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Spatial analysis of escape tactics of Iberian lizards

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Rémi dos Santos

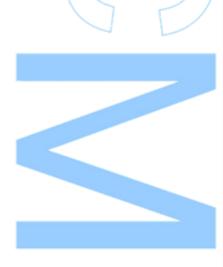
Mestrado em Ecologia, Ambiente e Território Departamento de Biologia 2016

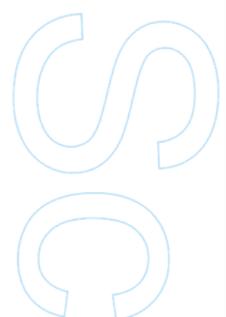
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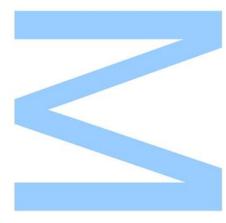
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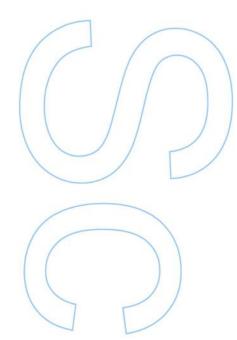
Mestrado em Ecologia, Ambiente e Território Departamento de Biologia 2016

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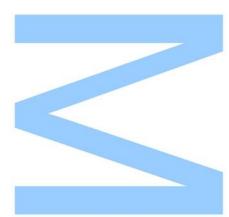


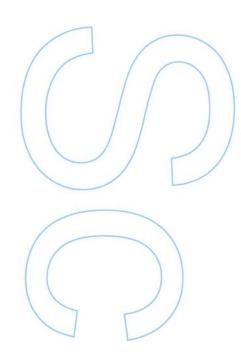


Todas as correções determinadas pelo júri, e só essas, foram efetuadas.

O Presidente do Júri,







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Abstract:

Lizards use flight as main anti-predator behaviour, frequently escaping to a refuge. This response is well studied in terms of morphology, physiology and reproductive biology, though the spatial context is frequently ignored. The home range influence or the spatial factors of refuge selection are not completely understood. This study aims to determine the influence of Podarcis bocagei home range on its escape behaviour and how is it established when facing a new area. This study was conducted inside a 400m² mesocosmos using 38 acclimatized adult individuals. Remote sense techniques were used in order to map the mesocosm, which resulted in an orthophoto, temperature and humidity map and refuge map. The individuals were approached with a constant pace and manually marked three georeferenced points in the orthophoto (predator location, starting and final escape locations). We estimated home-ranges using a 90% Characteristic Hull Polygon. This study revealed the home range is gradually established. At first, the individuals roam randomly through the mesocosm in an exploratory phase and then established a home range that decreased with the time. About the escape outside the home range, 25% of the escapes ended outside the homerange, although keeping short distance (about 50 cm). Lizards may temporally flee outside home range limits, but keeping a short distance allowing them to easily return, and hence, ensuring the mid-term persistence of their home ranges.

Resumo:

As lagartixas usam a fuga como principal comportamento anti predador, frequentemente escapando para refúgios. Esta resposta é bem estudada em termos de morfologia, fisiologia e biologia reprodutiva, mas o contexto espacial é frequentemente negligenciado. Além disso, a influência das áreas vitais e a interação com o complexo espacial não é totalmente compreendido. O objetivo deste trabalho é determinar a influência das áreas vitais no comportamento de fuga de *Podarcis bocagei* de um ponto de vista espacial, bem como analisar como estas se desenvolvem numa área totalmente nova. Este estudo foi realizado dentro de um mesocosmo de 400m² em 38 indivíduos adultos aclimatados. Técnicas de deteção remota foram utilizadas de forma a mapear a área de estudo, o que proporcionou uma ortofoto, mapas de temperatura, humidade e refúgios. Os indivíduos eram abordados diretamente e com passo constante e a sua posição era marcada manualmente por na ortofoto. As áreas vitais foram estimadas utilizando o método de Characteristic Gull Polygon a 90%. Este estudo demonstra que as áreas vitais são desenvolvidas gradualmente, onde inicialmente os indivíduos

permanecem numa fase exploratória, e depois vão criando uma área vital que vai decrescendo. Relativamente às fugas fora das áreas vitais, 25% das fugas acabaram fora das áreas vitais, no entanto mantinham se perto das mesmas (cerca de 50 cm). Estes resultados indicam que as lagartixas podem momentaneamente fugir para fora da área vital, mas mantêm-se próximas das mesmas de forma a conseguirem regressar, consequentemente assegurando a área a médio prazo.

Keywords: Podarcis bocagei, Spatial Analysis, Remote Sensing, Escape

Behaviour, Home Range

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Introduction

The behavioural decision between staying and running away in presence of a potential predator have always been a major challenge for all living animals because it involves a careful balance between fitness costs and benefits. In order to avoid being predated, some species developed different antipredator mechanisms, which are evolutionary adaptations intending the survival from a predatory approach. These can be divided in three different classes: behavioural, morphological or physiological (Ford & Reeves, 2008). The most common antipredator behaviours are the escape from the predator and "playing dead" (thanatosis), aiming at discouraging the predator. Another example is the syncing of the life-cycle and its emerging from young in huge number in a small time period, in some insects, for example the cicadas. This behaviour will ensure the prevailing of the species through the sacrifice of a small portion of the population (Williams, 1995). The aggressiveness of venomous snakes is also an antipredator behaviour, this aggressiveness may harm or be highly costly to the predator. In what regards the morphological antipredator mechanisms, the colouration similar to the environment (camouflage) is widely present through species and intends the avoidance of predators; in some cases the colouration may change actively as a threat warning (for example in cephalopods) (Holmes, 1940); The presence of some chemical compounds, either toxic or unpleasant somehow, is an example of the physiological class with the purpose of deviating the predator's attention. It is common for the species to have multiple antipredator mechanisms. In the case of reptiles, small lizards usually have a colouration similar to the environment as a camouflage, but they also rely on the escape strategy (Samia, Blumstein, Stankowich, & Cooper, 2015). It is also fairly common for the lizards to shed the tail as a distracting manoeuvre, gaining time to hide in a refuge while the predator concentrates in the still moving tail. Although this move will harm the lizard (mainly losing matter, energy and balance in locomotion) and influence future decisions, helps the lizard to survive and will soon regenerate (Salvador, Martin, & P. López, 1995). For some reptile species (especially small lizards) the escape is the most relying behaviour under predation risk, a trade-off between the cost of fleeing and the risk of capture (M. a. Carretero et al., 2006). Usually, the escape ends with the individual hiding in a refuge, though the escape might end quicker in case the prey fails to escape (lizard performance depends on the temperature) and the refuge is far or the predator is faster, feeding upon the prey. Therefore, the escape strategy has to be balanced to the threat and costs regarding the innumerable number of factors influencing it: e.g. the ability of the prey to be able to run, the distance from the individual to the refuge, the speed of the predator or its distance to the prey. The approach distance is the distance

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between the predator and the individual in the moment it starts the escape (approach distance); the flight distance is the distance between the individual and the refuge it hides (Cooper Jr, 1997). Although the refuge distance is the most related to the performance of the individual, the distance between it and the predator will certainly define the possibility of survival. Nevertheless, not only the distances, but also the thermal condition will affect the reptiles' escape behaviour since they are ectotherms. An individual with the body temperature close to the physiological optimum (preferred temperature) should start running later because he should be able to run faster. On the other hand, a colder (or too warm) individual, with low performance, should start the escape early, run slower and possibly hide in closer refuges. Yet, some other factors may also have influence, such as the gender, age class, body condition, parasitization and pregnancy in the case of females (Bauwens & Thoen, 1981). Although the escape behaviour is constantly occurring in natural conditions, to study it properly in controlled and replicable ways researchers simulate the predation situation. The researcher will act as a predator, approaching the individual until it starts to run away and then calculates the distances. These experiments can either be performed in open space or indoor, depending on the need to repeat the experiment with the same individual (Martin, 2002).

Also, some other factors must be taken such as the current activity of the individual: should an individual hunting lose its prey and hide or continue the hunt and risk being the prey? For lacertids many factors were already studied, the risk-benefit of being predated when individuals were mating, feeding, or even the stage of regeneration of the tail (the tail effect). Cooper, 2000 analysed the influence of a predation threat when feeding and concluded that two main factors would influence the risk-benefit of feeding when threat. First, the distance of the prey to the refuge: the probability of attacking the insect would decrease with the distance of the lizard to the refuge; and second: the size of the insect, if the insect was larger it would be more easily attacked, indicating that the lizard would accept that a greater energetic benefit would make up the risk. Additionally, the lizard would carry only larger insects to the refuge, eating the smaller ones right after the capture. In the case of reproductive behaviour. Braña, (1993) studied the effect of pregnancy in the escape behaviour, concluding that: First pregnant females present a lower body temperature than males and non-pregnant females; Second, the pregnant female changes its tactics from flight to crypsis, once the pregnancy highly reduces the effectiveness of the flight tactics. Third, once it shifted the tactics, the female will allow a closed approach from the predator and remain closed to the refuge. Cooper (1999) concluded that when conspecific males were present, both isolated and mate-guarding, they would initiate agonistic behaviour (aggressive or defensive social behaviour), and allowed a closer approach of the predator. On the contrary, in the presence of females

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and after courtship, isolated males would allow a closer approach than mate-guarding. Hence, these results indicated that the greater the reproductive benefits, the riskier the lizards accepted to be. In the case of tail loss (autotomy), lizards increase terrestrial locomotor performance due to the loss of traction caused by the tail friction with the substrate. Yet, for climbing movement this loss would negatively affect its ability to climb, once the tail is used as counterweight for balance (Brown, Taylor, & Gist, 1995). Although these risk-benefit factors are well known, there are some less studied aspects. The spatial context is poorly documented with many unknown connections to these escape behaviours. Although some studies include the spatial context (Castilla, 1998; Fisher, Suarez, & Case, 2002; S. M. Jones & Droge, 1980), none tries to find a relationship between the home range and these antipredator behaviours.

Independently of the prey characteristics, the escape behaviour takes place in a spatial context and the lizard can only take cost-effective decision as it takes the space into account. The concept of Home Range is widely used as an area where the individual lives, although sometimes is wrongly used as synonym of territory. Burt (1943) defined home range as: "the area over which the animal normally travels in food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range". In contrast, the territory is the part of the home range which is defended, either fighting or with aggressive gestures, from others of their kind. It is important to take into account that the home range is not static but may vary in size and location within the same individual, and across individuals might depend on the sex, age and/or season (Burt, 1943). Home range is hardly used homogeneously, most individuals will present a preferred area and will be mostly seen there (Harris et al., 1990). These areas, centres of activity or "core areas", represent the area with greater activity inside the home range (e.g. feeding, basking). These are generally the location of usual hunting trajectories and refuges. Similarly, others concepts are associated with home range: the utilisation distribution is generally two-dimensional (x, y) or three-dimensional (x,y,z) (Greenberg & McClintock, 2008; Monterroso, Sillero, Rosalino, Loureiro, & Alves, 2013) relative frequency of positions of an individual over a determined period of time (Van Winkle, 1975). In other words, the utilisation distribution will indicate the probability of an individual being within an area of its home range at any point in time. Although the home range is easily understood as a concept, its representation and accuracy with reality is not quite obvious and simple to obtain. Over time, different methods and protocols were developed in order to be able to illustrate it and gather further knowledge of its relevance. As one of the earliest techniques developed, and still one of the simplest, "Minimum Convex Polygon" (MCP) remains as one of the most frequently used (Harris et al., 1990). This technique will

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generate the smallest polygon containing all the detections of the input and requires at least three points for it to be able to calculate the home range, though the accuracy of the model will increase with the number of points. Although this technique may be used with grid trapping, telemetry data and any other point data, the results tend to be overestimated, which decreases the degree of reality of these findings. Yet, it is possible to use some variations of this technique, like 95% MCP or even 50% MCP (generally used for core areas) (Fieberg & Kochanny, 2010). These will ignore either 5% or 50% of the farthest detections, respectively. These alternatives ensure a more realistic model of the home range. Some other, more complex alternatives include Kernel Density Estimation (KDE), Local Convex Hull (LoCoH) or Characteristic Hull Polygons (CHP) (Downs et al., 2012). The kernel-based method is developed as a probability model and will calculate the likelihood of an individual being in a specific zone within the home range at any moment, forecasting the utilisation distribution (Worton, 1989). This technique produces accurate home ranges but does not generates boundaries, which means it expands to the infinity, or at least until the border of the study area (Jones, 1993). The LoCoH is essentially a non-parametric kernel that uses MCP construction. This way will produce results with boundaries and better convergence properties (Getz et al., 2007). It operates by the union of convex hulls associated with each point and its k-1 nearest neighbours (K-NNCH). It is greatly used with telemetry data due the quantity of data produced, hence diminishing the degree of error (Getz & Wilmers, 2004). There are two more modifications of LoCoH technique: fixed radius (r-NNCH) and adaptive (a-NNCH). Characteristic Hull Polygon (CHP) creates polygons using Delaunay triangulation which, unlike MCP, is able to have concave edges, be composed of disjoint regions and within the hull contain empty portions of unused space (Downs & Horner, 2009). These techniques will represent a possible home range and based on the individual distribution over a small period of time, which may or not be realistic for a longer time. Nonetheless, not only the technique will define the home range accuracy, but also the data source and its collection. These can be essentially done by three different methods. First, radiotelemetry, a geomatic technique that will collect the position by a radio signal emitted by a transmitter attached to the animal. This technique may be divided in three types of radio-telemetry: (1) Very High Frequency (VHF) radio tracking; (2) Satellite tracking and; (3) GPS tracking. The VHF radio tracking is the cheapest, presents a reasonable accuracy and may have a long life (depending of the transmitter and the battery). Though, has as main disadvantage the intensive labour needed for the collection of the data (Mech, 1983). The satellite tracking presents the least accuracy, but it is used mainly for long-range movements and does not need personnel in the field. In the case of GPS tracking, requires a high initial investment and is highly precise (Moen, Pastor, &

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Cohen, 1997). Uses a collar as transmitter which will record the position in specific time periods, however, the size of the collar and batteries only permit the use for large mammals and some birds. Second, GPS hand held is more local technique. In this case the user needs to carry the GPS device and position it in the exact location for the data collection. Depending on the device may be highly precise (in the case of RTK-GPS centimetre-level). There is a third technique, local plots, which is entirely manual. The plot consists in the division of the study area in quadrants of defined area (Ferner, 1974). Then the data is collected by recapture methods (which means high disturbance in the individuals). The quadrants allow a manual geo-referencing by measuring the distance to the nearest vector (Diego-Rasilla & Pérez-Mellado, 2003). The home ranges of lacertids are highly diversified, usually changing according to season, gender and ageclass. In the case of juveniles, (Aragón, Meylan, & Clobert, 2006) demonstrated that do not have a proper home range staying more in a state of dispersal. Due to sedentary habits, females present a smaller home range than males, generally smaller than the available area per lizard. Females have home range based on food, thermoregulation and shelter, while males are influenced by the presence of females, thus having larger home range. On contrary, males active habits of search for females and preys, result in a home range larger than the available area per lizard, which means an overlap of the home range between males (Rose, 1982). For territorial lizards, overlaps may be explained by the complexity and size of the home range, being impossible for them to survey all the area, defending mainly the core areas. Nevertheless, this can only explain small area overlaps (Ferner, 1974). In case of mating success, a larger home range increases the mating success, partially. In other words, for a territorial lizard, the increase of the home range means overlapping more females, which might prevent other males from mating with them. On the contrary, non-territorial lizards may increase the home range in order to overlap females, but will not prevent other males from doing the same; in this case the mating success would not increase (Censky, 1995). Nonetheless, it is expected the increase of the home range and overlap with females for non-territorial lizards in breading season (Salvador et al., 1995). Hence, the presence of females is considered the main factor influencing male home range during the breading season. However, food abundance reveals to be the key factor influencing males in non-breading seasons, as well as, females throughout the year (Rose, 1982). Home range can increase with age-class (SVL), which is strongly positively correlated (Perry & Garland, Jr, 2002), due to the increase of energetic needs (Rose, 1982). The diet is also influences the home range size, with each move up in the position of the food chain, about 90% of the energy is loss, meaning that higher position need a larger home range than a lower position. Then, carnivorous present the largest home range, as they are at the highest

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position on the food web, in opposition to herbivorous which represent a lower position (Perry & Garland, Jr, 2002). Omnivorous present the smallest home range, once the food abundance is much higher than in any other position (Perry & Garland, Jr, 2002). Finally, others factors may influence the home range on species-level base, which must be considered when the species is in study. Although the home range of the lizards are in general well studies, it is still unknown how the home range is established when arriving to a new location.

In this thesis the main aim is to understand the influence of the home range in escape behaviour of Iberian lizards and provide further knowledge on how the home range is defined and developed, and what influences the individual escape behaviour. Thus, the specific questions are: (1) Do Iberian lizards escape outside their home range? (2) How is the home range established in a new area? (3) Which spatial factors would affect the escape behaviour? and (4) How would the thermic and hydric heterogeneity affect the escape?

For the main question (1) we defined the null hypothesis (H_0) as no relation between the home range and the escape behaviour, meaning that lizards may flee randomly regardless the home range no matter the individual or the predator position, alternatively (H_1) there is a correspondence between the home range and escape behaviour, namely lizards would not flee outside the home range. For the secondary questions it is expected that: (2) the home range is not present in the first moments and the lizards will explore the area randomly and discover resources. Once the resources positions are known the individual will persist in an area close to the resources needed. It is also expected changes of the area during the study time; (3) since the mesocosm provides a heterogonous habitat containing the basic and essential resources it is expected that the main spatial factors would be the presence of many refuges with a thermal and hydric gradient in the area. Nevertheless, the lizard may take decisions mainly constrained by the nature of the predation risk and the associated costs involved; and (4) the individual will try to hide in a refuge with similar temperature to its current body temperature, minimising the thermal costs. However, it may not be possible if the temperature of the individual is low and his performance is compromised, in this case it will probably hide in a closer refuge and stay shortly.

Thus, these questions may be answered and in order to be able to repeat the experiments in the same individuals, a mesocosm was built and characterised with remote sensing techniques, in order to ensure high precision in all the different tasks, minimising the errors. The use of lizards, small, abundant and with almost no conservative concerns will ease the methodologies used.

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Materials and methods

Study location: Mesocosm

A mesocosm was built in order to have a controlled environment regarding space and its abiotic structures, hence minimizing the possible impacts of open space, like predation, on the species behaviour and consequently its spatial dynamics. The mesocosm is limited in monitoring time, size and mass of biotic and abiotic components, which restricts the interactions with the rest of the ecosystem. Hence, it cannot be taken as reality but as a simulation of a particularly small natural system (Van den Brink et al., 2005). In fact, a mesocosm is defined as a replicable and semi-controlled experimental area with the purpose of simulate a certain natural environment and its conditions (Odum, 1984). The mesocosm was built in the Professor Manuel de Barros Astronomic Observatory (41°06'22.6"N, 8°35'18.9"W, 230 m) and consisted in a 20x20 meter area surrounded by flat plastic fence including a variety of small vegetation, tree trunks and rocks. The mesocosmos also restricts the presence of terrestrial predators which could interfere with the experiments. In order to monitor the temperature and humidity conditions a total of 50 dataloggers (small devices that register these specific parameters every 15 minutes of a particular location), from which 26 would only record the temperature. It was assured the dataloggers would be evenly placed in open areas, rocks and vegetation, using a random algorithm. All dataloggers were georeferenced so it would be possible to generate temperature and humidity maps (Figure 1).

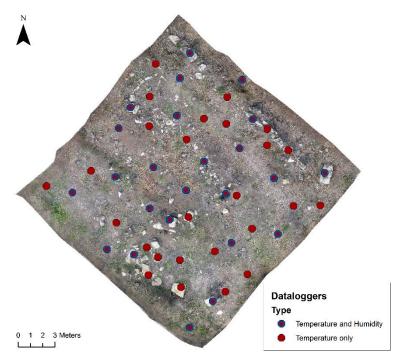


Figure 1 - Positions of the two types of dataloggers

Species used: Podarcis bocagei

A lacertid species were used in this study: Podarcis bocagei, which was chosen for being one of the most common lizards in north-west Iberian peninsula, and due to their conservation status, being classified as "Least Concern" by the IUCN red list (Miras et al., 2009; Sá-Sousa, Pérez-Mellado, & Martínez-Solano, 2009).

Podarcis bocagei (Figure 2) is a small diurnal insectivorous lizard from the family Lacertidae, and is an endemic species of the north-west Iberian Peninsula (Amaral et al., 2012; Galán, 1996), with most of its distribution being located north of the Douro river, Portugal (Sá-Sousa, 2001). This species is known to be active during all months, having minimal activity in the cold months (November to January) (Galán, 1999). P. bocagei have a maximum lifespan of four years, in which obtain sexual maturity in 11-12 months (Galán, 1996). During non-mating periods, there is a slight dimorphism, with the males being bigger than females (males average SVL, 60 mm and weight 4.68 g; females average SVL, 56 mm and weight 3.15 g). During the reproductive period (April to July) the males show a bright green colour in the dorsum, while females present a brown dorsum (Galán, 1996). Some females mimic the bright green colour of the males in the gravid phase, which is believed to be an hormonal response and will deter copulation attempts (Galán, 2000). This species has a stable population with no major threat to extinction (Sá-Sousa et al., 2009). This species do not have major conservation threats, though it usually co-exist with some possible predators, being the feral cat and small raptors the most common (Pérez-Mellado, Corti & Lo Cascio, 1997).



Figure 2 - Male Podarcis bocagei

Capture and measurement method

A total of 25 adult individuals (15 males and 10 females) were captured at Madalena beach, Vila Nova de Gaia (Portugal) (41°06'11.0"N 8°39'40.1"W), by noose (García-muñoz & Sillero, 2010). Only individuals with a snout-vent Length greater than

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45 mm (adults and sub-adults) were considered for the study (M. Carretero, Ribeiro, Barbosa, Sá-Sousa, & Harris, 2006).

The following data were recorded: gender and size class, weight, Snout-vent length (SVL), Trunk Length (TL), Head Length (HL), Head Width (HW), Head Height (HH); Front Limb Length (FLL) and Hind Limb Length (HFL) (Antigoni Kaliontzopoulou, Carretero, & Llorente, 2007). Pictures of the chest of each individual were taken for photoidentification. Lastly, each individual was marked with a combination of three non-toxic colour dye. This combination would indicate a unique code for each individual and its respectively measurements.

The photo-identification software I³S (Van Tienhoven, Den Hartog, Reijns, & Peddemors, 2007) was used in order to recognise the individuals in case of dye loss. The Interactive Individual Identification System (I³S) is a software originally developed with the purpose of recognising patterns in sharks (eg. spot position in *Carcharias taurus*) as an individual fingerprint. The algorithm was tested with other natural patterns like intersection among pectoral scales, which would be used as fingerprint for lizards (Pellitteri-Rosa et al., 2010).

Escape behaviour and Home range location

The study was conducted in the period between May 2016 and July 2016, performing the escape behaviour experiment two days a week and the home range experiment during the next five days.

The escape behaviour experiment consisted in a simulation of a predation approach (similar to Bulova, 1994), where the predator (researcher with similar clothes in every experiment) walked randomly with slow pace through the mesocosm until a lizard was seen and choose to initiate the experiment. Once a lizard was selected, the simulated predator started walking directly towards the individual until it would initiate the escape. At this moment, using a Trimble GeoExplorer 2008 XM GPS device (about 10 cm error), the location of the predator (Ap) and the location where the lizard started the escape (St) were marked. Keeping track of the escape trajectory, the final location (Fn), which corresponds to the refuge, was marked.

Concerning the home range experiment, the researcher walked slowly through a random trajectory in the mesocosm marking the position, with the use of Trimble GeoExplorer 2008 XM, of every lizard and the following data: activity – Thermoregulation, Active, Feeding, Mating, Mate Guarding, Fighting or Running; and position – in the Sun, in the Shade, Mixed location. Once the walking trajectory ended, the experiment stopped and the mesocosm was leaved unperturbed for about 30 minutes to one hour, then the experiment was repeated again with a new random trajectory.

Spatial analysis

Orthophoto

In order to map the study area, an orthophoto (Figure 3) was taken using a Canon PowerShot A495 and a stick, a sequential photo shoot in all the area was taken. For the creation of an orthophoto, a total of 1152 photos were taken and processed using a photogrammetry software, Agisoft Photoscan version 1.2.0 (Agisoft.com, 2015), resulting in a mosaic with all individual photos. An orthophoto is an aerial photo orthorectified, nullifying the tilt of the camera at the moment of capture. This way, an orthophoto is an accurate representation of an area used primarily for measurements of true distances (Schickler & Thorpe, 1998).



Figure 3 - Orthophoto of the mesocosm

Temperature and humidity map

In order to understand and record the thermal and moisture dynamics of the mesocosm, the dataloggers logs were analysed and arranged by day, so the changes of temperature and humidity could be followed. From the daily average temperature (°C) and relative humidity (%H) maps were created which describe the evolution of the conditions in the mesocosm through the study time. All maps were created using ESRI software "ArcGIS" resorting the "geostastical analyst" tools. The data was georeferenced and interpolated by ordinary kriging. This technique estimates values for unsampled areas through the weighing of the spatial component, meaning the spatial analysis is based on a semi-variogram, providing an unbiased interpolation and a minimum mean square estimation error (Krige, 1952).

Refuge map

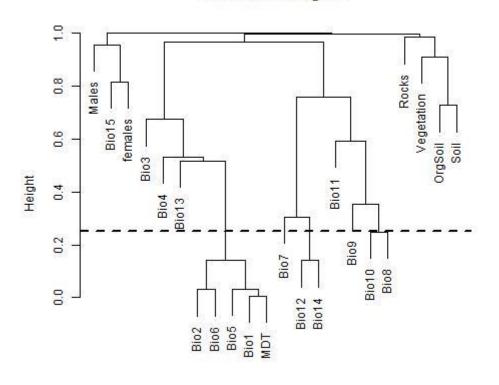
It is known that, when running from a predator, lacertids usually hide in refuges where will stay until for short periods of time and then resume its activity (Martin, 2002). For this reason, it is imperative a previous knowledge of the number of refuges of the mesocosm

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and its location. Using ESRI software "ArcGIS" and applying supervised maximum likelihood classification method, the orthophoto was classified in four different classes: Refuges, vegetation (as temporary/avoidance refuge), soil and organic soil. For the sake of this study a refuge was defined as a crack in a rock, small hole or even an entire rock in which the lizard could be hiding. The supervised classes were calculated with the help of four polygons for each class with about: (1) 620 000 pixels for refuges; (2) 210 000 pixels for vegetation; (3) 270 000 pixels for soil and; (4) 240 000 pixels for organic soil. After the classification was finished and the refuge map created, a manual *in situ* validation was done.

Ecological niche models

In order to understand the suitable habitat for each individual, ecological niche modelling techniques were used. Maxent was the tool selected in order to model the individuals, due to its performance (Phillips, Avenue, & Park, 1997). Initially, 22 variables were created: (Bio 1) Maximum temperature, (Bio 2) average daily maximum temperature, (Bio 3) minimum temperature, (Bio 4) average daily minimum temperature, (Bio 5) range of temperatures, (Bio 6) range of average temperatures, (Bio 7) maximum humidity, (Bio 8) average daily maximum humidity, (Bio 9) minimum humidity, (Bio 10) average daily minimum humidity, (Bio 11) range of humidity, (Bio 12) range of average humidity, (Bio 13) temperature seasonality, (Bio 14) humidity seasonality, (Bio 15) isothermality, organic soil, bare soil, vegetation, rocks, digital surface model, distance to males and distance to females. For the distance to males and to females, the individual to be modelled was excluded from the variable. All the variables were created using ESRI software "ArcGIS": the environmental variables were calculated and interpolated using Inverse Distance Weighting, the surface variables were calculated using Euclidean distance tool and the distance to females/males were calculated using all the presences of the individuals. Using these variables, a correlation dendrogram was created with a trend line at 0.75 and from the correlated variables one was selected to keep (Figure 4). The models were performed using a 16 variables.



Cluster Dendrogram

1 - var.dist hclust (*, "complete")

Figure 4 -Correlation cluster with trend line

Home range analysis

In order to determine the home range of each individual, a 90% Characteristic Hull Polygon (CHP) analysis was used. This analysis generates polygons using Delaunay triangulation, permitting concave edges, disjoint regions and empty portions of unused space (Downs & Horner, 2009) In order to eliminate outliers, the method ignores 10% of the marked points. The area of the home range per individual was then calculated. For the home range establishment was calculated generating CHP per individual through the four periods. Then the area was calculated and compared. In order to calculate the travelled distances by each individual, the home ranges locations of the individual were linked by day and distance was calculated in metres. The overlaps between home ranges were calculated using "Union" tool. These overlap were divided in three classes: Malefemale overlap, Male-male overlap and Female-female overlap, and represent the areas of the home range were executed overlap, and represent the areas of the home range were executed overlapping the home range and intersecting the final locations.

Statistical analysis:

In order to test the assumption of normality, the Kolmogorov-Simonov test was used. The Homoscedasticity was tested using Bartlett's test. For normal data and to compare two samples a t-student test was used, in the case of three or more samples comparison a ANOVA was performed. The home range establishment was divided in four periods and compared using ANOVA. Later, sequenced T-Student test were performed comparing paired periods. For the distances, a log transformation was implemented and a chi-square test performed in order to test the significance of the escapes outside the home range. For the influence of environmental variables (temperature and humidity) on the distances, a generalized linear regression (GLM) was performed.

Results

Home range analysis

A total of 46 *Podarcis bocagei* individuals were captured, though due to the low number of locations detected only 38 were considered for this study. The measurement recorded of the 38 individuals are presented in the Table 1 - Average size and weight of both male and female P. bocagei lizards

		SVL (cm)	Weight (g)				
Gender	N٥	ź	σ	ź	σ		
Male	25	60.4664	3.581383	4.7304	0.79602		
Female	13	56.52769	4.243348	3.481	0.803493		
Total	38	59.11895	4.212542	4.221553	1.063857		

Table 1 - Average size and weight of both male and female P. bocagei lizards

During the experiment three recaptures were performed, the number of individuals captured and the sightings recorded until the next recapture are present in the Table 2. The number of captures and sightings are slightly lower in the first recapture, having a greater decrease in the two next recaptures.

Table 2 – Number of individuals captured and sighted by gender during the four periods of experience

-	Capture)	Sighting	js	With Area		
	Males	Females	Males	Females	Males	Females	
Capture	25	13	24	11	18	9	
1 st recapture	19	9	21	12	12	4	
2 nd recapture	16	5	14	3	5	1	
3 rd recapture	8	1	6	1	4	1	

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During the experiment a total of 569 locations were recorded, the Figure 5 presents the location by gender in the mesocosm. Of all 569 locations, 140 were females and 429 males.

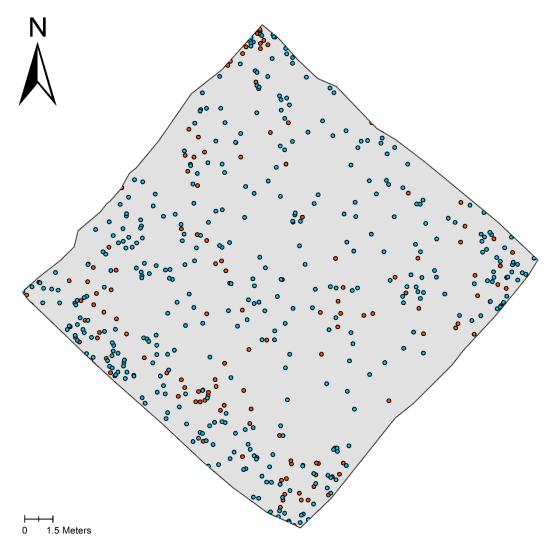


Figure 5 - Map representing the number of location recorded during all the experience. The blue marks represent the male lizards and the orange marks the females

Home range establishment

The establishment of the home range is described by its changes by shape, area and perimeter through the different periods. Throughout the four periods a significant shift was observed both in shape and size which visually (Figure 6) agrees with the repeated measures ANOVA performed (df=3, F=3.487, P=0.0361). Additionally, sequenced T-Student test proved that only the first period was significantly bigger (df=1, F=4.81, P=0.034), while period two and three (df=1, F=0.564, P=0.461) and period three and four (df=1, F=0.153, P=0.705) are not.

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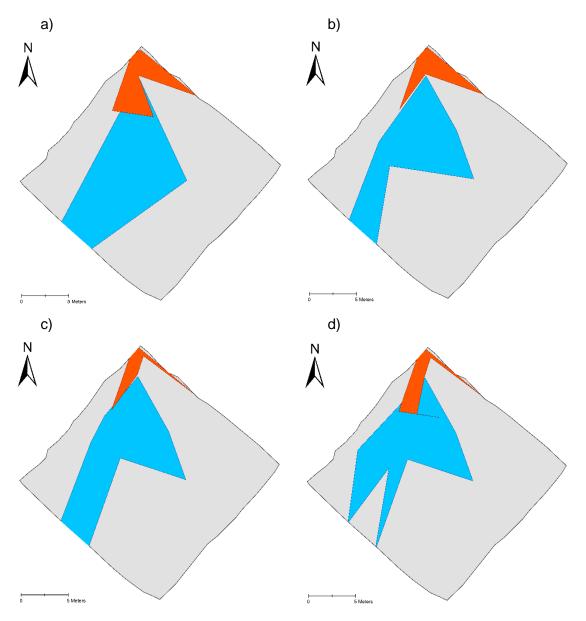


Figure 6 - Evolutions of two home ranges (orange - female and blue - male) over four periods

The home range size is highly variable both between gender level and individuals. Males tend to occupy a significantly bigger area (*t*=-3.2559, df=32.264, *P*=0.002658) than females. The males' perimeter is also significantly bigger (*t*=-2.2754, df=33.405, *P*=0.02942) than females (Table 3).

Table 3 - Average area	and perimeter	by gender
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	Area		Perimeter			
	ź	σ	ź	σ		
Female	39,46014	20,37611	48,50602	22,34812		

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Male	82,0174	52,08884	67,57504	29,39248
Total	66,74043	47,78488	60,72975	28,32614

Travel Distances

The travel distances represent the distances between all the points of the individual (Figure 7). It is observed there is a highly significant difference between the travel distance of males (average of 136.56m) and females (average of 63.04m) (t=-4.1913, df=30.976, P=0.0002143).

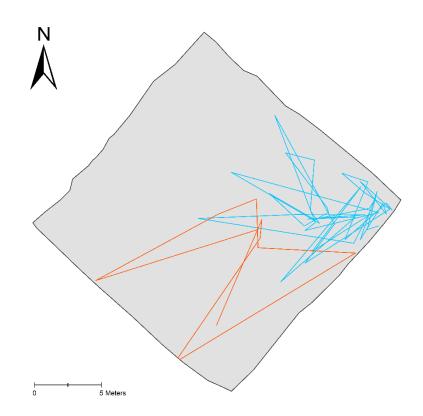


Figure 7 - Travelled distance of two individuals during the study period

Overlap of individuals

Overlapping home ranges of each individual provided three case scenarios (Figure 8): Male-Female overlapping, Male-Male Overlap and Female-Female Overlap. From these maps it is possible to recognise the areas of the mesocosm which are mostly used. The individuals overlap mostly in the western part of the mesocosm, reaching a total of 16 individuals overlapping in small areas. The same occurs with the Male-Male overlap, except for the number of individuals overlapping. In the Female-Female overlap, as random pattern occurs, some areas with a total of four females overlapping.

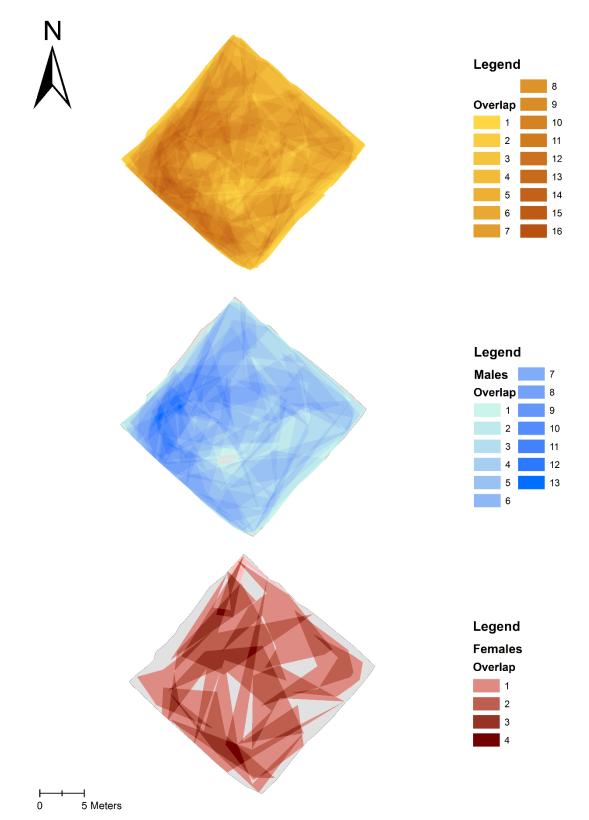
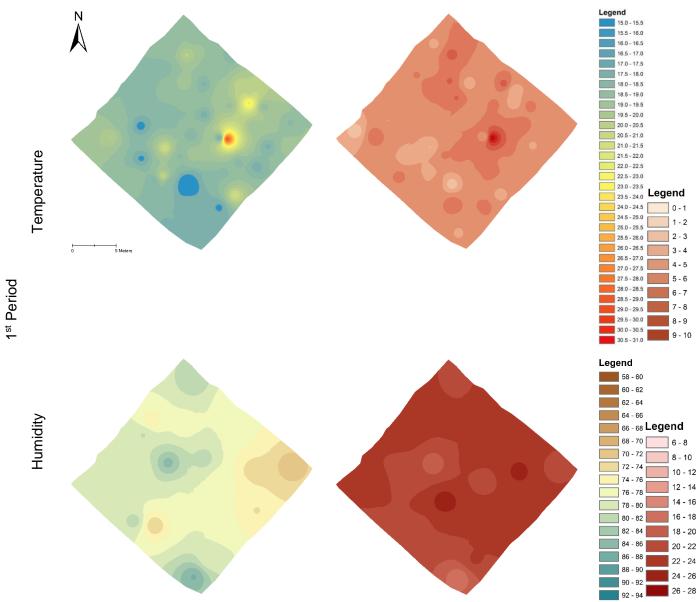
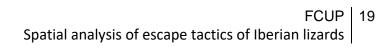


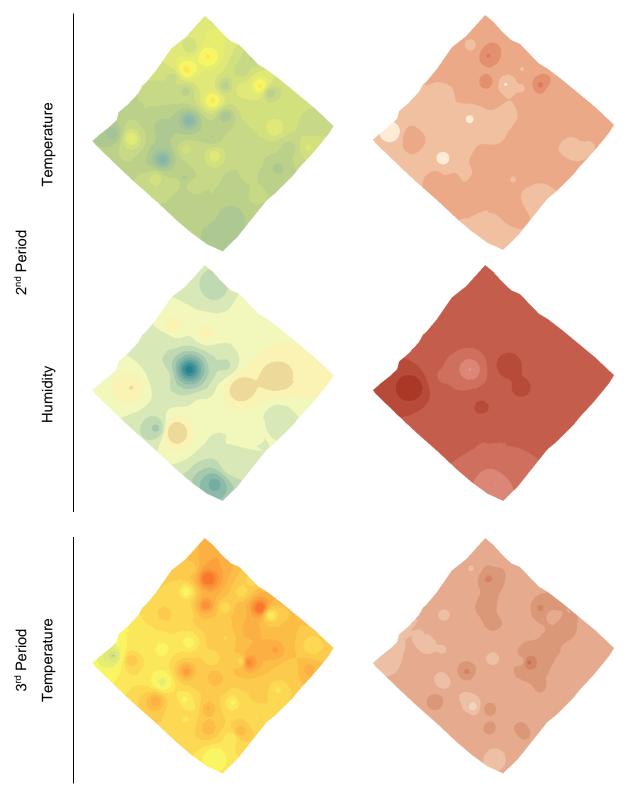
Figure 8 - Overlap of the home ranges which represents all individuals overlapping, male-male overlap and female-female overlapping, consecutively

Environmental conditions

During the four periods the environmental conditions suffer changes, namely in ground temperature and humidity (Figure 9). In the first period the mesocosm temperature would vary between 15°c and 22°c and gradually warmed up until an average of 28°c. In terms of humidity, it progressively decreased resulting in a drier environment, initially with an average 80%H and in the final period with an average 62%H.







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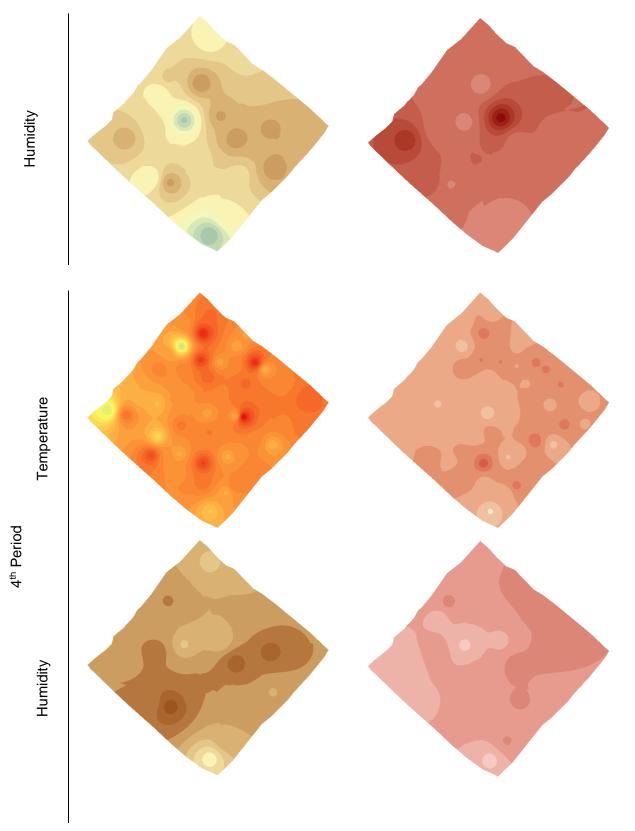


Figure 9 - Evolution of the environmental condition over the four periods. The left maps represent average temperature and humidity and the right maps represents its consecutive standard desviation

Ecological Niche Modelling

From the 32 models generated, all of them possessed an AUC higher than 0.823 (Table 4 - AUC and more important variables per individual). These models will try to identify the suitable habitat of each individual using the environmental conditions and locations found (Figure 10). From the 17 variables introduced to generate the model, six proved to be major contributors.

ا م بان بنام برما		le eth e wee e litu	Minimum	Minimum	Distance to	Distance to	Organia Cail
Individual	AUC	Isothermality	Temperature	Humidity	Females	Males	Organic Soil
BPB	0,8265	8,785	1,0356	4,6815	8,38	22,0365	5,7553
BPP	0,9106	11,8628	0,6695	33,3623	9,2819	1,9847	4,2517
BPW	0,9121	28,3487	7,9738	22,7966	4,4738	2,08	0,9017
BRP	0,8481	4,8604	16,8545	12,1012	4,8037	14,4674	11,6217
BRW	0,8856	1,4727	5,2479	2,5415	4,8158	9,9739	2,7458
BWB	0,8948	32,6846	4,6654	0,8736	34,9775	1,3039	3,73
BWP	0,8457	0,4742	6,3389	2,0994	7,9148	30,5169	4,3882
BWW	0,8755	48,057	0,0377	13,6293	0,7306	1,423	1,0626
PBG	0,9235	18,4144	2,2336	29,7426	1,1542	23,7425	3,5749
PPB	0,9821	11,2579	5,4805	0,0274	9,2778	1,1375	0,5233
PRB	0,8821	21,8444	6,0645	2,0925	23,4419	5,7431	6,9238
РҮВ	0,9646	0,1195	1,7652	4,2042	0,718	1,9196	2,1981
RBB	0.9511	7,555	20,68	14,4143	11,8494	2,2967	5,6711
RBG	0,873	3,2761	10,3288	16,6883	2,9615	2,9733	22,6675
RBR	0.9215	2,6323	0,3269	28,6013	19,2655	4,8726	1,067
RBW	0,9225	47,2843	1,1935	4,4555	8,1222	1,8768	0,3683
RBY	0,8982	0,1815	2,1681	17,8924	13,1227	2,1417	1,2568
RGB	0,9614	31,0282	5,2461	15,2128	9,9199	3,6723	1,2067
RPB	0,9037	4,8058	18,7645	2,1829	7,7134	11,7226	1,7775
RRB	0,9619	4,3599	32,9101	9,4075	0,7396	2,9192	2,0404
RWB	0,9061	3,4464	41,3848	7,5085	13,3151	9,2802	1,9716
WBB	0,9743	2,6752	3,071	9,2814	5,6108	0,843	44,5941
WBR	0,9257	8,4461	5,3949	18,0224	6,0768	10,9195	3,6022

Table 4 - AUC and more important variables per individual

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WBW	0,855	3,2542	2,5581	6,1294	2,2763	11,7202	45,1528
WBY	0,9108	4,5081	3,6114	17,2514	11,1791	32,8754	9,6647
WGB	0,885	17,3781	0,0693	23,9252	4,2353	9,6948	11,7862
WPB	0,8758	5,501	19,5716	4,5812	5,2902	5,6745	5,5682
WRB	0,977	5,1313	0,6483	1,3638	4,5753	0,8988	6,914
YPB	0,8231	2,5907	8,7395	1,7401	2,9408	12,5892	10,6843
YWB	0,9591	0,8416	1,631	1,4766	40,8599	5,7819	1,6108
YYB	0,9619	33,944	5,8934	17,559	8,5605	3,7642	1,4435

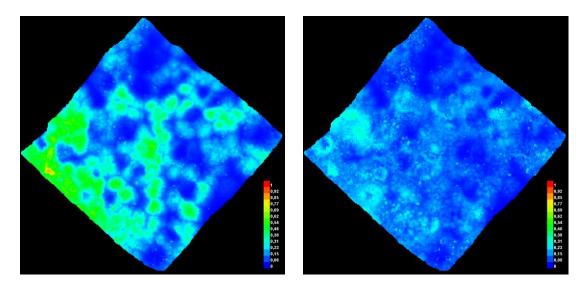


Figure 10 - Model of suitable area of one individual and its standard deviation

Distance analysis

A total of 72 final locations were recorded outside the home range of the individual and 216 inside the home range. This means that 25% of the escapes ended outside the home range (Figure 11), which represents a significant deviation from random escape choice using chi-square test ($df = 1, \chi^2 = 96, P = 1.1488 \times e^{-22}$).

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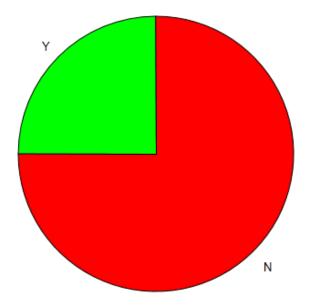


Figure 11 - Graph representing the percentage of individuals running outside the home range. Green represents the individuals running outside and the red the individuals staying inside

Generalized Linear Models were used to test the significance between the periods (time between recaptures), the approach distances and refuge distance, which did not prove to be significant (Figure 12).

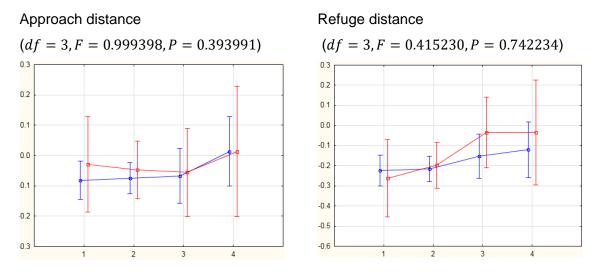


Figure 12 - GLM representing the significance between the distances, periods and the escapes inside and outside the home range

Then, GLM (Figure 13) were used in order to find the variable which represented the most important response in order to find its relationship. Although, none of the factors tested where significant, a positive trend in the approach distance, escape distance and thermoregulatory cost was suggested.

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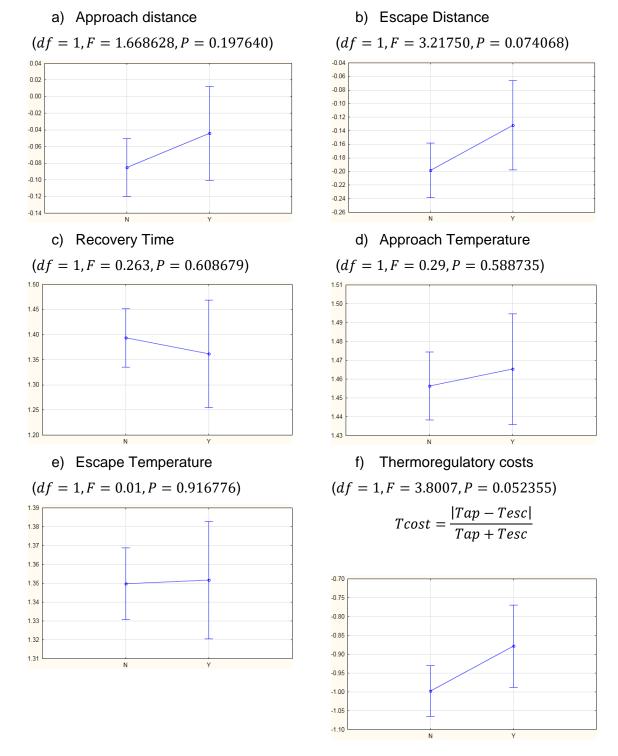


Figure 13 - GLMs representing the significance between the the escapes inside and outside the home range and: a) approach distance, b) escape distance, c) recovery time, d) approach temperature, e) escape temperature and f) thermoregulatory cost

Discussion

The morphological measures were in conformity with previous studies in relationship with significant differences of both size and weight between male and

females of *Podarcis bocagei* lizards (A. Kaliontzopoulou, Carretero, & Llorente, 2010; Antigoni Kaliontzopoulou et al., 2007; Antigoni Kaliontzopoulou, Carretero, & Llorente, 2008). Not only the average size was different, but also females with the same SVL that males weight less.

Over five hundred locations were recorded for all over the mesocosm, containing both males and females' locations. When visually analysing the overlap between the classification map and the locations, a major abundance over the rocks and vegetation locations is clear. These sightings are easily explained by the fact this species finds refuge by hiding in crevices, holes or under rocks (A. Kaliontzopoulou et al., 2010); though it is also known to hide from predators in dense vegetation (A. Kaliontzopoulou, Bandeira, & Carretero, 2013). Due to the sampling design, consecutive locations of the same individual recorded were separated in timeto prevent stress of the recaptures and remarking of the individuals. Additionally, the individuals were translocated from a known open space location to an entirely new and closed space, which means the individuals needed some time in order to establish their home range. Thus our analyses tested for temporal differences between the home range sizes of the period. This was, in fact, confirmed, suggesting a slight decrease likely associated to the familiarisation of the lizards with the spatial structure of the mesocosm. Though, when comparing paired periods, only the first period proved to be different, presenting a much larger area than the others. The results showed that in the first period the individuals presented an area much larger than in the later periods. These results may suggest the individuals, when facing an entirely new environment, in a colonisation-like scenario, do not have well delimited home range and persist in an exploration phase. Only later, with the information acquired during the explorations and social interaction, individuals may start to define a home range, still susceptible to the dynamic of the environment and social interactions. Finally, in the last periods there is a more specific home range well delimited that suffers mainly minimal changes.

Regarding the difference of home range size by gender, as expected, the males' present a home range significantly larger than the ones of the females. The males also presented significantly larger perimeter than females. Perry & Garland, Jr, 2002 described a strong positive relationship between the animal size and its home range. The results are also in conformity with the kind of activity developed by both gender during the time of the study (reproductive period): for males, the constant and active pursuit for females and food, will consequently lead to larger home ranges and try to include females home ranges within its own. On the other hand, females' main activity is the search for better food, which will result in smaller home ranges containing the essential resources for its survival. The results are in agreement with previous studies of Rose, 1982, in which the male home range not only have twice the size of the females but also exceeds the available area per male, meaning there is an overlap of home ranges between males (M. Carretero et al., 2006).

Concerning the overlap results, three maps were obtained: (1) it was analysed the overlap among all individuals; (2) only among males; (3) only among females. The first showed a clear preference of the individuals for the western part of the mesocosm, an area with more and higher vegetation. These results were expected once the *Podarcis* bocagei is known to be a ground-dwelling species with clear preference for vegetation, rocks and crevices rocks (A. Kaliontzopoulou et al., 2010). The overlap map (1) shows that the entire mesocosm is used as home range for one or more individuals; however, this may indicate that the mesocosm was too small for the number of individuals used. Another possible explanation is that the individuals are not in the same place at the same time also, chemical information contributes to minimize aggressions between "dear enemies" (P. Carazo, Font, & Desfilis, 2008; Pau Carazo, Font, & Desfilis, 2011). The overlap of all males (2) was a similar case, with the exception of a small area with no presence of any of the individuals. This area consisted in a lower zone with bare soil and no vegetation, which led to believe that this highly exposed area would hamper to hide in case of predation and this risk might not make up for the benefits of an unused area. Finally, the overlap of all fames (3) showed distinct results when compared with the male overlap, since females seem to have random home ranges throughout the available area, being present in areas with essentially rocks and underbrush. These results confirms the conclusions by Rose, 1982 in which females home ranges are specially related with food.

As for the environmental conditions, as expected, during the two months of the study numerous changes occurred, namely the area became warmer and dryer. The mesocosm changed in about six degrees its temperature and in 20% the humidity. Those two factors are strongly and inversely correlated with each other and related with the months of the year and time of the day. Nevertheless, these two environmental conditions did not affect the escape behaviour of the lizards significantly, remaining important for the preferential establishment of the home range. These data contradict the ones obtained by Martin & Lopez (1999), in which the temperature highly affects not only the escape behaviour but also the recovery time as a decisive factor for the choosing of the refuge. The present results did not show significance, though the sample size may not allow such big conclusions. Concerning the home range, the temperature and humidity is a key factor for its establishment once ectotherms actively suffer from environmental conditions (Carrascal & Díaz, 1989; Tracy & Christian, 1986; Waldschmidt, Tracy, & Jun, 1983).

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All ecological niche models obtained a high AUC which permits the assumptions of realistic conclusions. Both genders seem to be highly influenced by the isothermality, minimum humidity and distance to females. Each gender presented a characteristic variable that influenced its suitable habitat: for the females, the minimum temperature; and for the males, the distance to other males and the distance to the organic soil. In other words, the species seems to prefer a more constant temperature of the ground, with less daily variation. In an environment with much temperature variation the performance of the individual is affected and so are the activities. The minimum humidity can be clarified by the fact *Podarcis bocagei* is a species limited by humidity at both geographic and ecological scale (Ferreira, Santos, & Carretero, 2016; Sá-sousa, 2001). The third variable that influences both males and females is the distance to females, however the reasons seems to be opposite, for males a low distance have a major importance for the model, which is easily explained by the constant pursuit for females and including their home range in its own. On the other hand, females avoid short distances to other females in order to diminish competition for food, hence less overlaps. Additionally, females appear to be sensible to low temperatures. Regarding males, the distance to other males proved to be extremely important for the models, greater distance allows less competition not only for food and thermoregulatory spots but also for females. The other major variable is the organic soil, where males are especially fond of, trying to stay near. The organic soil seems to present higher values of temperature and a lower humidity comparing to the bare soil, thus facilitating the thermoregulation of the individuals. Another possible explanation for the organic soil preference may be the food availability (M. A. Carretero, 2004).

The travelled distances map represented the distances between the locations recorded and provides further knowledge about how the home range is delimited: where are the individuals' occasional sallies, what locations are part of the home range, direction of the movements, as well as how the home range evolved during the study time. As expected the males presented longer distances travelled which is in accordance with normal activity of males, mainly the pursuit for females and patrolling for male intruders (Rose, 1982).

Unexpectedly, some individuals run outside their home range. The results contradict the expected result, "the individuals do not run outside their home range", staying in a well-known location. In fact, all the mesocosm seems to be well-known by the individuals due to their sallies, and the home range should contain the essential resources which may not include refuges for all the thermal optimum. These results answer a question never tested before and that might change how the spatial context is analysed for behavioural studies once some factors not yet known may interfere with the escape. However, all the

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escapes outside the home range remain close (about 50 cm) to their limits, which corroborates the idea of the thermal optimum refuges. In other words, the individuals do not include in their home range all available refuges, but only the recurrent ones. However, only the movements of the individuals were considered, ignoring the predator influence in the escape behaviour. Factors like direction of approach are certain to affect this behaviour and may limit the options of the individual (Cooper, Pérez-Mellado, & Hawlena, 2007; Cooper W.E., 1997). From the response variables of the species (Approach distance, Escape distance, Approach temperature, Escape temperature, Recovery time) it was impossible to find a significant relationship. However, in three of these variables (approach distance, escape distance and thermoregulatory cost) it is visible a positive trend, in which running outside the home ranges proves to have a slight relationship with these variables. It is obvious the association between the escape distance and the fact the individual runs outside the home range, since the individual have to travel longer in order to exit the home range. Concerning the approach distance, it seems the individual starts to escape earlier so it can reach the selected refuge, leading to belief the individual does not stops at the first possible refuge but tries to go to a more thermally appropriate refuge. Finally, the thermoregulatory cost indicates that the fact individuals run outside the home range there is an increase of the cost to their temperature.

Conclusion:

This study intended to answer to a main question: "Do Iberian lizards escape outside their home range?", which was proved to be true. In fact, 25% of the escapes of the individuals in the study revealed to run outside the home range in order to achieve a refuge with thermal optimum. Despite the individuals running outside the home range, they stay close to it so it can ensure a mid-term persistence of the home range. Additionally, this study brings new insights about the establishment of the home range in a new area, that revealed to be inconsistent at first, where the individuals roam randomly through the mesocosm in an exploratory phase and then established a home range that decreased with the time. Contrary to previous studies, it was not possible to determine the relationship between thermic or hydric heterogeneity and the escape behaviour

Further recommendations for future studies would be to use a larger mesocosm for the same number of individuals. Additionally, other techniques for the recording of the locations for the home range would diminish the stress caused to the individual. Furthermore, the study should consider a longer period once the home range is known to dynamically change over time and is highly influenced by breeding period or nonbreeding period. Finally, it would be valuable to compare other species that are known to co-exist with *Podarcis bocagei*.

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FCUP | I Spatial analysis of escape tactics of Iberian lizards

Appendixes

Appendix I – Morphological data: Snout-vent length (SVL), Trunk Length (TRL), Head Length (HL), Head Width (HW), Head Height (HH); Front Limb Length (FLL); Hind Limb Length (HFL); Total Tail Size (Tltot) and Regenerated Tail Size (Tlori)

Code	Color	SVL	TRL	HL	HW	ΗH	FFL	FL	Tltot	Tlori	W (g)
F1	PPB	52,1	25,93	17,75	5,46	4,36	13,63	7,65	50,42	12,96	2,151
F2	PBP	60,97	34,19	21,24	6,54	5,44	15,08	7,95	90,01	74,51	3,917
F3	PRB	58,17	32,99	20,48	6,45	4,64	15,61	7,84	66,98	19,42	3,005
F4	PBR	59,26	31,09	21,61	6,33	5,11	15,99	7,22	56,65	17,4	3,084
F5	PGB	58,47	32,94	19,22	7,09	5,43	15,45	7,47	50,76	26,62	3,566
F6	PBG	51,2	26,83	19,04	6,04	4,59	14,9	7,11	85,76	85,76	2,159
F7	PBW	50,62	29,23	18,18	6,37	4,89	15,23	6,67	66,64	9,02	2,2
F8	PYB	58,46	32,14	21,07	6,81	5,47	15,33	7,39	77,15	44,71	3,975
F9	PWB	56,33	31,33	19,1	6,23	5,47	14,31	6,67	54,67	24,01	3,163
F10	PBY	54,16	30,46	10,01	6,15	4,98	13,79	7,22	18,52	10,43	2,329
F11	PBB	62,01	32,51	21,38	6,71	5,77	16,42	8,16	62,71	7,35	4,194
F12	RGB	60,56	38,15	21,59	6,93	5,75	15,25	7,09	98,03	53,62	4,098
F13	RBW	57,24	30,66	20,79	6,27	5,06	15,46	7,48	75,89	47,34	3,418
F14	RBR	58,22	30,65	21,62	6,63	5,28	15,06	8,13	89,16	77,01	3,648
F15	RRB	59,59	32,95	19,73	7,06	4,75	14,38	7,84	79,16	25,1	3,67
F16	RPB	49	27,74	18,59	5,81	4,76	14,73	6,72	83,97	83,97	2,172
F17	RBP	52,81	26,96	19,81	6,14	5,08	14,58	6,51	91,66	91,66	2,537

FCUP | II Spatial analysis of escape tactics of Iberian lizards |

F18 RYB 54,64 28,85 17,88 6,4 5,14 15,24 6,72 89,46 89,46 2,689 F19 RWB 59,22 33,25 19,44 6,5 5,53 15,92 7,36 64,25 25,01 3,903 M2 YYB 60,9 26,33 25,75 8,88 7 19,8 9,64 112,3 112,3 4,938 M3 WBW 63,49 30,64 26,44 8,41 6,71 20,01 9,25 81,33 19,43 4,907 M4 YWB 66,45 31,22 27,27 8,65 7,31 20,09 11,26 124,26 124,26 5,732 M5 YPB 58,17 26,19 23,67 7,81 5,76 19,13 9,28 105,93 105,93 3,895 M6 YRB 57,19 25,93 24,62 7,77 6,78 19,03 9,37 103,53 103,53 3,339 M8												
M2 YYB 60,9 26,33 25,75 8,88 7 19,8 9,64 112,3 112,3 4,938 M3 WBW 63,49 30,64 26,44 8,41 6,71 20,01 9,25 81,33 19,43 4,907 M4 YWB 66,45 31,22 27,27 8,65 7,31 20,09 11,26 124,26 124,26 5,732 M5 YPB 58,17 26,19 23,67 7,81 5,76 19,13 9,28 105,93 105,93 3,895 M6 YRB 57,19 25,93 24,62 7,77 6,78 19,03 9,37 103,53 103,53 3,897 M7 WBY 54,42 25,42 22,36 7,37 6,57 17,77 7,64 71,09 7,93 3,339 M8 WBP 62,02 31,37 23,57 26,22 18,24 8,56 30,28 20,87 4,079 M11 BRB	F18	RYB	54,64	28,85	17,88	6,4	5,14	15,24	6,72	89,46	89,46	2,689
M3WBW63,4930,6426,448,416,7120,019,2581,3319,434,907M4YWB66,4531,2227,278,657,3120,0911,26124,26124,265,732M5YPB58,1726,1923,677,815,7619,139,28105,93105,933,895M6YRB57,1925,9324,627,776,7819,039,37103,53103,533,807M7WBY54,4225,4222,367,376,5717,777,6471,097,933,339M8WBP62,0231,3723,598,176,318,61103,6956,084,539M9WBR57,8826,2725,448,516,3517,39,2892,1530,764,246M10WBB/YBB57,6925,7724,637,726,2218,248,5630,2820,874,079M11BRB55,426,1223,877,196,4417,687,8887,3433,613,626M12BPP59,6128,823,088,846,7517,038,476,5111,323,98M13BWP59,8828,8924,688,746,8619,5210,4579,5341,575,269M14BWR56,9626,1322,957,584,9518,329,3651,8751,873,8433,768 <td>F19</td> <td>RWB</td> <td>59,22</td> <td>33,25</td> <td>19,44</td> <td>6,5</td> <td>5,53</td> <td>15,92</td> <td>7,36</td> <td>64,25</td> <td>25,01</td> <td>3,903</td>	F19	RWB	59,22	33,25	19,44	6,5	5,53	15,92	7,36	64,25	25,01	3,903
M4YWB66,4531,2227,278,657,3120,0911,26124,26124,26124,265,732M5YPB58,1726,1923,677,815,7619,139,28105,93105,933,895M6YRB57,1925,9324,627,776,7819,039,37103,53103,533,807M7WBY54,4225,4222,367,376,5717,777,6471,097,933,339M8WBP62,0231,3723,598,176,318,61103,6956,084,539M9WBR57,8826,2725,448,516,3517,39,2892,1530,764,246M10WBB/YBB57,6925,7724,637,726,2218,248,5630,2820,874,079M11BRB55,426,1223,877,196,4417,687,8887,3433,613,626M12BPP59,6128,8924,688,746,8619,5210,4579,5341,575,269M14BWR56,9626,1322,957,584,9518,329,3651,8751,873,788M15BWW55,2225,4222,687,766,5918,899,1446,4738,433,768M15BWW55,2225,4222,687,766,5918,899,1446,4738,433,768 <td>M2</td> <td>YYB</td> <td>60,9</td> <td>26,33</td> <td>25,75</td> <td>8,88</td> <td>7</td> <td>19,8</td> <td>9,64</td> <td>112,3</td> <td>112,3</td> <td>4,938</td>	M2	YYB	60,9	26,33	25,75	8,88	7	19,8	9,64	112,3	112,3	4,938
M5YPB58,1726,1923,677,815,7619,139,28105,93105,933,895M6YRB57,1925,9324,627,776,7819,039,37103,53103,533,807M7WBY54,4225,4222,367,376,5717,777,6471,097,933,339M8WBP62,0231,3723,598,176,318,61103,6956,084,539M9WBR57,8826,2725,448,516,3517,39,2892,1530,764,246M10WBB/YBB57,6925,7724,637,726,2218,248,5630,2820,874,079M11BRB55,426,1223,877,196,4417,687,8887,3433,613,626M12BPP59,6128,823,088,846,7517,038,476,5111,323,98M13BWP59,8828,8924,688,746,8619,5210,4579,5341,575,269M14BWR56,9626,1322,957,584,9518,329,3651,8751,873,589M15BWW55,2225,4222,687,766,5918,899,1446,4738,433,768M16BRW60,2128,7724,468,396,6420,619,2981,6581,154,751M17 </td <td>M3</td> <td>WBW</td> <td>63,49</td> <td>30,64</td> <td>26,44</td> <td>8,41</td> <td>6,71</td> <td>20,01</td> <td>9,25</td> <td>81,33</td> <td>19,43</td> <td>4,907</td>	M3	WBW	63,49	30,64	26,44	8,41	6,71	20,01	9,25	81,33	19,43	4,907
M6YRB57,1925,9324,627,776,7819,039,37103,53103,533,807M7WBY54,4225,4222,367,376,5717,777,6471,097,933,339M8WBP62,0231,3723,598,176,318,61103,6956,084,539M9WBR57,8826,2725,448,516,3517,39,2892,1530,764,246M10WBB/YBB57,6925,7724,637,726,2218,248,5630,2820,874,079M11BRB55,426,1223,877,196,4417,687,8887,3433,613,626M12BPP59,6128,823,088,846,7517,038,476,5111,323,98M13BWP59,8828,8924,688,746,8619,5210,4579,5341,575,269M14BWR56,9626,1322,957,584,9518,329,3651,8751,873,589M15BWW55,2225,4222,687,766,5918,899,1446,4738,433,768M16BRW60,2128,7724,468,396,4420,619,2981,6581,154,751M17BPW61,4128,2323,48,857,4820,929,8288,498,496,471M17	M4	YWB	66,45	31,22	27,27	8,65	7,31	20,09	11,26	124,26	124,26	5,732
M7WBY54,4225,4222,367,376,5717,777,6471,097,933,339M8WBP62,0231,3723,598,176,318,61103,6956,084,539M9WBR57,8826,2725,448,516,3517,39,2892,1530,764,246M10WBB/YBB57,6925,7724,637,726,2218,248,5630,2820,874,079M11BRB55,426,1223,877,196,4417,687,8887,3433,613,626M12BPP59,6128,823,088,846,7517,038,476,5111,323,98M13BWP59,8828,8924,688,746,8619,5210,4579,5341,575,269M14BWR56,9626,1322,957,584,9518,329,3651,8751,873,589M15BWW55,2225,4222,687,766,5918,899,1446,4738,433,768M16BRW60,2128,7724,468,396,6420,619,2981,6581,154,751M17BPW61,4128,2323,48,386,7519,5310,6310,83539,45,154M17BPW61,4128,2325,48,857,4820,929,8288,496,487M18BPB <t< td=""><td>M5</td><td>YPB</td><td>58,17</td><td>26,19</td><td>23,67</td><td>7,81</td><td>5,76</td><td>19,13</td><td>9,28</td><td>105,93</td><td>105,93</td><td>3,895</td></t<>	M5	YPB	58,17	26,19	23,67	7,81	5,76	19,13	9,28	105,93	105,93	3,895
M8WBP62,0231,3723,598,176,318,61103,6956,084,539M9WBR57,8826,2725,448,516,3517,39,2892,1530,764,246M10WBB/YBB57,6925,7724,637,726,2218,248,5630,2820,874,079M11BRB55,426,1223,877,196,4417,687,8887,3433,613,626M12BPP59,6128,823,088,846,7517,038,476,5111,323,98M13BWP59,8828,8924,688,746,8619,5210,4579,5341,575,269M14BWR56,9626,1322,957,584,9518,329,3651,8751,873,589M15BWW55,2225,4222,687,766,5918,899,1446,4738,433,768M16BRW60,2128,7724,468,396,6420,619,2981,6581,154,751M17BPW61,4128,2323,48,386,7519,5310,63108,3539,45,154M17BPW61,8230,7924,718,036,6920,2510,89125,17105,155,154M18BPB63,1928,6525,478,017,2618,558,4283,2211,584,969M1	M6	YRB	57,19	25,93	24,62	7,77	6,78	19,03	9,37	103,53	103,53	3,807
M9WBR57,8826,2725,448,516,3517,39,2892,1530,764,246M10WBB/YBB57,6925,7724,637,726,2218,248,5630,2820,874,079M11BRB55,426,1223,877,196,4417,687,8887,3433,613,626M12BPP59,6128,823,088,846,7517,038,476,5111,323,98M13BWP59,8828,8924,688,746,8619,5210,4579,5341,575,269M14BWR56,9626,1322,957,584,9518,329,3651,8751,873,589M15BWW55,2225,4222,687,766,5918,899,1446,4738,433,768M16BRW60,2128,7724,468,396,6420,619,2981,6581,154,751M17BPW61,4128,2323,48,386,7519,5310,63108,3539,45,154M18BPB63,1928,6525,48,857,4820,929,8288,4988,496,487M19BWB61,8230,7924,718,036,6920,2510,89125,17105,155,15M20BRP64,6530,7924,738,046,7919,968,8463,3616,184,969 <td>M7</td> <td>WBY</td> <td>54,42</td> <td>25,42</td> <td>22,36</td> <td>7,37</td> <td>6,57</td> <td>17,77</td> <td>7,64</td> <td>71,09</td> <td>7,93</td> <td>3,339</td>	M7	WBY	54,42	25,42	22,36	7,37	6,57	17,77	7,64	71,09	7,93	3,339
M10WBB/YBB57,6925,7724,637,726,2218,248,5630,2820,874,079M11BRB55,426,1223,877,196,4417,687,8887,3433,613,626M12BPP59,6128,823,088,846,7517,038,476,5111,323,98M13BWP59,8828,8924,688,746,8619,5210,4579,5341,575,269M14BWR56,9626,1322,957,584,9518,329,3651,8751,873,589M15BWW55,2225,4222,687,766,5918,899,1446,4738,433,768M16BRW60,2128,7724,468,396,6420,619,2981,6581,154,751M17BPW61,4128,2323,48,386,7519,5310,63108,3539,45,154M18BPB63,1928,6525,48,857,4820,929,8288,4988,496,487M19BWB61,8230,7924,718,036,6920,2510,89125,17105,155,15M20BRP64,6530,7924,738,496,7919,968,8463,3616,184,969M21WGB59,1727,5425,178,017,2618,58,4283,2211,584,741 </td <td>M8</td> <td>WBP</td> <td>62,02</td> <td>31,37</td> <td>23,59</td> <td>8,17</td> <td>6,3</td> <td>18,61</td> <td></td> <td>103,69</td> <td>56,08</td> <td>4,539</td>	M8	WBP	62,02	31,37	23,59	8,17	6,3	18,61		103,69	56,08	4,539
M11BRB55,426,1223,877,196,4417,687,8887,3433,613,626M12BPP59,6128,823,088,846,7517,038,476,5111,323,98M13BWP59,8828,8924,688,746,8619,5210,4579,5341,575,269M14BWR56,9626,1322,957,584,9518,329,3651,8751,873,589M15BWW55,2225,4222,687,766,5918,899,1446,4738,433,768M16BRW60,2128,7724,468,396,6420,619,2981,6581,154,751M17BPW61,4128,2323,48,386,7519,5310,63108,3539,45,154M18BPB63,1928,6525,48,857,4820,929,8288,4988,496,487M19BWB61,8230,7924,718,036,6920,2510,89125,17105,155,15M20BRP64,6530,7924,738,496,7919,968,8463,3616,184,969M21WGB59,1727,5425,178,017,2618,578,4283,2211,584,741M22WPB58,627,5823,518,376,7218,1710,57100,1235,534,741 <td>M9</td> <td>WBR</td> <td>57,88</td> <td>26,27</td> <td>25,44</td> <td>8,51</td> <td>6,35</td> <td>17,3</td> <td>9,28</td> <td>92,15</td> <td>30,76</td> <td>4,246</td>	M9	WBR	57,88	26,27	25,44	8,51	6,35	17,3	9,28	92,15	30,76	4,246
M12BPP59,6128,823,088,846,7517,038,476,5111,323,98M13BWP59,8828,8924,688,746,8619,5210,4579,5341,575,269M14BWR56,9626,1322,957,584,9518,329,3651,8751,873,589M15BWW55,2225,4222,687,766,5918,899,1446,4738,433,768M16BRW60,2128,7724,468,396,6420,619,2981,6581,154,751M17BPW61,4128,2323,48,386,7519,5310,63108,3539,45,154M18BPB63,1928,6525,48,857,4820,929,8288,4988,496,487M19BWB61,8230,7924,718,036,6920,2510,89125,17105,155,15M20BRP64,6530,7924,738,496,7919,968,8463,3616,184,969M21WGB59,1727,5425,178,017,2618,558,4283,2211,584,741M22WPB58,627,5823,518,376,7218,1710,57100,1235,534,741	M10	WBB/YBB	57,69	25,77	24,63	7,72	6,22	18,24	8,56	30,28	20,87	4,079
M13BWP59,8828,8924,688,746,8619,5210,4579,5341,575,269M14BWR56,9626,1322,957,584,9518,329,3651,8751,873,589M15BWW55,2225,4222,687,766,5918,899,1446,4738,433,768M16BRW60,2128,7724,468,396,6420,619,2981,6581,154,751M17BPW61,4128,2323,48,386,7519,5310,63108,3539,45,154M18BPB63,1928,6525,48,857,4820,929,8288,4988,496,487M19BWB61,8230,7924,718,036,6920,2510,89125,17105,155,15M20BRP64,6530,7924,738,496,7919,968,8463,3616,184,969M21WGB59,1727,5425,178,017,2618,58,4283,2211,584,796M22WPB58,627,5823,518,376,7218,1710,57100,1235,534,741	M11	BRB	55,4	26,12	23,87	7,19	6,44	17,68	7,88	87,34	33,61	3,626
M14BWR56,9626,1322,957,584,9518,329,3651,8751,873,589M15BWW55,2225,4222,687,766,5918,899,1446,4738,433,768M16BRW60,2128,7724,468,396,6420,619,2981,6581,154,751M17BPW61,4128,2323,48,386,7519,5310,63108,3539,45,154M18BPB63,1928,6525,48,857,4820,929,8288,4988,496,487M19BWB61,8230,7924,718,036,6920,2510,89125,17105,155,15M20BRP64,6530,7924,738,496,7919,968,8463,3616,184,969M21WGB59,1727,5425,178,017,2618,58,4283,2211,584,741M22WPB58,627,5823,518,376,7218,1710,57100,1235,534,741	M12	BPP	59,61	28,8	23,08	8,84	6,75	17,03	8,4	76,51	11,32	3,98
M15BWW55,2225,4222,687,766,5918,899,1446,4738,433,768M16BRW60,2128,7724,468,396,6420,619,2981,6581,154,751M17BPW61,4128,2323,48,386,7519,5310,63108,3539,45,154M18BPB63,1928,6525,48,857,4820,929,8288,4988,496,487M19BWB61,8230,7924,718,036,6920,2510,89125,17105,155,15M20BRP64,6530,7924,738,496,7919,968,8463,3616,184,969M21WGB59,1727,5425,178,017,2618,58,4283,2211,584,741M22WPB58,627,5823,518,376,7218,1710,57100,1235,534,741	M13	BWP	59,88	28,89	24,68	8,74	6,86	19,52	10,45	79,53	41,57	5,269
M16BRW60,2128,7724,468,396,6420,619,2981,6581,154,751M17BPW61,4128,2323,48,386,7519,5310,63108,3539,45,154M18BPB63,1928,6525,48,857,4820,929,8288,4988,496,487M19BWB61,8230,7924,718,036,6920,2510,89125,17105,155,15M20BRP64,6530,7924,738,496,7919,968,8463,3616,184,969M21WGB59,1727,5425,178,017,2618,58,4283,2211,584,741M22WPB58,627,5823,518,376,7218,1710,57100,1235,534,741	M14	BWR	56,96	26,13	22,95	7,58	4,95	18,32	9,36	51,87	51,87	3,589
M17BPW61,4128,2323,48,386,7519,5310,63108,3539,45,154M18BPB63,1928,6525,48,857,4820,929,8288,4988,496,487M19BWB61,8230,7924,718,036,6920,2510,89125,17105,155,15M20BRP64,6530,7924,738,496,7919,968,8463,3616,184,969M21WGB59,1727,5425,178,017,2618,58,4283,2211,584,796M22WPB58,627,5823,518,376,7218,1710,57100,1235,534,741	M15	BWW	55,22	25,42	22,68	7,76	6,59	18,89	9,14	46,47	38,43	3,768
M18BPB63,1928,6525,48,857,4820,929,8288,4988,496,487M19BWB61,8230,7924,718,036,6920,2510,89125,17105,155,15M20BRP64,6530,7924,738,496,7919,968,8463,3616,184,969M21WGB59,1727,5425,178,017,2618,58,4283,2211,584,796M22WPB58,627,5823,518,376,7218,1710,57100,1235,534,741	M16	BRW	60,21	28,77	24,46	8,39	6,64	20,61	9,29	81,65	81,15	4,751
M19BWB61,8230,7924,718,036,6920,2510,89125,17105,155,15M20BRP64,6530,7924,738,496,7919,968,8463,3616,184,969M21WGB59,1727,5425,178,017,2618,58,4283,2211,584,796M22WPB58,627,5823,518,376,7218,1710,57100,1235,534,741	M17	BPW	61,41	28,23	23,4	8,38	6,75	19,53	10,63	108,35	39,4	5,154
M20BRP64,6530,7924,738,496,7919,968,8463,3616,184,969M21WGB59,1727,5425,178,017,2618,58,4283,2211,584,796M22WPB58,627,5823,518,376,7218,1710,57100,1235,534,741	M18	BPB	63,19	28,65	25,4	8,85	7,48	20,92	9,82	88,49	88,49	6,487
M21WGB59,1727,5425,178,017,2618,58,4283,2211,584,796M22WPB58,627,5823,518,376,7218,1710,57100,1235,534,741	M19	BWB	61,82	30,79	24,71	8,03	6,69	20,25	10,89	125,17	105,15	5,15
M22 WPB 58,6 27,58 23,51 8,37 6,72 18,17 10,57 100,12 35,53 4,741	M20	BRP	64,65	30,79	24,73	8,49	6,79	19,96	8,84	63,36	16,18	4,969
	M21	WGB	59,17	27,54	25,17	8,01	7,26	18,5	8,42	83,22	11,58	4,796
M23 WWB 62,2 27,03 25,84 8,34 6,78 19,62 9,82 77,41 77,41 4,912	M22	WPB	58,6	27,58	23,51	8,37	6,72	18,17	10,57	100,12	35,53	4,741
	M23	WWB	62,2	27,03	25,84	8,34	6,78	19,62	9,82	77,41	77,41	4,912

FCUP | III Spatial analysis of escape tactics of Iberian lizards |

M24	WYB	66,61	31,33	26,1	8,3	6,77	20,27		96,98	10,92	5,834
M25	WRB	65,03	31,09	26,77	8,7	7,4	19,07	9,51	83,67	43,51	5,395
M26	RBY	62,95	30,11	25,95	8,28	7,1	20,74	9,66	108,64	71,5	5,263
M27	RBB	63,97	30,43	24,5	8,41	7,23	18,89	9,46	108,94	52,69	5,467
M28	RBG	53,99	24,27	23,24	7,6	6,43	17,49	8,83	104,45	104,45	3,792