# Aggressive sexual behaviour and spatial distribution of the polymorphic lizard *Sceloporus minor* (Squamata: Phrynosomatidae) from Central Mexico

Aaron García-Rosales[1,3], Aurelio Ramírez-Bautista[1,*],
Pablo Octavio-Aguilar[2] & Miguel A. Armella-Villalpando[3]

[1] Laboratorio de Ecología de Poblaciones, Centro de Investigación Biológica, Instituto de Ciencias Básicas e Ingeniería, Universidad Autónoma del Estado de Hidalgo, Km 4.5 carretera Pachuca-Tulancingo, 42184, Mineral de La Reforma, Hidalgo, México

[2] Laboratorio de Genética de Poblaciones, Centro de Investigación Biológica, Instituto de Ciencias Básicas e Ingeniería, Universidad Autónoma del Estado de Hidalgo, Km 4.5 carretera Pachuca-Tulancingo, 42184, Mineral de La Reforma, Hidalgo, México

[3] Laboratorio de Ecología y Comportamiento Animal, Departamento de Biología, Universidad Autónoma Metropolitana-Iztapalapa, Av. San Rafael Atlixco No 186, Vicentina, Iztapalapa, 09340, CDMX, México

* Corresponding author: Aurelio Ramírez-Bautista, e-mail: ramibautistaa@gmail.com

**Abstract.** Intrasexual polychromatism has generally been linked to alternative reproductive and ecological tactics, where different morphs may exhibit differences in their behavioural, morphological, physiological, ecological, and life history characteristics. Therefore, these differences might favour the fitness of a certain morph over others. If multiple morphs are able to persist in the population however, they must have had similar fitness levels over a long period of time. This balance can be achieved via two processes: niche partitioning and negative frequency-dependent selection. The present study describes the aggressive sexual behaviour of the lizard *Sceloporus minor* and evaluates its possible relationships to ecological and behavioural aspects of two different male morphs (yellow and red) in a population from central Mexico. The results reveal that both the yellow and the red morphs are territorial. The home range (HR) of yellow males was 17 times larger than that of females, whereas the HR of red males was 13 times larger than that of females; however, there was no significant difference in HR size between morphs. Spatial distribution analysis indicated a pattern of regular distribution for adult *S. minor*. Our results also demonstrated that red males had more females within their HRs than yellow males had; however, yellow males were more aggressive than red males. In addition, both red and yellow morphs were similar in some other behavioural, ecological, and morphological traits, disproving the hypothesis that morphs in this population are maintained by niche partitioning. This leaves open the possibility that frequency-dependent selection maintains the polychromatism in this population.

Key words. Polychromatism, male morphs, niche partitioning, frequency-dependent selection.

## Introduction

In ecology, polymorphism is defined as the presence of two or more genetically determined morphs with stable frequencies that are too high to be considered a consequence of recurrent mutations (Galeotti et al. 2013). In recent years, the instances of intrasexual polychromatism seen in some squamate reptiles have attracted attention from evolutionary ecologists (Sinervo & Lively 1996, Sinervo et al. 2000, Zamudio & Sinervo 2000, Hamilton & Sullivan 2005, Lattanzio & Miles 2016, Scali et al. 2016, Sacchi et al. 2017, Yewers et al. 2017, Hernández-Gallegos et al. 2018, Paterson & Blouin-Demers 2018), especially in species in which colours co-vary with reproduc-

tive strategies (Thompson & Moore 1991, 1992, Sinervo & Lively 1996, Galeotti et al. 2013, Fitze et al. 2014). In many cases, intrasexual polychromatism has been linked to alternative reproductive and ecological tactics (Sinervo & Lively 1996, Svensson et al. 2001, Taborsky et al. 2008) that involve complex combinations of behavioural, morphological, physiological, and life history characteristics (Galeotti et al. 2013, Sacchi et al. 2017, Yewers et al. 2017, Hernández-Gallegos et al. 2018). The variation in some of these traits between morphs can improve their fitness, resulting in an asymmetry in the potential retention of resources, and, therefore, a relative dominance of a certain morph over others (Lattanzio & Miles 2016, Yewers et al. 2017, Hernández-Gallegos et al. 2018). If these

morphs are able to be persist in the same population, however, they must have had similar fitness levels over a long period of time (Lattanzio & Miles 2016). This balance can be achieved via processes such as niche partitioning and negative frequency-dependent selection (Lattanzio & Miles 2016, Scali et al. 2016).

The niche partition hypothesis proposes that individuals representing different morphs use different resources from the environment (e.g., space, shelter, food) to avoid strong competition for the same resource (Skúlason & Smith 1995, Lattanzio & Miles 2016, Scali et al. 2016, Paterson & Blouin-Demers 2018). For example, in the wall lizard (*Podarcis muralis)* and the tree lizard (*Urosaurus ornatus*), certain morphs of these species were shown to have predilections for certain types of prey that are only partially shared with other morphs (Lattanzio & Miles 2016, Scali et al. 2016, Paterson & Blouin-Demers 2018). In addition, differences in the spatial distribution of morphs have been recorded in *U. ornatus* (Paterson & Blouin-Demers 2018). On the other hand, negative frequency-dependent selection can sometimes maintain polymorphism, because this type of selection confers survival and/or reproduction advantages to rare morphs such that the fitness of a given phenotype depends on the frequencies of competing phenotypes (Sinervo & Lively 1996, Pryke et al. 2007). For example, frequency-dependent selection maintains polymorphism in the side-blotched lizard *Uta stansburiana*; in this species, morph frequencies change between years forming cycles, being a consequence of the different behavioural strategies exhibited by each morph (Sinervo & Lively 1996).

In lizards, polychromatism has been linked to behavioural tactics in several species, with certain colours being associated with the greater aggressiveness of males as compared to other conspecific morph(s) (Thompson & Moore 1991, 1992, Sinervo & Lively 1996). In many of these polymorphic species, one morph will be territorial, defending mating sites and/or females against other males, while the other morph(s) will achieve mating success by alternative means (Gross 1996). In addition, it has been found that some morphs differ in body size, aggression levels, spatial distribution within the landscape, size of territory and/or home range and quality of habitats used (Thompson & Moore 1991, Sinervo & Lively 1996, Lattanzio & Miles 2016, Scali et al. 2016, Paterson & Blouin-Demers 2018).

In the genus *Sceloporus*, it has been reported that some species exhibit morphological differences, such as coloration and body size within a given sex (i.e., intrasexual polymorphism); for example, *S. horridus* (Bustos-Zagal et al. 2014), *S. erythrocheilus* (Rand 1990), *S. grammicus* (Bastiaans et al. 2013), *S. minor* (Stephenson 2010, García-Rosales et al. 2017, 2019b), and *S. torquatus* (Domínguez-Guerrero 2015), amongst others. However, in several of these species, direct links between coloration, behaviour, and morphology have not been studied in detail, and there is only limited information by which to characterize coloration.

*Sceloporus minor* is a polychromatic species that has been relatively well studied in biological aspects such as systematics, reproduction, and morphology (Wiens et al. 1999, Ramírez-Bautista et al. 2008, Stephenson 2010, Stephenson & Ramírez-Bautista 2012, Ramírez-Bautista et al. 2014, García-Rosales et al. 2017, 2019a, b). The results of studies on morphology indicate that this species exhibits marked intra- and intersexual phenotypic variation in body size and coloration patterns in some of its populations (Wiens et al. 1999, Stephenson & Ramírez-Bautista 2012, García-Rosales et al. 2017). The polychromatism in this species is expressed in the dorsal coloration of males, which can be red, brown, yellow or blue, although not all morphs are found represented in the same population (Wiens et al. 1999, Stephenson 2010, Stephenson & Ramírez-Bautista 2012, García-Rosales et al. 2017, 2019b). Despite these advances in our understanding of this interesting and unusual species, many aspects of its intrasexual polymorphism remain poorly understood.

Therefore, the objective of this study was to describe the aggressive sexual behaviour of *S. minor* and to assess its possible relationships to aspects of the ecology and behaviour of two different male morphs (yellow and red) in a population from central Mexico. Our specific objectives were to: i) develop an ethogram describing the sexual and aggressive behavioural patterns of adult males from this population, ii) quantify home range sizes of both male morphs and adult females, iii) characterize the distribution and spatial association patterns for both male morphs and females, and iv) quantify and evaluate aspects of male space utilization, such as perch height, home range size, microhabitat, and other behavioural and morphological features. According to the niche partition hypothesis, different male morphs are expected to display differences in some of their behavioural and/or ecological attributes that allow them to differentially exploit resources in their environment, which in turn would reduce intrasexual competition for resources, facilitating the maintenance of polymorphism in this population.

### Material and methods
#### Study area

This study was conducted at El Enzuelado (20°35' N, 98°37' W) in the municipality of San Agustín Metzquititlán, Hidalgo, Mexico. El Enzuelado is located at an altitude of 1,955 m and has a vegetation of xerophilous scrub (Rzedowski 1978); the mean annual temperature is 17.5°C, and it receives an average of 496.7 mm of annual precipitation (Pavón & Meza-Sánchez 2009).

#### Fieldwork (Observations)

Fieldwork was carried out during September–November 2017 (approximately 90 consecutive days), a period corre-

sponding to the courtship and mating season of *S. minor* (Ramírez-Bautista et al. 2014). During this time, we searched for males that were perched on exposed structures (e.g., rock outcrops and branches) or performing behavioural displays (Zamudio & Sinervo 2000). Sexing was based on the (sexually dimorphic) colour pattern of each lizard (see García-Rosales et al. 2017), and we corroborated our records by checking for the enlarged postanal scales present only in males after an observation had been concluded. As each lizard was found, we recorded the general weather conditions and ambient temperature from one metre from the substrate with a Miller-Weber rapid-reading thermometer ($\pm$ 0.2°C). About five minutes later, the lizards were observed individually (focal observations with continuous recording; Altmann 1974, Martin & Bateson 2007) with binoculars from a distance at which lizards were not expected to feel intimidated (approximately 10 metres away; Simon 1975). Focal observations were made for 60 minutes per individual, and during this time, all observed behavioural expressions (aggressive and sexual) were recorded. Also, an attempt was made to identify whether the observed individual behaved territorially or not; to this end, we defined the HR as the area within which a specimen carried out all of its various activities (perching, foraging, and displaying) without directing aggression toward any other conspecific (Burt 1943), while territory was defined as the area defended by a specimen (Noble 1939, Nice 1941). Male territorial behaviour was classified as either passive or active defence. In passive defence, responses to intruders involved no direct physical contact (Marquez-Luna 2014); for example, the individual performed push-ups with lateral compression, revealing the colours of the belly and gular area (i.e., a full show; Table 1). Active defence was defined as responses involving direct physical contact (e.g., a fight) or when one individual rushed towards another individual (Table 1). However, when no aggressive behaviour was observed in the resident male (sometimes because there were no other males nearby), this behaviour was induced. To do so, on the day after an observation and in the first hours of activity of such an individual (between 9:00 and 10:00 a.m.), an intruding male (collected from approximately 100 metres away in the quest to avoid bias such as the phenomenon of the "beloved enemy"; Sachhi et al. 2009) was placed approximately one to two metres from the site where we had previously observed a resident male. A transparent thread was tied around the male intruder's waist, while the other end of the thread was tied to a wooden pole (Simon 1975). This thread measured approximately one metre in length, so that the intruder had some range of movement. After placing the intruder in position, we waited a maximum of 20 minutes for the resident male to come out of his hiding place so that we could record his behaviour (in all these experiments resident males emerged within less than 20 minutes). Because the behavioural expressions of resident males had all been observed previously, this experiment was only carried out to find out if these males were territorial or not (if they had not previously shown some type

of aggressive behaviour); therefore, if this male exhibited some active aggressive behaviour before 20 minutes of observation had elapsed, the individuals were immediately separated and observation was terminated at that moment (Simon 1975, Martin & Bateson 2007).

Estimates of home ranges (HRs) were calculated for each sex and morph based on the distance travelled during focal observations (Simon 1975), as well as recaptures of previously observed individuals that were obtained during daily tours throughout the sampling period (approx. three months; September–November 2017), thus obtaining more realistic estimates of HRs. All points of encounters were recorded with the help of a Garmin e Trex 10 GPS. In addition, the numbers of females in each observed male's HR was calculated (defined as the number of females found within the polygon that delimits the male's HR) as well as the type of microhabitat (rocks, trees, shrubs, and agaves) that he was observed using most frequently. After the observation and data collection period had been concluded, the height of the perch (measured with a conventional tape measure) where the male had been observed at the start of the observation was recorded. Finally, whenever possible, the observed lizard was captured to measure its snout–vent length (SVL), body mass, cloacal temperature with a thermometer (Miller and Weber Inc.), state of tail (complete or regenerated), and the coloration of its dorsal and ventral regions of the body, using a colour catalogue for fieldwork (Köhler 2012). The dorsal colour of each individual was recorded according to colour morph variation previously described in males from El Enzuelado (see García-Rosales et al. 2017, 2019b). Finally, each observed and collected lizard (males and females) was marked using phalangeal ectomization (toe clipping) and released at the site where it had been collected (García-Rosales & Martínez-Coronel 2016). This study was conducted according to the ethical guidelines and regulations for animal research of the Universidad Autónoma del Estado de Hidalgo and the official Mexican standard NOM-033-SAG/ZOO-2014 of policies for handling of animal specimens. All animal use was approved under collecting permit SGPA/DGVS/06183/17 issued by the Secretaría del Medio Ambiente y Recursos Naturales (SEMARNAT) of the Government of Mexico.

### Data analysis

Home range sizes were calculated applying the minimum convex polygon method (Simon 1975, Zamudio & Sinervo 2000, Duca et al. 2006) with the Biotas 2.0 Alpha software (Ecological Software Solutions LLC 2004). We used ANOVA to test for differences in HR sizes between red- and yellow-morph males, as well as females. Even though the latter are not territorial. Variables were normalized prior to analysis using a $\log_{10}$ transformation. Kruskal-Wallis tests were performed to compare the SVL of individuals that did not defend territories to those that defended their territories either actively or passively. Post-hoc tests were used to determine which specific groups were differ-

Table 1. Ethogram of the behavioural patterns registered in male *Sceloporus minor* at El Enzuelado. *Active aggressive behaviours, +passive aggressive behaviours. ˣ Descriptions of behavior patterns correspond to those given in Stephenson & Ramirez-Bautista 2012.

| Behaviour | Description | Category |
|---|---|---|
| Full show | Starts with strong wags (one to four) of tail from one side of the body to the other; then the lizard begins to take short leaps from one side to the other, elevating the forelimbs in the air. This is accompanied by lateral compression of the body that will expose the blue abdominal patches and also the extension of the throat (dewlap). | Aggressive+ |
| Push-up | Entire body is moved up and down vertically through bending and straightening of front legs. Cannot be performed while walking. | Aggressive+ |
| Touch | The male touches the body of his opponent with the tip of his snout. | Aggressive* |
| Aggressive bite | The male holds his opponent in his jaws, and usually shakes his head from side to side while still holding his opponent. | Aggressive* |
| Approach | Male moves toward opponent staring at him. | Aggressive* |
| Chase ˣ | Sprinting towards an opponent that results in displacement of the opponent. | Aggressive* |
| Retreat | Sprinting away from opponent. | Submissive |
| Dorso-ventral flattening | The belly, throat, and the four limbs are in contact with the ground. | Submissive or inactive |
| Without aggression | Males do not show any of the aforementioned aggressive behaviours. In fact, these males can be in contact without showing any kind of aggressive behaviour. | Without aggression |
| Courtship pushup | Slow vertical movement of the head accompanied by lateral compression of the body, exposing the blue ventral patches and expanding the gular sac; all this happens at the same time when the anterior extremities are flexed, which results in an elevation of the anterior half of the torso. Cannot be performed while walking. | Courtship |
| Cover the female | The male places the anterior half of his torso on top of the female while she is perched; thus, the dorsal region of the female body is in contact with the ventral region of the male's body. Sometimes, the male only places some portions of his forelimbs on the body of the female. | Courtship |
| Headbutt | The male pushes the female's body, often around the middle section, with his head without biting. This behaviour was not observed between males. | Courtship |
| Courtship bite | The male holds the tip of the female's tail in his jaws, smoothly and quickly opening and closing the jaw. No lateral movements of the head are performed as would be in fights with other males. | Courtship |
| Mating bite | The male bites the neck of the female in the lateral or dorsal region, while ventrally aligning his pelvic region with the ventral part of the female so that the hemipenis can be inserted upwards. This happens while the female is immobilized by the male, and she remains standing on all four limbs. | Mating |
| Perch | The individual bends the rear limbs and extends the forelimbs, causing the posterior venter to be in contact with the substrate while the middle and front portions are elevated. | Inactive |
| Foraging | The lizard sprints quickly towards a prey item, catches it in its mouth and returns to the place where it was perching, where it will now crush and ingest the prey item. | Feeding |

ent from each other (Zar 1999). We used non-parametric Spearman correlations to test whether male SVL predicted either HR size or the number of females within this area, as well as the size of an HR and the number of females within it; these analyses were performed separately for each morph and for all males combined. We used a non-parametric test because sample sizes were small for some tests and the corresponding HR size data could not be normalized (Zar 1999).

The spatial distribution pattern was analyzed for each male morph separately, for all males combined, and for all females with the $K_t$ function (Ripley 1981). The pattern of spatial association was analyzed between male morphs (i.e., red vs yellow), and between each morph and all females (i.e., red morph vs females; yellow morph vs females) with the $K_{12}$ function (Ripley 1981). The $K_t$ function calculates the distribution pattern (random, clumped, or regular) of a group of data, counting the individuals distributed around a random point located in each area. Up to 99 simulations were performed in each quadrant in ascending intervals of 0.1 m within a radius of 5 m, which is the limit proposed by De la Cruz (2006) and corresponds to less than one-third of the quadrant lengths and so decreases edge effects. If the value of $K_t$ exceeds or does not reach the confidence interval (CI) generated by the model, then a clumped or a random pattern is inferred, respectively. When the value of $K_t$ lies within the CI, the distribution pattern is deemed to be regular (Peter 1995). The $K_{12}$ analysis compares the degree of association between the spatial distribution of two groups of data (dependence, independence, or inhibition). The null hypothesis is that two groups of data are independent. If the values of $K_{12}$ are higher than the CI, a dependence (association) between groups is inferred; values below the CI indicate inhibition, and values within the

CI correspond to independence between the groups. Like the $K_t$ function, the $K_{12}$ function was calculated with a maximum radius of 5 m, with 99 simulations in each quadrant in ascending intervals of 0.1 m. Both $K_t$ and $K_{12}$ functions were calculated with the Spatial Analysis program (Duncan 1990).

Finally, in order to identify possible morphological, behavioural, and ecological differences between morphs, a generalized discriminant function analysis (GDFA) was undertaken, incorporating both categorical [aggressive behaviour (AB), state of tail (TS), and coloration of the ventral body patches (CVP); see Appendix 1] and continuous variables [HR area, SVL, number of females within a male HR (NF), perch height (PH), cloacal temperature (CT), and environmental temperature (ET)]. The type of microhabitat that all subjects used was rocks; therefore, these data were not used in this analysis. Afterwards, the variables with high correlations with the explanatory factors were used to separate groups of lizards, allowing us to perform a canonical correlation analysis (CCA). Tests were considered significant if $p \leq 0.05$. All statistical analyses were calculated using Statistica 7.0 (StatSoft, Inc., Tulsa, OK, USA). Means are presented as $\bar{x} \pm$ standard deviation.

## Results

A total of 23 adult females and 46 adult males were observed and used to calculate HRs (we categorized the individuals as adults, both male and female, according to the sizes reported by Ramírez-Bautista et al. (2014). The males were representative of 28 red morphs, 17 yellow morphs, and one grey-coloured male of unknown morph status (Table 2). This latter individual was approaching ecdysis when captured and could not be classified in any morph category; therefore, it was excluded from most subsequent analyses. Overall, we performed 2700 minutes of observation (45 males × 60 minutes per subject), in which 16 distinct behavioural expressions were recorded (Table 1). Of the 45 males analyzed, 37 (82.3%) were considered territorial; of these, 13 (35%) defended their territory only in an passive manner, and 24 (65%) employed both passive and active defence measures; eight males exhibited no territorial behaviour at all (17.7%). Males that did not defend their territories tended to be smaller ($\bar{x} = 71.5 \pm 3.2$ mm SVL, n = 8) than males that passively defended theirs ($\bar{x} = 72.6 \pm 3.3$ mm SVL, n = 13), which in turn tended to be smaller than males that actively defended their territories ($\bar{x} = 74.9 \pm 1.5$ mm SVL, n = 24), although these differences were not significant (H = 1.17, p = 0.57). Of the 28 red males we observed, 24 (86%) were territorial; nine (37%) defended their territory only passively, 15 (63%) engaged in both passive and active defence, and four (14%) did not defend their territories. Amongst the yellow males (n = 17), 13 (76.4%) were territorial; four (30.7%) defended only passively, nine (69.3%) did so with both passive and active measures, and four (23.6%) did not defend their territories. Females did not show territorial behaviour, and we observed multiple females coexisting in relatively small areas without any indications of aggression being apparent.

Observations of small adult males (62 to 72 mm) revealed that they were able to mate with females residing in the territories of larger males (73 to 84 mm) when these territory owners were not present (i.e., were removed experimentally from their territories), or when the resident male was located at the extremes of his territory (satellite behaviour). A small adult male would then approach such females slowly, behaving as if attempting to avoid detection by the resident male. Once near a female (~1 m of distance or less), he would begin to perform a courtship display (push-ups; Table 1) to encourage the female to accept him. Later, this male would start to follow the female around, bumping his head in the lateral region of her body or face (Table 1), followed by intervals when the male would bite the tip of the female's tail (Table 1). This type of behaviour was repeated several times, as the female usually walked away from the male initially. After several minutes of effort (on average 30 min per courtship), however, such a male was sometimes able to take hold of the courted female with a bite to her neck followed by positioning his cloaca near hers and copulating (Table 1). Following copulation, the male would cease all courtship and harassment towards the female, and both resumed non-mating activities. We only observed copulation events of non-territorial males that were 5–12 sec in duration.

The HRs of yellow- and red-morph males differed significantly from those of females (F = 23.2, p < 0.001). On average, the HRs of yellow males were 17 times larger than those of females (yellow males: $\bar{x} = 12.59 \pm 5.07$ m$^2$; females, $\bar{x} = 0.75 \pm 0.14$ m$^2$; t = 9.1, p < 0.001), whereas the HRs of red males were 13 times larger than those of females (red males: $\bar{x} = 9.41 \pm 2.22$ m$^2$; t = 7.4, p < 0.001); however, there was no significant difference in HR sizes between morphs (t = 1.6, p = 0.47). There was no relationship between HR and SVL for yellow males alone ($r_s = 0.23$, p = 0.45, n = 12) or red males alone ($r_s = -0.12$, p = 0.61, n = 19); however, across all males, there was a significant positive relationship between HR and SVL ($r_s = 0.97$, p = 0.006, n = 31). On the other hand, there was no correlation between HR size and the number of females within this area for yellow morphs alone ($r_s = 0.13$, p = 0.60, n = 17), red morphs alone ($r_s = 0.20$, p = 0.29, n = 28), nor for all males combined ($r_s = 0.16$, p = 0.26, n = 45). There was no relationship between male SVL and the number of females within male HRs for yellow morphs alone ($r_s = 0.49$, p = 0.10), but there was a positive relationship for red morphs alone ($r_s = 0.44$, p = 0.05), and for all males combined ($r_s = 0.55$, p = 0.0011).

The spatial distribution analysis (Ripley's $K_t$ function) indicated a pattern of regular distribution for adult *S. minor*, but with a different radius for each of three groups considered (Table 3). Yellow-morph males exhibited a regular distribution pattern, in a radius of 2.4–5.0 m; red-morph males also had a regular distribution pattern, but in a radius of 3.6–4.8 m (Table 3). For all males grouped together, there was a regular distribution pattern in a radius of 4.0–5.0 m; females presented the same pattern, in a radius

Table 2. Descriptive statistics from observations of male morphs of *Sceloporus minor* at El Enzuelado. We report the body size (SVL) of each observed lizard, its HR area, and the number of females found within its HR. Null values (–) in the SVL column indicate individuals that could not be collected and measured. Observation 7 refers to a male that was molting and its original colour could not be identified; therefore, it does not feature in the table.

| | Yellow morph | | | | Red morph | | |
|---|---|---|---|---|---|---|---|
| Observed individual | SVL (mm) | Home range size (area m²) | Number females within home range | Observed individual | SVL (mm) | Home range size (area m²) | Number females within home range |
| 1 | 65.35 | 14.47 | 1 | 3 | 81.17 | 9.80 | 3 |
| 2 | 77.91 | 7.87 | 2 | 6 | – | 2.11 | 1 |
| 4 | – | 1.59 | 2 | 11 | 79.29 | 10.31 | 2 |
| 5 | – | 1.61 | 1 | 13 | – | 1.62 | 2 |
| 8 | – | 0.49 | 1 | 15 | 84.24 | 1.02 | 5 |
| 9 | 80.82 | 6.32 | 3 | 16 | 79.50 | 5.20 | 2 |
| 10 | 75.32 | 47.96 | 2 | 17 | 80.61 | 0.73 | 1 |
| 12 | – | 1.74 | 1 | 18 | 75.80 | 0.60 | 1 |
| 14 | 63.21 | 1.72 | 1 | 20 | – | 0.86 | 2 |
| 19 | 73.43 | 2.94 | 1 | 22 | 74.74 | 34.18 | 3 |
| 21 | 63.95 | 3.03 | 1 | 23 | 77.51 | 3.62 | 2 |
| 29 | 65.78 | 5.60 | 2 | 24 | 78.82 | 0.56 | 3 |
| 30 | 83.07 | 5.95 | 4 | 25 | 63.22 | 1.70 | 1 |
| 31 | 82.17 | 10.86 | 1 | 26 | 73.74 | 19.84 | 3 |
| 34 | 78.87 | 75.43 | 2 | 27 | 70.14 | 5.44 | 2 |
| 38 | 62.02 | 13.88 | 2 | 28 | 62.40 | 0.72 | 1 |
| 42 | – | 134.74 | 0 | 32 | – | 0.82 | 0 |
| | | | | 33 | – | 16.68 | 3 |
| | | | | 35 | 74.51 | 1.94 | 3 |
| | | | | 36 | – | 23.06 | 0 |
| | | | | 37 | 82.08 | 1.12 | 2 |
| | | | | 39 | 75.74 | 19.04 | 2 |
| | | | | 40 | – | 42.53 | 1 |
| | | | | 41 | – | 13.90 | 3 |
| | | | | 43 | 80.74 | 6.03 | 3 |
| | | | | 44 | – | 4.64 | 5 |
| | | | | 45 | 65.97 | 2.05 | 1 |
| | | | | 46 | 67.70 | 33.57 | 2 |

Table 3. Spatial distribution patterns of the lizard *S. minor*. Ripley's K (t) function was performed with a confidence interval of 95% (99 simulations) and steps of 0.1 m. The hyphen (-) indicates a random distribution pattern, the plus sign (+) indicates a regular distribution pattern, and the X shows an aggregate pattern.

| | Distance in m | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0.2 | 0.4 | 0.6 | 0.8 | 1 | 1.2 | 1.4 | 1.6 | 1.8 | 2 | 2.2 | 2.4 | 2.6 | 2.8 | 3 | 3.2 | 3.4 | 3.6 | 3.8 | 4 | 4.2 | 4.4 | 4.6 | 4.8 | 5 |
| All males | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | + | + | + | + | + | + |
| Red morph | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | + | + | + | + | + | + | + | x |
| Yellow morph | – | – | – | – | – | – | – | – | – | – | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| Females | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | + | + | + | + | + | + | + | + | + |

of 3.4–5.0 m (Table 3). Spatial association analysis (Ripley's $K_{12}$ function) indicated that there was intermittent dependence (association) between morphs at a radius of < 1.0 m, but red males exhibited an association with females at a radius of < 1.0 m, and yellow males showed an intermittent association with females at a radius of < 1.4 m (Table 4). The HRs of adult males did not overlap with those of other adult males, at least not at the same time. When the owner of an HR was experimentally removed, this area was subsequently occupied by a male neighbour. The HRs of

Table 4. Spatial association patterns of *S. minor* male morphs and females. The K (12) function of Ripley was performed using a confidence interval of 95% (99 simulations) and steps of 0.1 m. The hyphen (-) indicates independence and the plus sign (+) indicates dependence (association).

| | Distance in m | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0.2 | 0.4 | 0.6 | 0.8 | 1 | 1.2 | 1.4 | 1.6 | 1.8 | 2 | 2.2 | 2.4 | 2.6 | 2.8 | 3 | 3.2 | 3.4 | 3.6 | 3.8 | 4 | 4.2 | 4.4 | 4.6 | 4.8 | 5 |
| Red males vs yellow males | + | – | + | + | + | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Females vs red males | + | + | + | + | + | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Females vs yellow males | + | + | – | + | – | + | + | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |

both small males (young but sexually mature) and females, however, overlapped with those of the adult males.

The GDFA did not show up significant differences between morphs ($F_{20,3} = 0.75$, $p = 0.71$). Considering the canonical values obtained from the comparison between morphs, however, it was observed that for all measured attributes, yellow males differed significantly from red males ($t_{22} = 10.4$, $p < 0.001$, Fig. 1). In addition, the association matrix showed 100% segregation between character states. The reason why the GDFA did not reveal significant differences, even though the association matrix values were a 100% segregated between morph character states, is because morphs shared certain attributes, and the variables associated with these attributes were correlated (categorical interactions; Fig. 1). Based on the GDFA, the variables were separated, and a CCA was conducted with only those variables that showed higher values of correlation. The variables "colour" and "number of females in the male HR" were used as contrast attributes (factors) and the descriptors (state of the tail, ventral patch colour, aggressive behaviour) as dependent variables. The result indicated a significant correlation between the state of a male's tail and dorsal colour ($R = -0.31$, $p < 0.05$), the number of females within the HR of a male and the state of the tail ($R = -0.21$, $p < 0.05$), and the male aggressive behaviour index and number of females ($R = 0.20$, $p < 0.05$); only the latter exhibited a positive correlation. In addition, when obtaining the weighted average for each morph, it was observed that males of the red morph had more females in their HRs ($\overline{x} = 1.08$) than yellow males ($\overline{x} = 0.87$). Within the attributes, a correlation was observed between the state of the tail and the coloration of the ventral patches ($R = -0.20$, $p < 0.05$), and state of the tail and aggressive behaviour ($R = -0.27$, $p < 0.05$). That is to say, the darker the tone of the ventral patches, the less the damage to the tail; similarly, the higher the aggressive behaviour score, the less damage there is to the tail (regenerated tail; see categories in Appendix 1).

## Discussion

Both theory and empirical evidence have linked polychromatism to alternative reproductive tactics (Gross 1996, Sinervo & Lively 1996, Taborsky et al. 2008), with individuals using different strategies to achieve reproductive success (Taborsky et al. 2008). In certain species with polymorphism, such as the lizards *Uta stanburiana* and *Urosaurus ornatus*, one type of morph will be territorial, while the other type will create mating opportunities by alternative means (i.e., non-territorial satellites: Sinervo & Lively 1996, Moore et al. 1998). The results of our study demonstrate that this is not the case for *S. minor*, since, in general, both morphs in our study population are usually territorial. It was observed, however, that a few individuals of each morph were not territorial (17.7%); notably, non-territorial males were smaller on average than those that were territorial. A territory, unlike a home range (HR), is an exclusive area that is defended against conspecifics (Schoener 1968), and such areas are acquired by winning contests (Stamps & Krishnan 1994). Consequently, one interpretation of this finding is that smaller individuals do not defend territories until they reach the minimum size necessary for being able to successfully compete. On the other hand, individuals that did not exhibit territorial behaviour (active, passive, or both) might not have received a sufficient stimulus to express such behaviour (Martin & Bateson 2007). That is, an intruder male might not have been placed in an area that was exclusive to a resident male, or perhaps the intruder male was not perceived as a threat to the resident (Martin & Bateson 2007).

Home range sizes did not differ between male morphs, but did differ between males and females, with female HRs being smaller than those of males. Several factors are known to affect HR size in lizards, such as sex, body size,
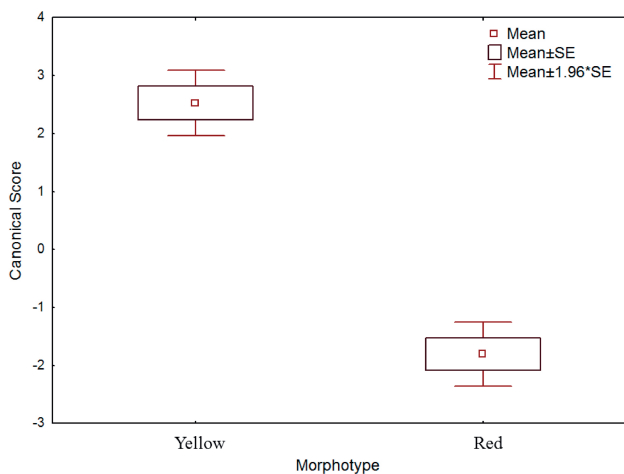


Figure 1. Box plot of canonical values obtained from the GDFA. Eigenvalue = 4.97, cumulative variance = 100%.

time of year, type of foraging behaviour, population density, energy requirements, social behaviour, and availability of mates (Rose 1982, Perry & Garland 2002). Body size generally correlates positively with HR size, because larger animals can move farther than small ones to exploit their resources (Rocha 1999). Previous studies of *S. minor* morphology showed that there were no significant differences in body size or other morphometric characters between morphs in this population (García-Rosales et al. 2019b); therefore, it was expected that HR size would also be similar between the morphs. Males of this population are larger in body size than females (García-Rosales et al. 2017), which in turn might be a major factor in explaining the difference in HR size between the sexes. This difference in HR size, however, might also be a consequence of the need for adult males of relatively large body size to claim large areas in order to include many females in that area (Ruby & Dunham 1987, Rocha 1999). The HRs of adult males did not overlap with each other; this result suggests mutual exclusion, which constitutes direct evidence of territoriality, and also suggests that the size of the HR could coincide with the size of the territory (Rocha 1999). The HRs of males often overlapped with those of multiple females, which probably forms part of a strategy by larger males to increase their probabilities of mating (Ruby & Dunham 1987). However, neither the overlap of HR between males and females, nor the closeness between sexes, can ensure the reproductive success of the male (Haenel et al. 2003).

The spatial distribution analysis revealed a regular distribution pattern across all groups we examined, but with different radii (Table 2). This pattern usually occurs in species living in homogeneous environments (Octavio-Aguilar et al. 2019), especially in species where multiple groups compete and defend different resources in the environment (Giesselmann et al. 2008). Red males exhibited a pattern of regular distribution at a greater radius than yellow males, suggesting that red males defend larger territories than do yellow males. It was also observed that females had a regular distribution with a greater radius than do yellow males. This latter outcome might reflect the greater number of females found in the territories of red males; that is, if red males defend larger territories that contain more females than yellow males do, it follows that females would show a distribution pattern more similar to that of red males than that of yellow males. Huey (1991) argued that lizards can maximize their fitness by claiming for themselves areas that provide greater and better food resources, a lower rate of predation, and suitable temperatures. In this respect, because the habitat of this population of *S. minor* is relatively homogeneous, the territories that these lizards defend are expected to be of similar quality; therefore, this pattern of regular distribution would be created by the density of organisms in this area (Grigoropoulou & Butt 2010). It will be necessary for generating a more robust conclusion, however, both to measure the density of adult *S. minor* in the area and to quantify the quality of the habitats used by them. The pattern of association between male morphs and between each male morph

and all females showed an intermittent dependence at distances of less than 1.4 m (except between red males and females, where a constant association was observed). This pattern of association at short distances could be a function of the visual signalling that these lizards use (Font et al. 2010), since such signals are normally transmitted better across short distances and without physical barriers that prevent individuals from seeing each other (Font et al. 2010).

On the other hand, we found no correlation between HR size and the number of females within the HR (either by morphs separately or considering all males), although there were differences between the numbers of females found in the HRs of each morph, in that red males had more females than did yellow males. Yellow males, however, were more aggressive than were red males (R = 0.20). This information, together with that provided by García-Rosales et al. (2019b), who indicated that there are no morphometric differences between morphs, would suggest that the high number of females found in red male HRs is unrelated to male size, male aggressive behaviour, or HR *per se*. Likewise, we recorded that the yellow males had a higher frequency of regenerated tails than did red males (R = -0.31). This could be a consequence of the greater aggressiveness displayed by the yellow males, since a higher frequency of tail loss has been recorded in species with a higher degree of aggressiveness (García-Rosales & Martínez-Coronel 2016). In turn, this higher frequency of tail loss or regenerated tails recorded for the yellow morphs can result in reduced access to females, as has been demonstrated to be the case in *Iberolacerta montícola* (Martín & Salvador 1993) and *Psammodromus algirus* (Salvador et al. 1995). The state of the tail (complete or regenerated), can indicate to male or female conspecifics the ability of an individual to escape from predators; thus, the possession of an intact tail can be a sign of its bearer's ability to avoid predators, while a regenerated tail would indicate its bearer to be less able to escape without incurring damage (Martín & Salvador 1993, Salvador et al. 1995). Together with morphology, coloration, and behaviour, these might be elements (characteristics) that the female evaluates in considering whether or not to copulate with a male (Martín & Salvador 1993). Female choice in this population could therefore involve evaluating the state of the courting male's tail or by using dorsal colour as an indicator of male quality (genetic or resources), but variation in male aggressive behaviour might then be irrelevant.

A large body size and high degree of aggressiveness can facilitate dominance, in turn conferring an advantage in access to resources (Archer 1988). The most aggressive individuals are more successful in the competition for resources (space and food, among others). Thus, an aggressive individual could have an HR that is both larger and of better quality than those of less aggressive individuals. In support of this, Civantos (2000) demonstrated that the most aggressive lizards established larger HRs than less aggressive ones, which was something Fox (1983) had observed before in *Uta stansburiana*. In this study, however,

we found that males of the more aggressive yellow morph have an HR that is similar in size to those of the less aggressive red morph. This result might be related to the quality of male HRs; perhaps yellow males have HRs of better quality than those of red morphs. This prediction could be tested in future studies by assessing the quality of male HRs, and testing for a morph-specific difference.

Several studies of polymorphic lizards have mentioned that morphs can differ in their morphology, behaviour, and ecology (Thompson & Moore 1991, 1992, Sinervo & Lively 1996, Lattanzio & Miles 2016, Scali et al. 2016, Paterson & Blouin-Demers 2018). Specifically, they can differ in body size (Thompson & Moore 1991, Sinervo & Lively 1999), spatial distribution within the landscape (Paterson & Blouin-Demers 2018), aggressiveness (Sinervo et al. 2000), size of territory and/or home range (Thompson & Moore 1991, Sinervo &Lively 1996), quality of habitats used (Paterson & Blouin-Demers 2018), and trophic ecology (Lattanzio & Miles 2016, Scali et al. 2016). In this study, however, we found no differences in certain ecological attributes, such as the type of microhabitat used by each morph, perch height, and HR size. Together with information previously provided by García-Rosales et al. (2019b), specifically the fact that these authors did not find differences in morphology or diet between morphs, this suggests that the polymorphism in this population is probably not maintained by means of niche partitioning (Skúlason & Smith 1995, Lattanzio & Miles 2016, Scali et al. 2016, Paterson & Blouin-Demers 2018), since both morphs exploit the same resources. This could be explained by one of at least three hypotheses: one, that resources are so abundant at this site that morphs do not have to compete for access to them; two, the morphs are maintained by their different reproductive qualities, and each morph is evolutionarily stable; or three, the maintenance of these morphs at this site is due to frequency-dependent selection, where the fitness of a morph depends on the frequencies of the other morphs with which it competes (Sinervo & Lively 1996, Pryke et al. 2007).

In conclusion, our results demonstrate that there are differences between morphs in aggressive behaviour and in the number of females found in their respective HRs. Both red and yellow morphs, however, were similar in some other behavioural, ecological, and morphological traits (this last trait was not evaluated in this study; see García-Rosales et al. 2019b), rejecting the hypothesis that morphs in this population are maintained by niche partitioning. This leaves open the possibility that frequency-dependent selection maintains the polymorphism in this population. It is necessary, however, to measure the availability, abundance, and quality of the resources that these lizards utilise, as well as to monitor them for a longer period of time, recording the frequency of morphs by year. Doing so should allow us to corroborate more robustly which mechanism(s) maintain(s) the polymorphism in this population (Sinervo & Lively 1996, Lattanzio & Miles 2016, Scali et al. 2016).

## References

Altmann, J. (1974): Observational study of behavior: sampling methods. – Behaviour, **49**: 227–267.

Archer, J. (1988): The behavioural biology of aggression. – Cambridge University Press, Cambridge.

Bastiaans, E., G. Morinaga, J. G. Catañeda-Gaytan, J. C. Marshall & B. Sinervo (2013): Male aggression varies with throat color in 2 distinct populations of the mesquite lizard. – Behavioral Ecology, **24**: 968–981.

Burt, W. H. (1943): Territoriality and home range concepts as applied to mammals. – Journal of Mammalogy, **24**: 346–352.

Bustos-Zagal, M. G., R. Castro-Franco, J. Manjarrez & V. Fajardo-Guadarrama (2014): Variación morfológica asociada a los patrones de color de la garganta, en lagartijas *Sceloporus horridus* (Sauria: Phrynosomatidae). – Acta Zoológica Mexicana, **30**: 357–368.

Civantos, E. (2000): Home-range ecology, aggressive behaviour, and survival in juvenile lizards, *Psammodromus algirus*. – Canadian Journal of Zoology, **78**: 1681–1685.

De la Cruz, M. (2006): Introducción al análisis de datos mapeados o algunas de las (muchas) cosas que puedo hacer si tengo coordenadas. – Ecosistemas, **15**: 19–39.

Domínguez-Guerrero, S. F. (2015): Patrones reproductores, polimorfismos morfológicos y sistemas de apareamiento en una población de *Sceloporus torquatus* (Squamata: Phrynosomatidae) en Toluca, Estado de México. – Master's Thesis. Universidad Autónoma del Estado de Hidalgo, Hidalgo, México.

Duca, C., T. J. Guerra & M. A. Marini (2006): Territory size of three Antbirds (Aves, Passeriformes) in an Atlantic forest fragment in southeastern Brazil. – Revista Brasileira de Zoologia, **23**: 692–698.

Duncan, R. P. (1990): Spatial Analysis Programs. – Statistical Analysis Software Package. Lincoln University, Canterbury, New Zealand.

Fitze, P. S., V. Gonzalez-Jimena, L. M. San-Jose, B. Heulin & B. Sinervo (2014): Frequency-dependent sexual selection with respect to progeny survival is consistent with predictions from rock-paper-scissors dynamics in the European common lizard. – Frontiers in Ecology and Evolution, **2**: 77. https://doi.org/10.3389/fevo.2014.00077.

Font, E., P. Carazo, G. Pérez i de Lanuza & D. Barbosa (2010): Comportamiento y comunicación animal: ¿Qué nos enseñan los lagartos?. – Acta Zool lilloana, **54**:11–34.

Fox, S. F. (1983): Fitness, home-range quality and aggression in *Uta stansburiana*. – pp. 149–168 in: Huey, R. B., E. R. Pianka

& T. W. Schoener (eds): Lizard Ecology: Studies of a Model Organism. – Harvard University Press, Cambridge, Mass.

Galeotti, P., R. Sacchi, D. Pellitteri-Rosa, A. Bellati, W. Cocca, A. Gentilli, S. Scali & M. Fasola (2013): Colour polymorphism and alternative breeding strategies: effects of parent's colour morph on fitness traits in the common wall lizard. – Evolutionary Biology, **40**: 385–394.

García-Rosales, A., R. Cruz-Elizalde, A. Ramírez-Bautista & V. Mata-Silva (2019a): Feeding ecology of two populations of *Sceloporus minor* (Squamata: Phrynosomatidae) inhabiting contrasting environments in central México. – Salamandra, **55**: 103–114.

García-Rosales, A. & M. Martínez-Coronel (2016): Frecuencia de pérdida de la cola en un ensamble de lagartijas de Oaxaca, México. – Acta Zoológica Mexicana, **32**: 174–181.

García-Rosales, A., A. Ramírez-Bautista & B. P. Stephenson (2019b): Comparative morphology and trophic ecology in a population of the polymorphic lizard *Sceloporus minor* (Squamata: Phrynosomatidae) from central Mexico. – PeerJ 7:e8099, https://doi.org/10.7717/peerj.8099.

García-Rosales, A., A. Ramírez-Bautista, B. P. Stephenson, R. N. Meza-Lázaro & A. Nieto-Montes de Oca (2017): Comparative morphology and genetics of two populations of spiny lizards (genus *Sceloporus*) from Central Mexico. – Zoologischer Anzeiger, **267**: 21–30.

Giesselmann, U. C., T. Wiegand, J. Meyer, M. Vogel & R. Brandl (2008): Spatial distribution of communal nets in a colonial breeding bird: benefits without costs?. – Austral Ecology, **33**: 607–613.

Grigoropoulou, N. & K. R. Butt (2010): Field investigations of *Lumbricus terrestris* spatial distribution and dispersal through monitoring of manipulated, enclosed plots. – Soil Biology and Biochemistry, **42**: 40–47.

Gross, M. R. (1996): Alternative reproductive strategies and tactics: diversity within sexes. – Trends in Ecology and Evolution, **11**: 92–98.

Haenel, G. J., L. C. Smith & H. B. John-Alder (2003): Home-Range Analysis in *Sceloporus undulatus*. II. A Test of Spatial Relationship and Reproductive Success. – Copeia, **2003**: 113–123.

Hamilton, P. S. & B. K. Sullivan (2005): Female Mate Attraction in Ornate Tree Lizards, *Urosaurus ornatus*: a Multivariate Analysis. – Animal Behaviour, **69**: 219–224.

Hernández-Gallegos, O., G. Granados-González, J. L. Rheubert, M. Villagrán-Santa Cruz, E. Peña-Herrera & K. M. Gribbins (2018): Lack of spermatogenic variation in a polymorphic lizard, *Sceloporus aeneus* (Squamata: Phrynosomatidae). – Acta Zoologica, **100**: 359–364.

Huey, R. B. (1991): Physiological consequences of habitat selection. – The American Naturalist, **137**: 95–115.

Köhler, G. (2012): Color catalogue for field biologists. – Herpeton, Offenbach, Germany.

Lattanzio, M. S. & D. B. Miles (2016): Trophic niche divergence among colour morphs that exhibit alternative mating tactics. – Royal Society Open Science, https://doi.org/10.1098/rsos.150531.

Márquez-Luna, U. (2014): Efecto de la abundancia floral y la calidad del néctar en la conducta y tamaño del territorio en dos especies de colibríes. – Master's Thesis. Universidad Autónoma del estado de Hidalgo, Hidalgo, México.

Martin, J. & A. Salvador (1993): Tail loss reduces mating success in the Iberian rock-lizard, *Lacerta monticola*. – Behavioral Ecolology and Sociobiology, **32**: 185–189.

Martin, P. & P. Bateson (2007): Measuring behaviour: An introductory guide (3a ed.). – Cambridge University Press.

Moore, M. C., D. K. Hews & R. Knapp (1998): Hormonal control and evolution of alternative male phenotypes: generalizations of models for sexual differentiation. – American Zoologist, **38**: 133–151.

Nice, M. M. (1941): The Role of territory in bird life. – The American Midland Naturalist Journal, **26**: 441–487.

Noble, G. K. (1939): The Role of dominance in the social life of birds. – The Auk, **56**: 263–273.

Octavio-Aguilar, P., A. P. Martínez-Falcón, A. Sánchez-González, A. Rojas-Martínez, A. Meerow, A. Ramírez-Bautista, R. Ortiz-Pulido, P. Caballero-Cruz, G. N. Hernández-Rico & C. S. Berriozabal-Islas (2019): Influence of microhabitat on functional attributes of two columnar cacti with different distribution ranges. – Journal of Arid Environments, **162**: 18–25.

Paterson, J. E. & G. Blouin-Demers (2018): Male throat color polymorphism is related to differences in space use and in habitat selection in tree lizards. – Journal of Zoology, **306**: 101–109.

Pavón, N. P. & M. Meza-Sánchez (2009): Cambio climático en el Estado de Hidalgo. – Universidad Autónoma del Estado de Hidalgo, Pachuca.

Perry, G. & T. Garland (2002): Lizard home ranges revisited: Effects of sex, body size, diet, habitat and phylogeny. – Ecology, **83**: 1870–1885.

Peter, H. (1995): Spatial pattern analysis in ecology based on Ripley's K-function: introduction and methods of edge correction. – Journal of Vegetation Science, **6**: 575–582.

Pryke, S. R., L. B. Astheimer, W. A. Buttemer & S. C. Griffith (2007): Frequency-dependent physiological trade-offs between competing colour morphs. – Biology Letters, **3**: 494–497.

Ramírez-Bautista, A., O. Ramos-Flores, B. P. Stephenson & G. R. Smith (2008): Reproduction and Sexual Dimorphism in Two Populations of *Sceloporus minor* of the Guadalcázar Region, San Luis Potosí, México. – Herpetological Journal, **18**: 121–127.

Ramírez-Bautista, A., B. P. Stephenson, C. Serrano-Muñoz, R. Cruz-Elizalde & U. Hernández-Salinas (2014): Reproduction and sexual dimorphism in two populations of the polymorphic spiny lizard *Sceloporus minor* from Hidalgo, México. – Acta Zoologica, **95**: 397–408.

Rand, M. S. (1990): Polymorphic sexual coloration in the lizard *Sceloporus undulatus erythrocheilus*. – The American Midland Naturalist, **124**: 352–359.

Ripley, B. D. (1981): Spatial Statistics. – Wiley, New York.

Rocha, C. F. D. (1999): Home range of the tropidurid lizard *Liolaemus lutzae*: sexual and body size differences. – Revista Brasileira de Biolología, **59**: 125–130.

Rose, B. (1982): Lizard home ranges: methodology and functions. – Journal of Herpetology, **16**: 253–269.

Ruby, D. E. & A. E. Dunham (1987): Variation in home range size along an elevational gradient in the iguanid lizard *Sceloporus merriami*. – Oecologica, **71**: 473–480.

Rzedowski, J. (1978): Vegetación de México. – Limusa Wiley, Mexico.

Sacchi, R., F. Pupin, A. Gentilli, D. Rubolini, S. Scali, M. Fasola & P. Galeotti (2009): Male–male combats in a polymorphic lizard: residency and size, but not color, affect fighting rules and contest outcome. – Aggressive Behavior: Official Journal of the International Society for Research on Aggression, **35**: 274–283.

Sacchi, R., S. Scali, M. Mangiacotti, M. Sannolo, M. A. Zuffi, F. Pupin, A. Gentilli & X. Bonnet (2017): Seasonal variations of plasma testosterone among colour-morph common wall lizards (*Podarcis muralis*). – General and Comparative Endocrinology, **240**: 114–120.

Salvador, A., J. Martin & P. Lopez (1995): Tail loss reduces home range size and access to females in male lizards, *Psammodromus algiricus*. – Behavioral Ecology, **6**: 382–387.

Scali, S., R. Sacchi, M. Mangiacotti, F. Pupin, A. Gentilli, C. Zucchi, M. Sannolo, M. Pavesi & M. A. L. Zuffi (2016): Does a polymorphic species have a "polymorphic" diet? A case study from a lacertid lizard. – Biological Journal of the Linnean Society, **117**: 492–502.

Schoener, T. W. (1968): Sizes of feeding territories among birds. – Ecology, **49**: 123–141.

Simon, C. A. (1975): The influence of food abundance on territory size in the iguanid lizard *Sceloporus jarrovii*. – Ecology, **56**: 993–998.

Sinervo, B. & C. M. Lively (1996): The Rock-Paper-Scissors Game and the Evolution of Alternative Male Strategies. – Nature, **380**: 240–243.

Sinervo, B., D. S. Miles, W. A. Frankino, M. Klukowski & D. F. De Nardo (2000): Testosterone, endurance, and Darwinian fitness: natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. – Hormones and Behavior, **38**: 222–233.

Skúlason, S. & T. B. Smith (1995): Resource polymorphisms in vertebrates. – Trends in Ecology and Evolution, **4**: 238–239.

Stamps, J. A. & V. V. Krishnan (1994): Territory acquisition in lizards: II. Establishing social and spatial relationships. – Animal Behavior, **47**: 1387–1400.

Stephenson, B. P. (2010): A Study of the Biological Significance of a Male Color Polymorphism in the Lizard *Sceloporus minor*. – Ph.D. thesis, University of Miami, Coral Gables, FL.

Stephenson, B. P. & A. Ramírez-Bautista (2012): Did Sexually Dimorphic Dorsal Coloration Evolve by a Pre-existing Bias in Males in the Lizard *Sceloporus minor*? – Evolutionary Ecology, **26**: 1277–1291.

Svensson, E., B. Sinervo & T. Comendant (2001): Density-dependent competition and selection on immune function in genetic lizard morphs. – Proceedings of the National Academy of Science, **98**: 12561–12565.

Taborsky, M., R. F. Oliveira & H. J. Brockmann (2008): The evolution of alternative reproductive tactics: concepts and questions. – pp. 1–21 in: Oliveira, R. F., M. Taborsky & J, Brockmann (eds): Alternative reproductive tactics. – Cambridge University Press.

Thompson, C. W. & M. C. Moore (1991): Throat color reliably signals status in male tree lizards, *Urosaurus ornatus*. – Animal Behavior, **42**: 745–753.

Thompson, C. W. & M. C. Moore (1992): Behavioral and hormonal correlates of alternative reproductive strategies in a polygynous lizard: tests of the relative plasticity and challenge hypotheses. – Hormones and Behavior, **26**: 568–585.

Wiens, J. J., T. W. Reeder & A. Nieto-Montes de Oca (1999): Molecular phylogenetics and evolution of sexual dichromatism among populations of the Yarrow's spiny lizard (*Sceloporus jarrovii*). – Evolution, **53**: 1884–1897.

Yewers, M. S. C., T. S. Jessop & D. Stuart-Fox (2017): Endocrine differences among colour morphs in a lizard with alternative behavioural strategies. – Hormones and Behavior, **93**: 118–127.

Zamudio, K. R. & B. Sinervo (2000): Polygyny, mate-guarding, and posthumous fertilization as alternative male mating strategies. – Proceedings of the National Academy of Science, **97**: 14427–14432.

Zar, J. (1999): Biostatiscal Analysis. – Prentice Hall, Englewood Cliffs.

## Appendix 1.

Categorical variables used in the GDFA.

| Categorical variables | Category | | | | | |
| --- | --- | --- | --- | --- | --- | --- |
| | 1 | 2 | 3 | 4 | 5 | 6 |
| Aggressive behaviour | Not aggressive | Passive | Active | | | |
| State of the tail | Regenerated | Complete | | | | |
| Colour of the ventral body patches | Spectrum blue | Cobalt blue | Ultramarine | True blue | Smalt blue | Sky blue |