecko of São Vicente *Tarentola substituta*

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Apendix II – Communications in international congresses

Pereira J, Lopes E, Carretero MA, Vasconcelos R (2018). Social life or comfortable home? Factors involved in refuge selection in Cape Verde geckos. Abstract book XV Congresso Luso-Español de Herpetologia, Salamanca, España: 43-44.

Libro de resúmenes

Livro de resumos

Abstract book

XV Congreso Luso-Español de Herpetología / XIX Congreso Español de Herpetología "BIOLOGÍA Y CONSERVACIÓN DE HERPETOS EN EL ANTROPOCENO"

XV Congresso de Herpetologia Português-Espanhol / XIX Congresso Espanhol de Herpetologia
"BIOLOGIA E CONSERVAÇÃO DOS HERPETOS NO ANTROPOCENO"

XV Portuguese-Spanish Herpetology Congress / XIX Spanish Congress of Herpetology
BIOLOGY AND CONSERVATION OF HERPS IN THE ANTHROPOCENE

Salamanca, 5-8 Septiembre de 2018

Asociación Herpetológica Española (AHE)
Associação Portuguesa de Herpetologia (APH)

XV Congreso Luso-Español de Herpetología / XIX Congreso Español de Herpetología "BIOLOGÍA Y CONSERVACIÓN DE HERPETOS EN EL ANTROPOCENO". Salamanca, 5-8 de Septiembre de 2018 @2018 Salamanca.

CITACIÓN PROPUESTA:

Autores del resumen. Título del resumen. En: XV Congreso Luso-Español de Herpetología / XIX Congreso Español de Herpetología, Libro de resúmenes. Colino-Rabanal, V.J., Lizana, M. & Morales, J.J. (eds). 2018, Salamanca, España. Página. ID comunicación.

El Libro de Resúmenes se ha impreso antes del desarrollo del propio Congreso. Una versión actualizada del mismo estará disponible para su descarga en la página web del Congreso: herpiberica2018.usal.es. Esta versión on-line incluirá todos los cambios que tengan lugar a lo largo del evento e incorporará también los resúmenes y las conclusiones de los workshops, el simposio de Tortugas marinas y del propio Congreso de acuerdo a las directrices del VIII Centenario de la Universidad de Salamanca.

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Vitamin D dietary availability in gravid female rock lizard induces anticipatory maternal effects in the offspring

Males of many species produce chemical signals to attract females to their territories. In some cases, the presence and abundance of some compounds in the chemical signals depend on the availability of particular food resources in the environment. Since females are attracted by males' scents, it would be likely that females were just looking for the food resources that males have used to produce these signals. Females of the Carpetan rock lizard (*Iberolacerta cyreni*) are attracted by the smell of provitamin D3 in scent marks produced by males. Here, we supplemented gravid females of I. cyreni with provitamin D3 and vitamin D3 to examine how these food resources associated with the scent of males may act over the offspring. Because vitamin D3 has an important role in calcium metabolism, we attended to traits related to bones and muscles. Our results suggest that increasing the availability of the resource (vitamin D3) to mothers may provoke positive effects on the locomotor capability of offspring, increasing their climbing performance, and also on their dispersal decisions, decreasing their propensity to disperse in spite of their better locomotor performance. This latter result suggests that the amounts of provitamin D3 and vitamin D3 inside the body of the mother could act as an informative cue of the habitat quality for the offspring.

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Vida social ou casa confortável? Factores envolvidos na selecção de refúgios em osgas cabo-verdianas

Em pequenos sedentários ectotérmicos, a ecologia espacial resulta do jogo entre múltiplos factores, às vezes conflituantes, como variáveis abióticas e interacções bióticas. Avaliar os custos e benefícios destas pressões é crucial para tomar decisões comportamentais correctas em termos de fitness. A osga endémica insular *Tarentola substituta* habita áreas rochosas e áridas onde os refúgios são limitados, a densidade de conspecíficos alta e os predadores escassos. Efectuaram-se duas experiências paralelas para testar o papel de factores ecológicos e sociais na selecção de refúgios por esta osga: no laboratório e numa área árida representativa da ilha de São Vicente, Cabo Verde, onde só ocorre esta espécie de réptil. A 1ª realizou-se para analisar o papel dos factores ecológicos (temperatura, refúgio) e sociais (presença de conspecíficos) na escolha de refúgios. Efectuaram-se observações independentes num terrário de indivíduos isolados ou em combinações de dois de diferentes idades e sexos, permitindo-lhes escolher quatro tipos de refúgio: de alta/baixa qualidade, perto/longe duma fonte de calor. Os resultados sugerem que as osgas seleccionam refúgios maiores em detrimento da presença de conspecíficos, mas nem sempre da qualidade térmica. Em termos sociais, o género, idade e diferenças de tamanho entre indivíduos moldaram os padrões de agregação, influenciando a frequência de ocorrência. Estes resultados estão de

acordo com observações de campo, sugerindo a selecção de rochas como refúgios diurnos de acordo com as propriedades térmicas e agregações sociais sobretudo envolvendo machos e fêmeas adultos, mas não juvenis. Na experiência de campo, 10 estações foram amostradas relativamente à presença de osgas (considerando idade, sexo e tipo de agregação) e disponibilidade de refúgios de alta qualidade. Depois, a densidade desses refúgios foi manipulada para determinar quais os efeitos na escolha destes pelas osgas. Os resultados revelaram fidelidade em agregações macho/fêmea, mesmo depois da perturbação dos refúgios. Rochas maiores foram de novo o refúgio preferido, corroborando estudos anteriores. Por fim, notou-se um distúrbio menor nas estações onde refúgios de alta qualidade foram adicionados, provendo dados importantes para guiar a gestão da espécie. Em suma, estes resultados combinados fornecem informação sobre a ecologia espacial em ectotérmicos em condições de baixa predação, recursos limitados e alta competição intraespecífica, como as dos sistemas insulares.

Social life or comfortable home? Factors involved in refuge selection in Cape Verde geckos

In small sedentary ectotherms, spatial ecology results from the interplay between multiple, often conflicting factors, including abiotic environment and biotic interactions. Evaluating the costs and benefits of these pressures is crucial to make correct behavioural decisions in terms of fitness. The endemic island gecko *Tarentola substituta* inhabits arid rocky habitats where refuges are limited, density of conspecifics is high, and predators are almost absent. Two parallel experiments were conducted to determine the roles of ecological and social factors in refuge selection by this gecko: one in the lab, and another in a representative arid area of São Vicente Island, Cabo Verde, where only this reptile species is present. The first determined the roles of ecological (temperature, shelter size) and social (conspecifics' presence) factors in refuge selection. Independent observations of solo and pair combinations of different size and sex classes were set in a terrarium, allowing selecting four refuge options: cold small, hot small, cold large and hot large rock. Results suggest that geckos primarily select larger shelters trading-off the presence of conspecifics and, but not always, thermal quality. In social terms, the gender and age, and size disparity shaped the patterns of aggregation. These results reasonably match field observations, suggesting selection of rocks as diurnal retreats according to their thermal properties, and social aggregations mainly involving adult males and females but not juveniles. In the field experiment, 10 quadrats were surveyed for geckos (considering size, sex and aggregation) and high-quality refuge availability. Subsequently, the density of high-quality refuges was manipulated to determine its effects on refuge choice by geckos. Results showed aggregation fidelity in male/female, even after refuge disturbance, and bigger rocks as preferred refuges. After the addition of high quality refugia, the disturbance due to rock turning had less impact. This indicates future guidelines regarding the species management. Overall, this combined evidence provides insights on the spatial ecology of ectotherms under conditions of low predation, limited resources and high interspecific competition such as those prevailing on island systems.