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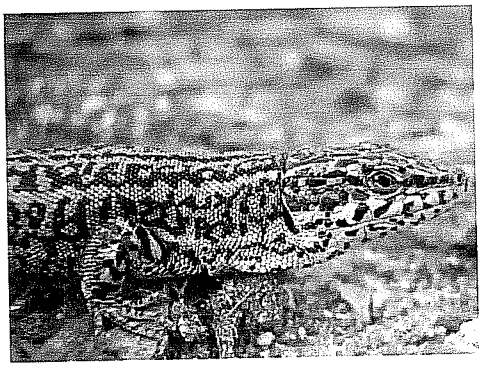
The relationship between field-determined putative territorial strategies and spatial and non-spatial learning in males of Carbonell's wall lizard, *Podarcis carbonelli berlengensis*.



Dissertation to fulfilment requirements for the Degree Master of Ethology

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Abstract

In a spatial context an animal, can orient itself to find a specific goal by having a spatial strategy or possessing a behavioural flexibility that enables it to respond to alterations in the environment. It was suggested that spatial cognition may have a social context. Therefore, I expected that putative territorial male lizards would perform better in a spatial learning task than putative non-territorial ones. If the males possessed behaviour flexibility while orienting them, I expected that non-territorial males would have better performances in a non-spatial task.

Lizards were tested in an arena where a heated quadrant was the goal. I conducted two experiments in which the lizards could achieve the goal associating three cues in the spatial learning experiment and by associating only two cues: one to a positive reinforcer (heated quadrant) and another to a negative reinforcer (not heated), in the non-spatial experiment.

Apparently, male lizards did not use visual cues in the spatial and non-spatial experiment, but they showed some spatial learning in the spatial experiment as expressed by a decrease in the latency and an overall preference for the goal quadrant. Although putative territorial males had apparently better performances, I only observed a statistically significant difference between the two groups in the frequencies of quadrant use and standard deviation of latency on the spatial learning experiment. The fact that the comparisons between male groups were not clear could be explained because these lizards were isolated during one month prior to the experiements and this could confound some of their characteristics that influence spatial strategies.

Keywords: Carbonell wall lizard, putative territorial strategies, spatial learning and non-spatial learning.

Resumo

A maioria dos animais poderá demonstrar uma aprendizagem espacial quando procuram refúgio, parceiros, forrageiam ou mesmo quando fogem de predadores. No seu ambiente natural, os répteis demonstram que conseguem aprender e recordar tarefas espaciais. Foi sugerido que o contexto social poderá funcionar como uma vantagem selectiva para mecanismos espaciais cognitivos e desta forma seria de esperar que uma variação intrasexual pudesse influenciar uma cognição espacial.

Num contexto espacial, os animais poderão usar uma estratégia espacial, na qual relacionam diversas pistas com o objectivo, ou possuírem uma flexibilidade comportamental para responder a diversas alterações do ambiente de forma a alcançar o objectivo. Esta flexibilidade comportamental é bastante importante, pois os animais que possuem uma flexibilidade elevada poderão alternar a sua resposta comportamental mesmo quando as pistas, o objectivo ou ambos, se alteram de uma forma inesperada.

Neste trabalho estudei a variação intrasexual dos machos da lagartixa de Carbonell num teste de estratégia espacial (aprendizagem espacial) e num teste de flexibilidade comportamental (aprendizagem não-espacial). No campo, apesar de não ter testado completamente o comportamento territorial, observei durante algum tempo, o uso de espaço por cada macho e considerei um macho putativamente territorial quando ocupava uma área de ± 4 m^2 e um macho putativamente não-territorial quando ocupava uma área superior. Neste estudo, refiro-me aos

putativamente territoriais como machos territoriais e aos putativamente não-territoriais como machos não-territoriais.

Se a variação intrasexual afecta uma cognição espacial, seria de esperar que os machos territoriais possuíssem um melhor desempenho que os machos não-territoriais. Se, na verdade, as lagartixas machos se orientam através do uso de uma flexibilidade comportamental, então seria de esperar que os machos não territoriais tivessem melhor desempenho na experiência de aprendizagem não-espacial.

Tanto a experiência de aprendizagem espacial como a de aprendizagem não-espacial foram feitas numa arena circular com tampo metálico coberto por areia. Por baixo desse tampo, existiam 4 lâmpadas. No entanto, somente uma das lâmpadas era acesa por sessão o que gerava um quadrante aquecido que denominei de quadrante objectivo. Na experiência de estratégia espacial utilizei três pistas pretas: quadrado, círculo e triângulo. O círculo situava-se sempre no quadrante aquecido. Esta experiência teve uma duração de 16 dias em que, a partir do 7 dia, o círculo foi degradado a 50% (foi removido uma determinada quantidade do preto do círculo mantendo sempre a mesma forma); no décimo dia o círculo foi degradado a 75% e ao décimo terceiro dia o círculo foi removido. Para testar uma aprendizagem espacial, baseada nas pistas visuais, realizei um dia de teste em que a pista triangular e a pista quadrangular foram trocadas.

Na experiência de estratégia não-espacial usei duas pistas pretas em que uma assinalava o reforço positivo (quadrante aquecido) e outra assinalava um reforço negativo (quadrante não-aquecido). A experiência teve uma duração de oito dias em que nos últimos quatro dias as pistas foram trocadas (a pista que assinalava anteriormente o reforço positivo passou a assinalar o reforço negativo).

As observações foram analisadas com os programas Measuring in Motion, R, SPSS e JMP. Usei ANOVA factorial de medidas repetidas para analisar os efeitos de grupo, dia e territorialidade e pista, e também para comparar o último dia de treino e o primeiro dia de teste. Só apresentei as médias dos ângulos que apresentavam uma tendência direccional.

Na experiência de estratégia espacial os machos não apresentaram um padrão de movimento aleatório na arena e mostraram aprendizagem, pois a latência diminuiu ao longo dos dias. Neste trabalho cronometrei a latência desde os primeiros movimentos dos quadris da lagartixa até parar pelo menos durante 30 segundos para termorregular. Não observei nenhuma alteração entre o último dia de treino e o teste. Os machos territoriais apresentaram aparentemente um desempenho melhor, no entanto só observei uma diferença estatística entre os machos territoriais e não-territoriais nas frequências de uso de quadrantes e desvio padrão da latência na experiência de aprendizagem espacial. Quando analisei os ângulos isoladamente, os dados mostraram que as lagartixas não se orientavam para o quadrante aquecido.

Na experiência de estratégia não-espacial não observei uma alteração da latência ao longo dos dias. No entanto os machos mostraram uma preferência pelo uso da quadrante aquecido.

Tanto na experiência de aprendizagem espacial como na de aprendizagem não-espacial, os machos de lagartixas de Carbonell não demonstraram uma aprendizagem baseada nas pistas visuais. No entanto, os machos não utilizaram uma estratégia aleatória e demonstraram aprendizagem espacial. Deste modo sugiro que as lagartixas usam um modelo de deslocação, pois reduziram ao longo dos dias o comprimento do seu trajecto até ao quadrante aquecido. Neste trabalho as lagartixas poderão não ter associado cada uma das pista à localização do quadrante aquecido devido à posição das mesmas, por variarem em cada sessão e porque o gradiente de temperatura poderá desviar a atenção às pistas. Estes resultados diferem dos que foram obtidos com tartarugas e cobras, mas não diferem dos de outras lagartixas. Este facto poderá ser devido a diferenças fisiológicas e filogenéticas entre os animais e diferenças metodológicas entre os estudos.

Neste estudo não observei a flexibilidade comportamental, pois os machos não conseguiram utilizar a informação potencialmente dada por cada pista e assim não perceberam quando as pistas foram invertidas. O facto de outros estudos, com répteis, terem observado uma flexibilidade comportamental poderá ser explicado devido às diferenças acima mencionadas.

Os machos territoriais apresentaram um melhor desempenho geral em ambas as experiências. No entanto só observei uma diferença estatística nas frequências e no desvio padrão da latência, na experiência de estratégia-espacial. Não observei diferença estatística de latência e frequências entre os machos territoriais e não-territoriais. O facto da comparação entre os machos territoriais e não-territoriais ser confusa poderá ser devido a estes animais terem estado isolados um mês antes da experiências o que poderá ter confundido as características que influenciam as estratégias espaciais de cada grupo. Um modo de evitar a perda de algumas destas características em cativeiro seria o implantar as lagartixas com hormonas, já que as hormonas têm um efeito na capacidade cognitiva espacial e também no tamanho da área vital.

Em conlusão, seria interessante testar em mais espécies de lagartixas o modelo de deslocação e averiguar especificamente se as lagartixas possuem ou não uma aprendizagem tigmotáctica. Neste trabalho a aprendizagem tigmotáctica foi dificultada devido ao quadrante aquecido variar aleatoriamente em cada sessão. Seria também interessante testar se as hormonas influenciam ou não o desempenho em tarefas de aprendizagem espacial e não-espacial de lagartixas.

Palavras-chave: Lagartixa de Carbonell, estratégias putativas territoriais, aprendizagem espacial e aprendizagem não-espacial.

Introduction

When solving a spatial task any animal requires sensory abilities to perceive the environment and memory to remember that environment in the future. Therefore, most animals may show spatial learning because they have an internal representation of the location of the goal and how to reach it (Shettleworth, 1998). The capacity to encode spatial relationships from landmarks and other environmental cues generally influences the ecological and life history traits of species (diet, locomotion, sensory modalities, body size, lifespan, etc.) (Dingle, 1998). Most work in spatial learning and memory has been done on rodents and birds, whereas reptiles and fishes have remained relatively unstudied (Day, 2003; Day et al., 1999; Holtzman, 1998; Holtzman et al., 1999; López et al., 2001; López et al., 2003; López et al., 2004).

Field studies strongly suggest that reptiles can learn and remember spatial tasks performed in their natural environment in turtles (Yeomans, 1995; Cain et al., 2005), in lizards (Jenssen, 2002; Freake, 2001; Freake, 1999), in snakes (Lawson, 1994)).The crested anoles, *Anolis cristatellus*, a non-ranging species, show homing ability because the lizards returned to their territories from presumably unfamiliar release points (Jenssen, 2002). Therefore, it is suggested that the selective advantage for cognitive spatial mechanisms may have a social context that function within the boundaries of their territory (Jenssen, 2002). According to this suggestion, one would expect that intrasexual variation affects spatial cognition in lizards.

Studies of intrasexual variations allow comparisons of differing behavioural phenotypes without the confounding effect of sex (Moore, 1991). Furthermore and reptiles are good study subjects for they have a wide variation in reproductive strategies (Godwin & Crews, 2002). Moreover, it was observed that hormonal levels affect cognition (Janowsky, 2006; Sandstrom et al., 2006). Therefore, spatial cognition could be affected by intrasexual variation either because the mental map is a flexible cognitive system (Jenssen, 2002) or because males with different reproductive tactics may have different levels of hormones which alter their cognitive abilities (Janowsky, 2006; Sandstrom et al., 2006; Isgor & Sengelaub, 1998).

Few laboratorial studies have tested spatial abilities of reptiles (Day, 2003; Day et al., 1999; Holtzman, 1998; Holtzman et al., 1999; López et al., 2001; López et al., 2003; López et al., 2004). To my knowledge, only another study tested the influence of lizard intrasexual variation in the accomplishment of a laboratory task (Stapley & Keogh, 2004). In that experiment, non-territorial males of yellow-bellied water skink, *Eulamprus heatwolei* were less wary of a novel environment, spending more time in the open, moved further, and were more likely to flee inside their refuge during a simulated predator attack than did their territorial counterparts (Stapley & Keogh, 2004). Only two recent spatial learning experiments were done with lizards (Day et al., 1999; Day et al., 2001). However, these studies did not find the use of visual cues in the spatial strategy of lizards (Daudin's fringe-fingered lizard, *Acanthodactylus boskianus*, and scutellated fringe-fingered lizard, *Acanthodactylus scutellatus*). Among the reptiles, both snakes and turtles showed a spatial learning based on visual cues (Holtzman et al., 1999; Holtzman, 1998; Avens & Lohman, 2003; López et al., 2001)

While the animals are orienting themselves, they have the ability to alter efficiently response strategies (Day et al., 1999). This ability is called *pliancy* and describes the behavioural flexibility that animals have to encode complex relationships between stimuli and reinforcers (Day et al., 1999). The presence of high *pliancy* is very important because animals with such high pliancy can use the information to select a behavioural response strategy caused by stimuli, reinforcers, or both unexpectedly change (Day et al., 1999). Therefore in a spatial context, an animal may use a type of spatial learning that relates cues with the specific goal or possess the behavioural flexibility to respond to several alterations in the environment to find the specific goal. The ability to learn that a particular conditional stimulus may signal the goal (positive reinforcer) on some occasions, but might also be either irrelevant or signal the non-goal (negative reinforcer) on other occasions, allows for greater flexibility in understanding the relationships among environmental stimuli (Day, 2003). Few experiments have studied *pliancy* with reptiles: turtles (López et al., 2004) and lizards (Day et al., 1999).

I studied the intrasexual variation of males of Carbonell's wall lizards, in two types of learning tasks (spatial and non-spatial). *Podarcis carbonelli berlengensis* is an insular subspecies that can be found in Berlenga Island and in the coast area of Peniche (adjacent to the island) (Sá-Sousa et al., 2000; Sá-Sousa & Harris, 2002). I used this subspecies because previous field studies showed that these male lizards may have three different spatial strategies: territorial males (surrounded by several females and moving in a 24.63 m^2 home range), monogamous males (moving in a smaller home range of 2.01 m^2), and non-territorial males (moving in a larger home range of 162.85 m^2 and chased away when attempting to enter into the area of a territorial male) (Ferreira, 2002; Vicente, 1989). Therefore, non-territorial males have much larger home ranges than the territorial and monogamous males. Although I did not test fully the territorial behaviour of males, I observed the use of space and considered that the males that settled in a smaller area (±4 m^2) were putatively territorial and the males that settled in a larger area were putatively non-territorials. In this study, I deemed putative territorial males as territorial and the putative non-territorial as non-territorial males. My experiments were made in a circular arena where a heated quadrant was the experimental goal. The two experiments have different methods to observe different responses. In the spatial learning experiment, the information to identify the goal is given by the association of three visual cues and in the non-spatial experiment, the information to identify the goal was only given by a single cue. I expected that putative territorial males would have better performances in a spatial learning task, for they have to be aware of neighbours and local features of the area. An improved spatial learning would be advantageous for the territorial male because he could anticipate social interactions or avoid risky encounters with specific individuals. However, if there is not a selective advantage for cognitive spatial mechanisms to have a social context than I expect that territorial and non-teritorial males would not differ in the spatial learning task.

The non-spatial learning that I conducted was similar to the reversal of simultaneous discrimination (O'Keefe & Nadel, 1978; Day, 2003) and intended to test whether there was an effect of intrassexual variation in the behavioral flexibility. Both groups of males would not differ on the acquisition of the original visual discrimination, as this task requires only simple stimulus-response association. I hypothesised that non-territorial males should be better at the non-spatial learning experiment since that it would be advantageous for these males to alter their responses with alterations of the environment for they have large home ranges and consequently with potentially more diverse habitats.

Methods

Subjects

I captured twenty male lizards of Carbonell wall lizard on the 9th and 10th of April, 2006, in the southern area of the Island Berlenga Grande (UTM 0456158 Lat 4362953 Log). To distinguish males with different spatial strategies, I followed a two-step protocol. First, I captured males by nosing, marked them dorsally with a non-toxic pen, and released them. After marking about 40 individuals, I conducted hourly scans, during three days, to observe the use of space of each lizard. Therefore, I named putative territorial the males those who settled in an area of 4 m^2 and putative non-territorial those who settled in a larger area, but I did not test completely their territorial behaviour. In this study, I deemed the putative territorial males as territorial and the putative non-territorial as non-territorial males. There was a statistical difference between the two groups of males in holding an area of 4 m^2 (Kruskal-Wallis test: $H_{11} = 16.4$; $P < 0.005$). I measured all males (territorial: SVL: 6.09±0.43 cm; non-territorial: 5.93±0.46 cm) and weighed them (territorial: 6.04±0.90 g; non-territorial: 5.39±0.57 g) after capture. There was no difference between the body mass index of the two groups of males (Paired *t* test: t_{12} = 2.040, *P*=0.56). All animals were transported in cloth bags with vegetation in an icebox. The trip to the laboratory lasted less than 3 hours.

During all the experiments, the lizards remained in glass terraria (22x39x30 cm) with coconut fibre as substrate. All the terraria had a UV lamp (30 W) (12L:12D cycle) and I placed a thermal cable on one side of the terrarium to provide a heat gradient. Black cardboard was used between adjacent terraria to prevent animals from watching each other. I fed periodically the lizards with *Tenebrio molitor*, crickets, mashed fruit, and all males had *ad libitum* access to water. I separated the 20 males in two groups. In group A, the males performed the spatial learning experiment first with an interval of 16 days between experiments. Males in group B performed the non-spatial experiment first. Initially each group had 5 males of territorial and 5 of non-territorial males.

There was no significant change in lizards' body mass from the day of capture and the last day of experiment (Wilcoxon test: Z = -1.33, P = 0.21), indicating a sufficient food supply. The males were not released to their natural environment because the Berlenga Island is a natural reserve and their release could endanger the natural population. The Instituto de Conservação da Natureza and the Reserva Natural da Berlenga gave the official permits to capture the animals and perform all of these experiments.

Apparatus

I built a circular arena with 1 m diameter by 0.8 m height (Fig. 1). I covered the walls with white paper and placed atop the arena a cone of cloth as an attempt to provide homogenous surroundings. In the vertex of the cover cloth there was a camera (LEGO cam) recording all sessions. Beneath the arena there were four light bulbs of 100 W each. I turned on only one light bulb per session to create a heated quadrant, which I defined as the goal quadrant. All animals were exposed to the same thermal gradient (Fig. 2, 3). Before each session I turned on a bulb for at least 30 minutes. The metal floor was covered with white sand.

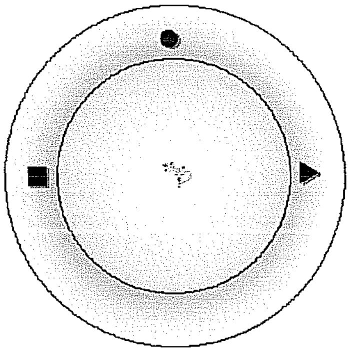


Figure 1. Design of the arena (1 m diameter, 0.8 height) where spatial and non-spatial experiments were performed. The arena was divided in four quadrants and beneath the table there was a 100 W light bulb that provided a thermal gradient. Only one light bulb was turned on per session and I called the heated quadrant as the goal quadrant. The walls of the arena were painted white and a cone of white cover tissue was used to prevent the lizards from using other cues in the room. The cues represented in this figure were used in the spatial learning experiment (see text for details).

The cues were affixed on the wall of the arena with Velcro (21 cm above the floor of the arena). In the arena, the position of the goal quadrant in the arena was switched randomly between sessions to reduce the influence of potentially outside cues (e.g.:magnetic field position). I mixed the sand before each experimental male lizard was tested to avoid chemical cues. The test sequence for each lizard was random. I used the Excel random generator which light bulb to turn on and lizard test sequence.

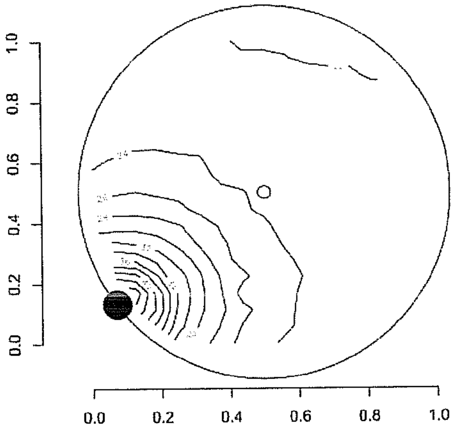


Figure 2. Isothermal lines represented in the arena. The circle represents the circle cue that was always above the heater zone in the heated gradient. The isothermal lines were determined with temperatures measured in a 5 cm x 5cm grid.

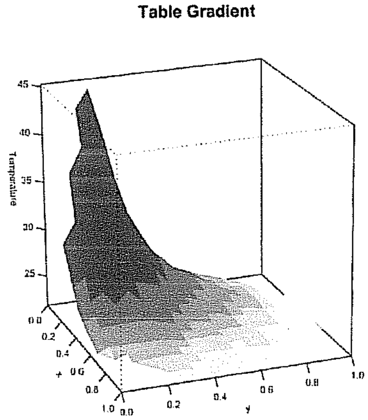


Figure 3. Representation of the thermal gradient. The position of the ligh bulb in the arena is represented as (0,0) in the x-axis.

EXPERIMENT 1: SPATIAL LEARNING

Apparatus

I used three visual cues: a circle, a square, and a triangle. As colour may be important in lizard displays, I choose to use black visual cues (Brattstrom, 1978). The diameter of the circle, the side of the square, and the side of the triangle were all 7 cm. The circle was always in the heated quadrant, the square on the left side and the triangle on the right of the circle.

Test procedures

The spatial learning experiment lasted for 16 days with 3 sessions per day. Before release, in the arena, I put the lizard inside a box placed in the center on the arena for 3 minutes. Afterwards, I removed the box and the lizard was allowed to move freely for 10 minutes in the arena.

Training

The training lasted 15 days. I conducted four blocks of experiments. The first block lasted 6 days. The second lasted 3 days and it was when I degraded the circle to 50%. The third block also lasted 3 days and I degraded the circle to 75%. In the last block. I removed the circle cue (Fig. 4).

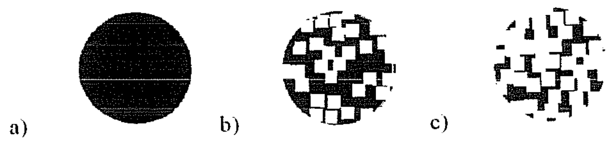


Figure 4. Circle cue used on the spatial learning experiment: a) 100%; b) degraded 50% and c) degraded 75%. I degraded the circle as removing an amount of black maintaining the general form, using the R program. The cue degraded 50 % was used on 7th day till 9th day and the cue degraded 75% was used on the 10th day and 12th day. On the 13th day the circle cue was removed.

I observed time spent in the goal quadrant, frequency of occurrence in the four quadrants, and latency until first thermoregulatory event . Frequency was determined every 30 seconds after the

EXPERIMENT 2: NON-SPATIAL LEARNING

Apparatus

I used two 7 cm black cues: on the shape of an **A** and the other with the shape of a **Z**. One of the cues served as a positive reinforcer (above the heated quadrant) and the other served as a negative reinforcer (above the opposite non- heated quadrant). The purpose of using alphabetic cues was to provide context-free cues. I affixed the cues facing each other on the wall of the arena with Velcro.

Test procedures

The non-spatial learning experiment lasted 8 days with 3 daily sessions. To avoid the influence of predisposition to the cues per se in these males, half of the males had the **A** cue in the heated quadrant and whereas the other half had the **Z** cue. In each session to quiet down the lizards, I put the lizard in an icebox for 3 minutes (9.71 ± 1.48 °C), 1 minute in the box (same as the spatial learning experiment) at room temperature and during 5 minutes the lizards was allowed to move freely in the arena.

Training

Training lasted 4 days and I observed the frequency in the quadrants, latency and two-thirds angle. The definitions of latency and frequency were the same as the spatial learning experiment.

Test

The test lasted 4 days and the cues were swapped so that the cue that was in the goal quadrant was moved to the opposite quadrant. I expected that if the lizards associated the stimuli with the reinforcer there would be an increase of the latency, a decrease in the frequency of the goal quadrant, and that the two-third angle would depart more from 0°.

Statistics

All observations were analysed with the programs Measuring in Motion, R, SPSS, and JMP programs. For all statistical tests I considered $\alpha=0.05$. I used a repeated measures factorial ANOVA to analyse the effects of group, day, and territoriality in both experiments and the effect of cues on the non-spatial experiment. Moreover I compared the last day of training and the first day of test. I only determined the mean angle if the angles passed the Rayleigh test. The results from two territorial males and three non-territorial males were not used eliminated due to the absence of response.

Results

EXPERIMENT 1: SPATIAL LEARNING

On the training and test there was no effect of group (group A did first the spatial learning experiment and group B did first the non-spatial learning experiment) on the latency, standard deviation of latency (errors) time spent in the goal quadrant and use frequency of the four quadrants (Table 1, 2, 3, 4, 5, 6, 7, 8). Therefore, I considered all males as belonging to the same group. Latency and errors of latency were not normal distributed; I used a Box-Cox transformation to do Repeated Measures ANOVA.

Training

There was an effect of day on the latency, errors of latency and on the time spent in the goal quadrant (Table 1, 2, 3), but I did not observe an effect in the frequencies of the four quadrants (circle, square, triangle cues and no cue) (Table 4).

Table 1 – Comparisons of latency between territorial and non-territorial males in training on the spatial learning experiment.

Source	DF	F ratio	P
group	1	0.1238	0.7257
territoriality	1	4.1837	0.0434
day	11	2.6974	0.0038*
group*day	11	1.024	0.4294
terri*day	11	1.6708	0.0875

Note. Repeated-measures factorial ANOVA results for latency with treatment blocks defined by group (group A did first the spatial learning experiment and group B did first the non-spatial learning experiment), territoriality (territorial and non-territorial males) and day (4th till 15th day). Statistical significant results are marked with asterisk. Df = degrees of freedom; *F* ratio = Fisher's value; P = associated probability.

Furthermore I observed an interaction between group (which experiment was first performed) and day in the latency and time spent in the goal quadrant (Table 1, 3), and no interaction between group and frequencies (Table 4). However, I did not observe an interaction between day and territoriality in the latency, errors of latency, time spent in the goal quadrant, and frequencies (Table 1, 2, 3, 4). The analysis of the frequencies showed that the frequency of the goal quadrant was different from those of other three quadrants (Table 4).

Table 2 – Comparisons of standard deviation of latency between territorial and non-territorial males in training on the spatial learning experiment.

Source	dF	F ratio	P
group	1	0.5646	0.4543
territoriality	1	5.13	0.0258*
day	10	3.5404	0.0004*
group*day	10	1.2762	0.2522
terri*day	10	1.8092	0.0667

Note. Repeated-measures factorial ANOVA results for errors of latency with treatment blocks defined by group (group A did first the spatial learning experiment and group B did first the non-spatial learning experiment), territoriality (territorial and non-territorial males) and day (4th till 15th day). Statistical significant results are marked with asterisk. df = degrees of freedom; *F* ratio = Fisher's value; P = associated probability.

Table 3 – Comparisons of time spent in the goal quadrant between territorial and non-territorial males in training on the spatial learning experiment.

Source	**dF**	**F ratio**	**P**
Group	1	3.8487	0.0547
territoriality	1	0.4683	0.4966
day	11	3.1824	0.0007*
Group*day	11	3.0743	0.0011*
terri*day	11	1.1646	0.3178

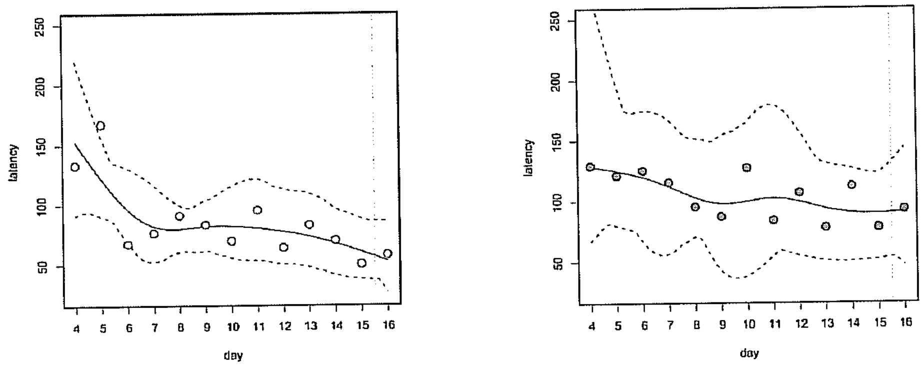
Note. Repeated-measures factorial ANOVA results for time spent in the goal quadrant with treatment blocks defined by group (group A did first the spatial learning experiment and group B did first the non-spatial learning experiment), territoriality (territorial and non-territorial males) and day (4th till 15th day). Statistical significant results are marked with asterisk. df = degrees of freedom; *F* ratio = Fisher's value; P = associated probability.

Apparently, territorial males have better performances than the non-territorial males regarding the latency and standard deviation of latency (Fig. 5, 6). However, I only observed an effect of territoriality in the frequencies (Table 4) and in the errors of the latency (Table 2). In training there was no difference between territorial and non-territorial males in latency and time spent in the goal quadrant (Table 1, 3). Regarding the two-thirds angle, only non-territorial males showed a directional tendency on the 5th, 12th and 15th day (Fig. 7) (Table 9). The paths taken by two territorial and non-territorial males on the 4th day of experiment were much longer than those turn by the same animals on the 15th day of experiment (Fig. 8).

Table 4 – Comparisons of frequencies of the four quadrants between territorial and non-territorial males in training on the spatial learning experiment.

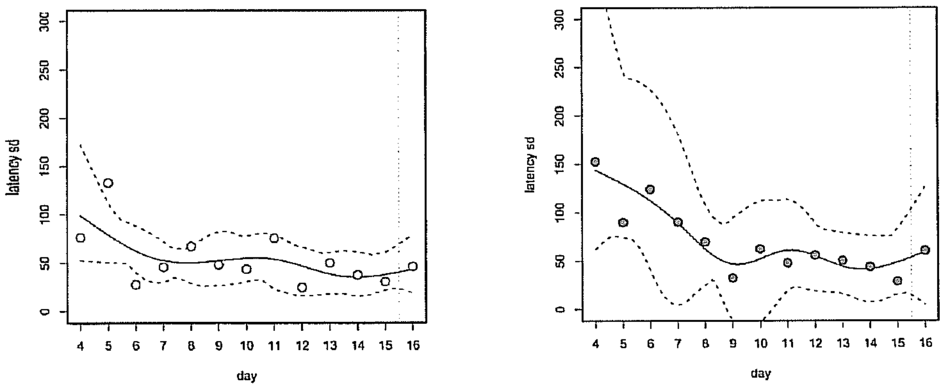
Source	dF	F ratio	P
group	1	1.3611	0.2449
territoriality	1	5.7104	0.0179*
day	11	0.1597	0.9992
quadrant	3	990.9408	<.0001*
group*day	11	0.2662	0.9915
terri*day	11	0.503	0.9018

Note. Repeated-measures factorial ANOVA results for frequencies in the four quadrants with treatment blocks defined by group (group A did first the spatial learning experiment and group B did first the non-spatial learning experiment), territoriality (territorial and non-territorial males), day (4th till 15th day) and quadrant (circle, square, triangle, no cue). Statistical significant results are marked with asterisk. df = degrees of freedom; *F* ratio = Fisher's value; P = associated probability.



a) b)

Figure 5. Mean latency for each day, on the spatial learning experiment, for: a) territorial and b) non-territorial males. The observation only started on the 4th day of training. The circle was degraded to 50% on the 7th day, to 75% on the 10th day and removed on the 13th day. The solid line represents a spline and the confidence interval (represented by the stippled line) was 95% and was created by bootstrapping of the spline. The vertical dotted line represents the swapping of the square and triangle cue.



a) b)

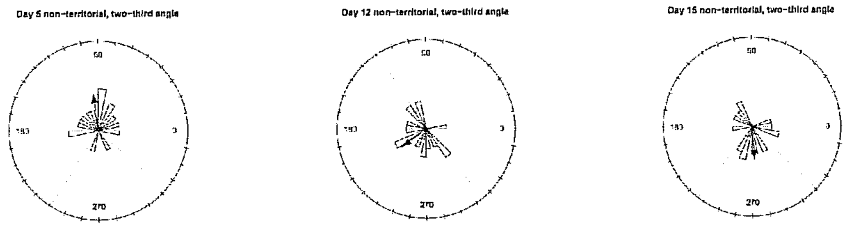
Figure 6. Mean standard deviation of latency, on the spatial learning experiment, for: a) territorial and b) non-territorial males. The solid line represent a spline and the confidence interval (represented by the stippled line) was 95% and was created by bootstrapping of the spline. The vertical dotted line represents the swapping of the square and triangle cue.

Test

Regarding the latency, time spent in the goal quadrant and frequencies of the four quadrants there was no difference between the last day of training and test in (Table 5, 6, 7, 8). In the test for territorial and non-territorial males the goal quadrant continued to have higher frequencies than the other three quadrants (Fig.9, 10) (Table 8). Regarding the two-thirds angle none of the males had a directional tendency in the test (Table 9).

Table 9 – Associated probability of the Rayleigh test, for each day of spatial learning experiment in the two-thirds angle for territorial (n=8) and non-territorial males (n=7). Significant values are marked with asterisk.

	4	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Territorial	0.77	0.42	0.22	0.25	0.11	0.71	0.07	0.51	0.34	0.59	0.17	0.70	0.23
Non-territorial	0.30	0.01*	0.56	0.18	0.18	0.20	0.30	0.53	0.05*	0.98	0.20	0.01*	0.77



a) b) c)

Figure 7. Rose diagrams, for two-thirds angle, on days that non-territorial males showed a directional tendency, on the spatial learning experiment. The black arrow represents the mean and intensity of the angle and the stippled lines represent 95% confidence interval. The heated quadrant is represented between 45° and 315° and the circle cue is represented at 0°.

There was no effect of territoriality in the test for latency, errors of latency, time spent in the goal quadrant, and frequencies (Table 5, 6, 7, 8). Moreover I did not observe any interaction between day or group and between territoriality and day in the latency, errors of latency, time spent in the goal quadrant, and frequencies (Table 5, 6, 7, 8).

Table 5 – Comparisons of latency between territorial and non-territorial males in the last day of training and test, on the spatial learning experiment.

Source	**dF**	**F ratio**	**P**
group	1	0.2097	0.6526
territoriality	1	2.4116	0.1382
day	1	1.8581	0.1979
group*day	1	0.0405	0.8439
terri*day	1	0.2267	0.6426

Note. Repeated-measures factorial ANOVA results for latency with treatment blocks defined by group (group A did first the spatial learning experiment and group B did first the non-spatial learning experiment), territoriality (territorial and non-territorial males) and day (15th day and test). Statistical significant results are marked with asterisk. df = degrees of freedom; *F* ratio = Fisher's value; P = associated probability.

Table 6 – Comparisons of standard deviation of latency between territorial, and non-territorial males in the last day of training and first day of test on the spatial learning experiment.

Source	dF	F ratio	P
group	1	0.3293	0.5717
territoriality	1	0.0003	0.9865
day	1	3.4752	0.0864
group*day	1	2.4684	0.142
terri*day	1	0.7865	0.3925

Note. Repeated-measures factorial ANOVA results for errors of latency with treatment blocks defined by group (group A did first the spatial learning experiment and group B did first the non-spatial learning experiment), territoriality (territorial and non-territorial males) and day (4th till 15th day). Statistical significant results are marked with asterisk. df = degrees of freedom; *F* ratio = Fisher's value; P = associated probability.

EXPERIMENT 2: NON-SPATIAL LEARNING

There was no effect of group (group A did first the spatial learning experiment and group B did first the non-spatial learning experiment) in the frequencies of the four quadrants (heated, non-heated, left and right of the heated quadrant) on the 4th and 5th day of experiment (Table 10). Also there was no effect of group in the latency on training, test and last day of training with first day of test (Table 11, 12, 13). I did not observe an effect of cue type (A or Z) on the latency during training, test, and last day of training with first day of test and frequencies during the last day of training and first day of test (Table 10, 11, 12, 13). I performed a Box Cox transformation to normalize latency and standard deviation of latency.

Table 7 – Comparisons of time spent in the goal quadrant between territorial and non-territorial males in the last day of training and test, on the spatial learning experiment.

Source	dF	F ratio	P
group	1	0.3663	0.5549
territoriality	1	0.8725	0.3664
day	1	0.2604	0.6191
group*day	1	0.0937	0.7647
terri*day	1	0.025	0.8771

Note. Repeated-measures factorial ANOVA results for time spent in the goal quadrant with treatment blocks defined by group (group A did first the spatial learning experiment and group B did first the non-spatial learning experiment), territoriality (territorial and non-territorial males) and day (15th day and test). Statistical significant results are marked with asterisk df = degrees of freedom; *F* ratio = Fisher's value; P = associated probability.

Table 8 – Comparisons of frequencies between territorial and non-territorial males in the last day of training and test, on the spatial learning experiment.

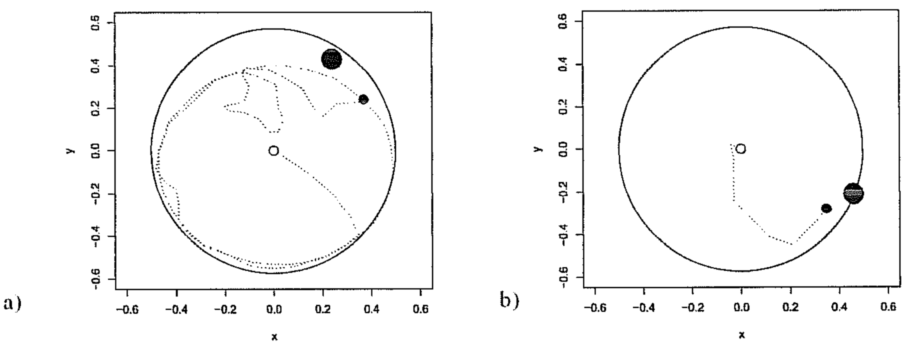
Source	dF	F ratio	P
group	1	0.1094	0.7417
territoriality	1	0.3244	0.5705
day	1	0.0894	0.7656
quadrant	3	99.539	<.0001*
group*day	1	0.1736	0.6778
terri*day	1	0.0143	0.9052

Note. Repeated-measures factorial ANOVA results for frequencies with treatment blocks defined by group (group A did first the spatial learning experiment and group B did first the non-spatial learning experiment), territoriality (territorial and non-territorial males) and day (15th day and test). Statistical significant results are marked with asterisk. df = degrees of freedom; *F* ratio = Fisher's value; P = associated probability.

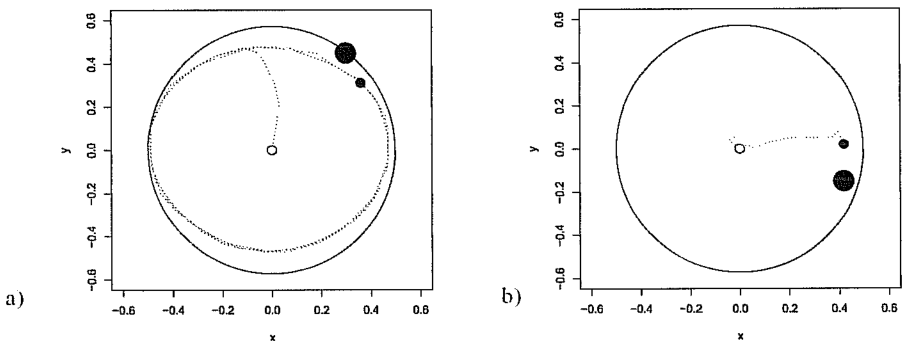
Training

There was no effect of day or territoriality on the latency (Table 11) (Fig 11). I could not statistically test the frequencies training because the time of experiment was not enough for the animals to generate treatable statistically. Both territorial and non-territorial males did not show a directional tendency in the two-thirds angle during training (Table 13).

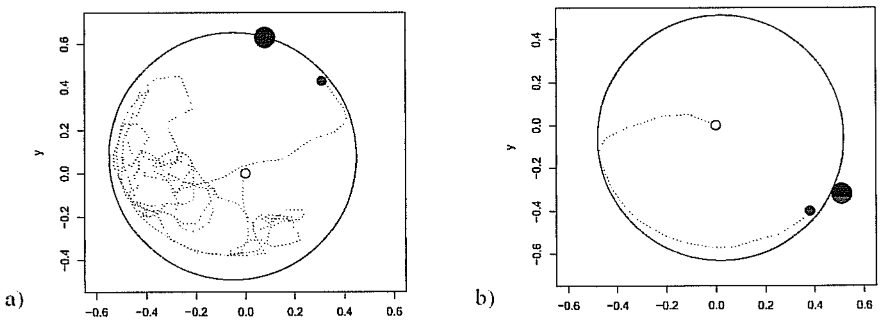
Territorial male



Non-territorial male



Territorial male



Non-territorial male

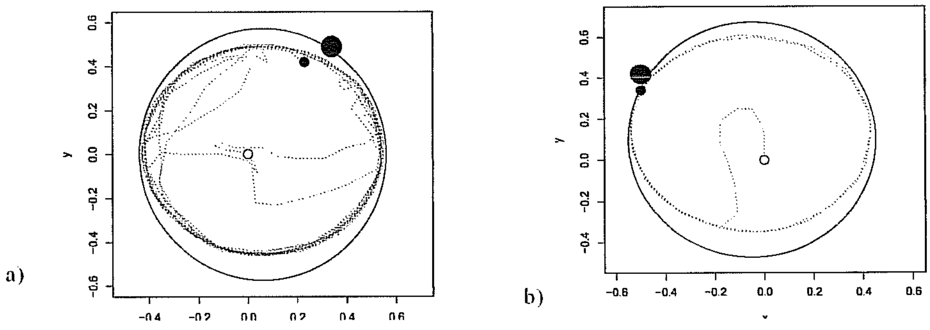
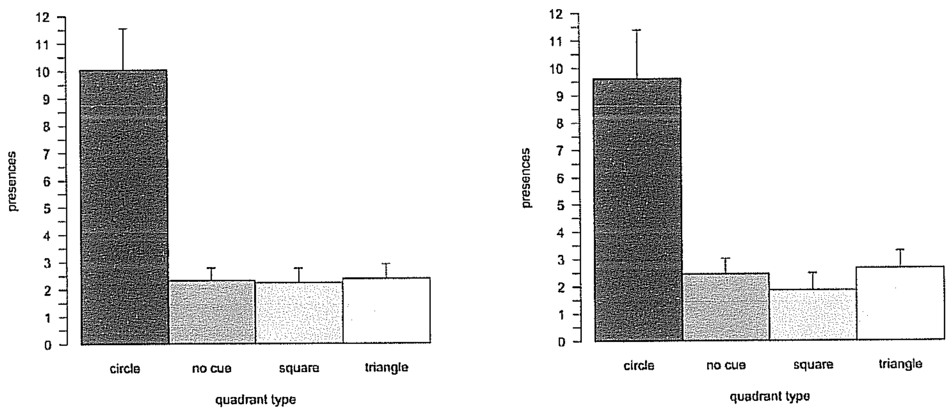


Figure 8. Paths performed during on the spatial learning experiment by 2 territorial males and 2 non-territorial males during the first day of observations (4th day of training) and the last day of training (15th). The paths taken in the last training day were more direct than those during the 4th day of training. The represented paths are from the last session of each day. The beginning of the path is marked with a white circle and the end is marked with a black cue. The larger black circle shows the position of the circle cue that marked the goal quadrant. The paths are somewhat ellipsoidal due to the shape of the arena.

Test

I did not observe an interaction between territoriality and day or between group and day in latency and frequencies of the last day of training and first day of test (Table 11, 10). There was no effect of day, territoriality in the latency during the test of non-spatial learning experiment and no interaction was observed between group and day and between territory and day (Table 13).



a) b)

Figure 9. Mean of frequencies, on the four quadrants: a) on the last day of training (15th day) and b) the test (16th day) for territorial males, on the spatial learning experiment. The lines represent the confidence interval for 95%. Regarding frequencies territorial males did not show any difference between the last day of training and the test day.

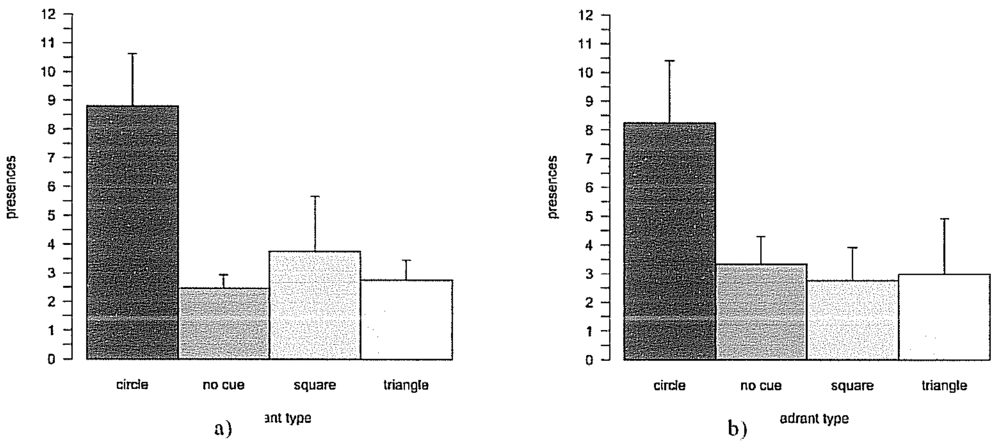


Figure 10. Mean of frequencies, on the four quadrants, on: a) the last day of training (15th day) and b) the test (16th day) for non-territorial males, on the spatial experiment. The lines represent the confidence interval for 95%. Regarding frequencies territorial males did not show any difference between the last day of training and the test day.

There was a difference in the frequency of the heated quadrant and the other three quadrants when I compared the last day of training and first day of test on the non-spatial learning experiment (Fig. 12 and Fig. 13 ((Table 10)). Also I did not observed an effect of day and territoriality in the frequency of the heated, not heated, left and right of the goal quadrant (Table 10). There was no interaction between day and group and between day and territoriality on the frequencies (Table 10). I did not statistical test the frequencies on the four days of training due to the same reason explained in the previous section. Only non-territorial males did show a directional tendency in the two-thirds angle on the test (Table 14). The mean angle on the 4th day was 286.94 and on the 5th day was 115.64.

Table 10 – Comparisons of frequencies between territorial and non-territorial males in the last day of training and first day of test, on the non-spatial learning experiment.

Source	dF	F ratio	P
group	1	0.0874	0.7694
cue	1	0.0265	0.871
territoriality	1	3.8099	0.0769
day	3	0.0265	0.871
quadrant	1	59.0504	<.0001*
group*day	1	0.7545	0.3872
terri*day	1	1.9793	0.1871

Note. Repeated-measures factorial ANOVA results for latencies with treatment blocks defined by group (group A did first the spatial learning experiment and group B did first the non-spatial learning experiment), cue (A and Z), territoriality (territorial and non-territorial males), day (4th day and 5th) and quadrant (heated, not heated, left and right of the heated quadrant). Statistical significant results are marked with asterisk. df = degrees of freedom; *F* ratio = Fisher's value; P = associated probability.

Discussion

There was no evidence that the males of Carbonell wall lizard used visual cues in the spatial and non-spatial learning experiments. However males used preferentially the goal quadrant and that suggests that they were not using space randomly. Furthermore, the lizards showed learning because there was a decrease time until thermorregulating (latency). Apparently the males of Carbonell wall lizard were using some sort of spatial strategy and I suggest that the lizards were using a movement algorithm whereby they reduce their path in relation to the goal. Therefore, the lizards, as the days passed by, could become more efficient in adjust their position with respect to the heated quadrant.

Table 11 – Comparisons of latency between territorial and non-territorial, in the training, on the non-spatial experiment.

Source	dF	F ratio	P
group	1	3.0283	0.0911
cue	1	0.004	0.9505
territoriality	1	0.7816	0.383
day	3	0.7045	0.5558
group*day	3	1.4069	0.2573
terri*day	3	0.0538	0.9833

Note. Repeated-measures factorial ANOVA results for latencies with treatment blocks defined by group (group A did first the spatial learning experiment and group B did first the non-spatial learning experiment), cue (A and Z), territoriality (territorial and non-territorial males) and day (15th day and test). Statistical significant results are marked with asterisk. df = degrees of freedom; *F* ratio = Fisher's value; P = associated probability.

Lizards can use a variety of visual cues such as brightness, colour, and shape as features for discrimination (Day et al., 2003; Day et al., 1999; Ord et al., 2002; Head et al., 2005). In this study, male lizards apparently did not use the visual cues. This absence of use was either because cues where misplaced for detection by the lizards, for their position and characteristics in the arena, or because lizards could not perceive information from the cues. It known that lizards discriminate better the position (left and right) than the visual features of shelters (Day et al., 2003). Therefore, a lizard in its natural environment could probably use a combination of visual features and position for orienting themselves, and therefore be in disadvantage in the present laboratory tasks for the position of the goal quadrant and cues varied randomly throughout the sessions.

Table 12 – Comparisons of latency between territorial and non-territorial males in the last day of training and first day of test, on the non-spatial learning experiment.

Source	dF	F ratio	P
group	1	3.1197	0.0941
cue	1	0.6711	0.43
territoriality	1	1.0841	0.3114
day	1	0.0008	0.9774
group*day	1	0.2818	0.6061
terri*day	1	0.4393	0.5211

Note. Repeated-measures factorial ANOVA results for latencies with treatment blocks defined by group (group A did first the spatial learning experiment and group B did first the non-spatial learning experiment), cue (A and Z), territoriality (territorial and non-territorial males) and day (4th day and 5th day). Statistical significant results are marked with asterisk. df = degrees of freedom; *F* ratio = Fisher's value; P = associated probability.

Table 13 – Comparisons of latency between territorial and non-territorial in the test on the non-spatial experiment.

Source	dF	F ratio	P
group	1	2.4978	0.1271
cue	1	0.0283	0.8694
territoriality	1	0.256	0.6175
day	3	0.4952	0.6881
group*day	3	2.8941	0.0496
terri*day	3	1.2109	0.3208

Note. Repeated-measures factorial ANOVA results for latencies with treatment blocks defined by group (group A did first the spatial learning experiment and group B did first the non-spatial learning experiment), cue (A and Z), territoriality (territorial and non-territorial males) and day (5th to 8th day). Statistical significant results are marked with asterisk. df = degrees of freedom; *F* ratio = Fisher's value; P = associated probability.

Animals can use different orientation mechanisms (spatial strategies) and different strategies (spatial and non-spatial strategies) to find the location of a goal. Whether an animal uses one or the other depends on its sensory abilities and the conditions imposed by the environment (Rodrigo, 2002). I suggest that males of Carbonell wall lizard, in these laboratory tasks, could have more sensory abilities to detect and perceive temperature gradient than the visual cues. Also the linear temperature gradient could be shadowing the visual cues because when a stimulus is perceived as relevant to the prediction of the goal, the attention to that stimulus is increased (Sansa & Prados, 2003). However, the males were not using the heated gradient as a cue because they did not show a specific orientation to the heated quadrant at the two-thirds angle. Only during just a few days did males present a direccional tendency and most of these angular means were not close to the cue. Although I did not observe an orientation based on the heated quadrant I do not put aside the possibility because it was difficult to the lizard to orient himself, considering that the goal quadrant changed randomly in every session.

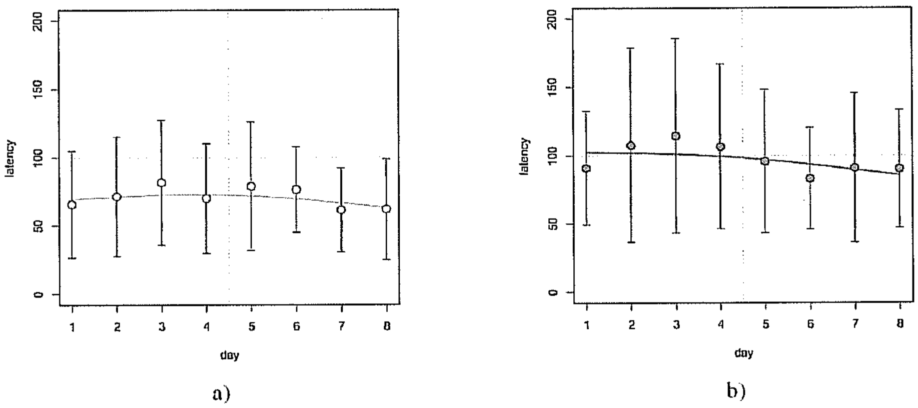


Figure 11. Mean of latency for each day for: a) territorial and b) non-territorial males, on the non-spatial experiment. The vertical lines represent the confidence interval for 95%. The stippled line represents the switch of the cues (the cue that indicated the heated quadrant on the 4th day was on the opposite quadrant on the 5th day).

The fact that a male thermoregulated, circle the arena and then came back to the goal quadrant may be an indicator that the lizard could use a path integration process (Rodrigo, 2002). This means that the lizards keep track of their current position in relation to a known position using the information gathered their movement. Path integration has been observed in snakes (Holtzman et al., 1999). Furthermore, lizards use olfactory cues and the coming back to the goal quadrant could show that the males had marked previously the quadrant during the same session (Main & Bull, 1996).

Reptiles show different abilities in spatial learning tasks. It was observed that turtles show spatial learning because there was a significant loss of performance in the probe trials when cues where removed, occluded, or transposed in the group (López et al., 2001; López et al., 2004; López et al., 2003; Rodríguez et al., 2002). The fact that spatial strategy based on visual cues is observed in turtles but not in lizards could be explained by the physiological and phylogenetic differences between turtles and lizards (Day, 2003). Moreover, it was found that snakes used a spatial strategy based on the visual cues (Holtzman, 1998; Holtzman et al., 1999). This could probably happen because Holtzman task was more ecologically relevant to the snakes than mine was to the males of *Podarcis*. Therefore my lizards could show enhanced spatial ability in a differently designed task.

My results and previous studies showed that lizard performance in a spatial task contains unusual elements, such as the high error rate and the high variability of the lizards in their overall performance to solve the spatial task at hand. Also, lizards rarely approach the goal directly (Day et al., 1999). The way which by lizards learn the spatial tasks is very different from that observed in mammals, birds, turtles, and snakes under similar conditions (Avens & Lohman, 2003; Holtzman, 1998; Holtzman et al., 1999; López et al., 2001; Rodríguez et al., 2002; Day et al., 1999). This could be explained by the fact that the spatial tasks are similar in all groups and could not be the most appropriate or ecologically relevant tasks for lizards to solve. It should be interesting to test spatial skills directly in the field in this specie, to test whether they have the ability to orient themselves. If this specie shows spatial skills in their natural environment it may show that apparently this specie cannot transfer any spatial abilities when tested in laboratory, even for tasks that require similar capabilities.

To my knowledge, this was the only study to view intrasexual variations in behavioural flexibility. I cannot say that the pliancy model is applicable to my lizards for the males did not achieve the reversal of visual discrimination or even the visual discrimination. The fact that the males did not achieve the visual discrimination could be explained because either they could not perceive the cues or those four days were not enough for the lizards to learn. I suggest that these males were also using a movement algorithm but an effect of day in the latency was not observed, on the non-spatial experience, perhaps on account of the few days of experiment.

Behavioural flexibility in laboratory tasks was observed in mammals (Tsuchida et al., 2002; Palencia & Ragozzino, 2006; Martin et al., 2006; Schrijver et al., 2004), birds (Range et al., article in press; Lissek et al., 2002), turtles (López et al., 2004), and lizards (Day et al., 1999). The fact that I did not observe behaviour flexibility in *Podarcis carbonelli berlengensis* could be due to physiological differences of turtles and lizards (Day, 2003). However, *Acanthodactylus boskianus* and *Acanthodactylus scutellatus* showed a behavioural flexibility when their cues were swapped (Day et al., 1999). This could happen because of the different methods of Day *et al.*(1999) and those used here. My positive reinforcer was a heated quadrant and the negative reinforcer was a non-heated quadrant and Day *et al.*(1999) used mealworms as positive reinforcer and mealworms soaked with quinine, salt and water as a negative reinforcer. As I have suggested before, perhaps the lizards were using a movement algorithm and thus could not perceived the visual discrimination and the reversal of the visual discrimination. Moreover, lizards were only tested for the reversal of visual discrimination only when did 10 correct responses in 12 sessions (Day et al., 1999). Carbonell wall lizard only had four days of training and this could probably be not enough for them to learn the visual discrimination and thus could not learn the reversal of visual discrimination.

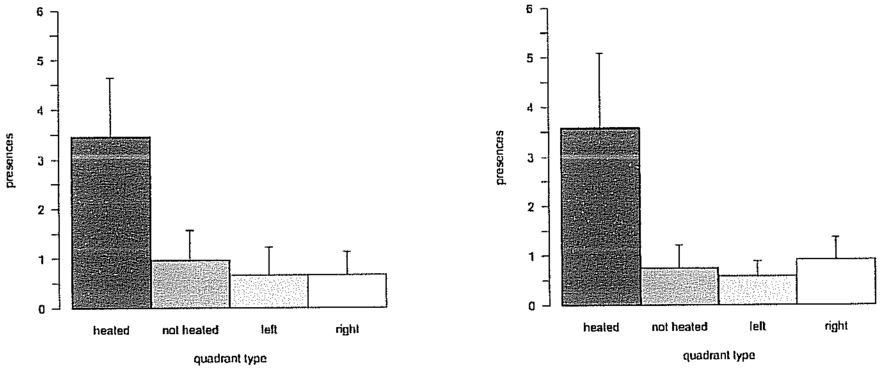


Figure 13. Mean of frequencies, on the four quadrants, on the last day of training (4th day) and the first day of test (5th day) for territorial males, on the non-spatial experiment. The lines represent the confidence interval for 95%. Territorial males did not show any difference between the last day of training and the first day of test for frequencies.

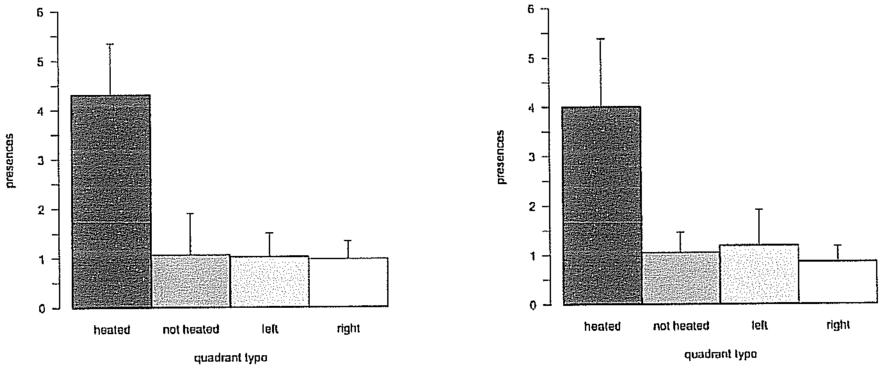


Figure 14. Mean of frequencies, on the four quadrants, on the last day of training (4th day) and the first day of test (5th day) for non-territorial males, on the non-spatial experiment. The lines represent the confidence interval for 95%. Territorial males did not show any difference between the last day of training and first day of test for frequencies.

When I compared the two groups of males, the results were inconclusive. There was no statistical difference in the latency, in the time spent in the goal quadrant on the spatial learning experiment, and no difference in the latency and frequencies of the quadrants on the non-spatial experiment. It seems that both territorial and non-territorial males learned how to reach the goal using the same method since there was no interaction between territoriality and day on both experiments. However, the territorial males apparently had slightly better performances and I observed a statistical difference in the frequencies of the quadrant use and in the standard deviation of latency on the spatial learning experiment. This would be consistent with the idea that there is a selective advantage for the cognitive spatial mechanism to have a social context. Males that settled in smaller areas would have to be aware of the neighbours and local features of the area and an enhanced spatial cognition would permit the male to place itself and other individuals in space and time (Jenssen, 2002). An improved spatial learning would be advantageous for the territorial male because he could anticipate social interactions and avoid risky encounters with specific individuals. However, when I compared the angles only non-territorial males showed a directional tendency on some days and some observations. Furthermore the means of the angles rarely pointed to the goal.

In the spatial experiment, the reverse was observed for the angles. The fact that comparisons of the angles between the males are clear could be explained because the males were using a movement algorithm and they did not have to be aware, in a first instance of the position of the heated quadrant and therefore did not moved directly towards the goal. Although angles would not give information about the effect of territoriality, the other data apparently give an indication that there is an effect of territoriality in the spatial cognition. The differences between the males are not clear and could probably be explained because they where isolated one month prior to experiences and this could confound some characteristics that affect their spatial and non-spatial capabilities. I did only observed an effect of territoriality in the two-thirds angle, on the non-spatial learning experiment, and this could be related to the fewer days of experiment and less time in the arena.

It is widely accepted that steroids affects alternative male behaviours and it was proposed a relative plasticity hypothesis that suggests that fixed differences between alternate phenotypes are due to organisational actions of steroid hormones, whereas more plastic differences are due to activation influences of these hormones (Moore, 1991). Lizards, elevated plasma androgens in the hatchling development in lizards affect aggressiveness, endurance, throat colour determination in adults (Hews & Moore, 1996; Hews et al., 1994; Moore, 1991). It was also observed in the prenatal environment that hormones affect home ranges (Sherry et al., 1996; Isgor & Sengelaub, 1998). In the specie *Anolis cristatellus,* territorial males can maintain territory during several years (Stapley & Keogh, 2004). It should be interesting to understand if the Carbonell wall lizard is able to do the same. If so, this could indicate that a male will have a predisposition to be territorial. Although I could not find a statistical difference between the males, I suggest that apparently intrasexual variation has some effect in the spatial cognition and if there is a predisposition of a male to become territorial, then these concomitant predisposition to have an improved spatial cognition.

However, it was observed that some male-typical behaviours in lizards are not affected by early action of steroids in hatchling development but are affected by the seasonally increase testosterone (Lovern et al., 2001). The latter behaviours include fullshow displays (aggressive behaviour that is performed with the body held perpendicular to that of the opponent), bites (Smith & Jonh-Alder, 1999) and the ability to acquire high-quality territories (Torkaz, 1995; DeNardo & Sinervo, 1994a; DeNardo & Sinervo, 1994b). Also, the acquisition of a territory could be done by change (*Anolis aeneus* (Stamps & Krishman, 1998)) or by opportunity (yellow-throated sneakers have the ability to acquire territory when a territorial male disappear (Sinervo et al., 2000)). All these observations suggest that there will be no predisposition to be a territorial male and therefore to have an improved spatial ability.

Table 14 – Associated probability of the Rayleigh test, for each day of non-spatial learning experiment on the, in the two-thirds angle for territorial (n=8) and non-territorial males (n=7). Significant values are marked with asterisk.

day	1	2	3	4	5	6	7	8
Territorial	0.54	0.30	0.81	0.95	0.47	0.29	0.64	0.61
Non-territorial	0.47	0.88	0.96	0.02*	0.00*	0.27	0.27	0.75

Consequently, male lizards of *P. carbonelli berlengensis* showed a spatial strategy and I suggest they may use a sort of movement algorithm where, they adjust, with time their position in relation to the heated quadrant. Apparently, there is an effect of intrasexual variation in spatial learning. Although males did not orient themselves using the heated quadrant, I did not put aside this possibility and it should be interesting to study the effects of heated gradients with several different thermal profiles. The data from my experiments alone are insufficient to draw conclusions about the effect of intrasexual variation in spatial and non-spatial learning, but apparently there is a learning effect. The relationship between intrasexual variation and spatial capabilities could be further tested by including more lizard species. Also, it will be interesting to study the effect of intrasexual variation on other nonspatial pliancy-dependent tasks. Most studies in spatial learning and memory have focused primarily on rodents and birds, whereas reptiles and fish have remained relatively unstudied (Day, 2003; Day et al., 1999; Holtzman, 1998; Holtzman et al., 1999; López et al., 2001; López et al., 2003; López et al., 2004). Therefore it is necessary to study a broader range of species to develop general theories of the evolution of learning processes and their neural basis (Day, 2003). It will also be interesting to study the effects of hormone manipulations in spatial and non-spatial learning since there is evidence that hormones is one of the factors that affects cognitive strategy (Janowsky, 2006). Considering that spatial cognition in lizards would be affected by androgens, it will be interesting to test if these effects would be organizational or activacion.

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