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# Female choice and male aggression in the polymorphic lizard *Sceloporus minor*

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## Abstract

In comparison with some other vertebrate groups, female choice in lizards is relatively poorly understood. In contrast, aggressive behavior in lizards has been better studied; nevertheless, there are many genera and even whole families for which little or no information on aggressive behavior has been described. Therefore, the objective of this study was to experimentally evaluate the importance of morphometric traits, body coloration, and behavioral attributes of male *Sceloporus minor* from a population in central Mexico in order to (1) determine whether female choice exists in this species, and if so, identify which features of males females are using to do so, and (2) identify the phenotypic features of males that predict dominance status in contests between dominant and subordinate males. We found that females of *S. minor* indeed show a preference for males on the basis of ventral patch color; specifically, females chose males with ventral patches of Spectrum Blue or True Blue over males with ventral patches of other blue hues, but found no evidence of choice based on other morphological characters examined. Results also showed that winner (i.e., dominant) males exhibited more aggressive behaviors and were larger in body size than subordinate (i.e., loser) males. Notably, we found no support for a role of male polymorphic dorsal coloration on either female choice or male contest outcome. The results of this study showed evidence of female choice and male-male competition, suggesting that in this population, males exhibit intrasexual interactions to compete for resources such as territories and produce displays that serve in part to attract females.

**KEYWORDS**
aggressive behavior, body coloration, dominance status, intersexual selection, morphometric traits, polychromatic lizard

## 1 | INTRODUCTION

Behavior is one of the most easily observable aspects of an organism's phenotype (Font, 2002; Martin & Bateson, 2007). Among vertebrates, fish, birds, and mammals are the most studied groups with respect to behavior (Font, 2002; Font et al., 2010); in contrast, squamates (especially lizards) are comparatively poorly studied (Font, 2002; Font et al., 2010). For example, female choice has been studied in many vertebrate groups; however, in non-avian reptiles, this phenomenon has been less well documented (Hamilton & Sullivan, 2005; LeBas & Marshall, 2000; Olsson & Madsen, 1995; Tokarz, 1995). On the other hand, aggressive behavior in some groups of lizards has been relatively well studied, both in natural conditions and captivity; this includes representatives of the families Scincidae,

  

Iguanidae, Phrynosomatidae, and Lacertidae, among others (Borja, 2002; Carpenter, 1995; Cooper & Vitt, 1988; Olsson, 1994; Sacchi et al., 2009). Even so, there are genera and even entire families of lizards for which little or no information on aggressive behavior has been described (Font, 2002; Font et al., 2010); detailed information is even scarcer in lizards that exhibit color polymorphisms, where aggressive behavior can vary among morphs (Bastiaans et al., 2013; Sacchi et al., 2009; Sinervo & Lively, 1996).

Many lizard species use visual signaling systems extensively. Diurnal lizards, in particular, tend to have large eyes suitable for photopic vision (Font et al., 2010; LeBas & Marshall, 2000). Therefore, intra- and interspecific signaling often take the form of stereotyped postures and movements, as well as displays of conspicuous color features, some found all over the body and others restricted to specific regions (Font, 2002; Font et al., 2010). The regional distribution of these color features in lizards is related to their environment. Species expressing such color features on relatively exposed areas (e.g., the dorsum), or even over the entire body, generally occur in environments with low predation pressure (Stuart-Fox & Ord, 2004), and/or forest habitats with closed canopy cover and few patches of light (Wiens et al., 1999). In contrast, species occurring in environments with high predation pressure usually restrict conspicuous coloration to body regions not easily observed by potential predators and only reveal these color features in specific social contexts, such as agonistic or courtship interactions (e.g., gular or ventral abdominal areas; Font, 2002; Font et al., 2010).

Regardless of the presence (and extent) of any conspicuous coloration, males of the same species generally use similar reproductive tactics, and their fitness is usually dictated by variation in one or more secondary sexual traits (e.g., body size and color pattern; Andersson, 1994). However, males of some species occur in different phenotypes (morphs), which present an intrinsic evolutionary problem; if morphs differ in their fitness, less successful morphs should eventually disappear from the population (Gross, 1996). Therefore, for multiple morphs to be maintained in the same population, they must achieve equal fitness over time (Lattanzio & Miles, 2016). Consequently, multiple mechanisms have been proposed to explain this phenomenon, including frequency-dependent selection, niche partitioning, and assortative mating (Lattanzio & Miles, 2016; Sinervo & Lively, 1996). Such variation, as seen in polymorphic species, leads to increased complexity in behavioral and mating systems (Bastiaans et al., 2013; Sacchi et al., 2009; Sinervo & Lively, 1996). In lizards, color polymorphism has been linked to variation in behavioral tactics in several species, with certain colors associated with more aggressive behavior of males as compared to the corresponding conspecific morph(s) (Sinervo & Lively, 1996; Thompson & Moore, 1991, 1992). Likewise, these morphs can differ in body size, life history traits, physiology, and size of territory and/or home range, among other characteristics (García-Rosales, Ramírez-Bautista & Stephenson, 2019; García-Rosales et al., 2021; Lattanzio & Miles, 2016; Sinervo & Lively, 1996; Thompson & Moore, 1991). For example, in the side-blotched lizard *Uta stansburiana*, orange morph males (ultra-dominant) exhibit higher levels of testosterone, a greater degree of aggressiveness, and defend larger territories with a greater number of females as compared to blue and yellow morphs (Sinervo & Lively, 1996; Sinervo et al., 2000). In turn, blue morphs (mate-guarders) show higher levels of testosterone, a greater degree of aggressiveness, and larger territories compared with yellow morphs. As a result, yellow males (sneakers) are forced to use alternative ecological and reproductive strategies so as not to interact directly with the orange and blue morphs (Sinervo & Lively, 1996; Sinervo et al., 2000). Notably, a red or orange morph is dominant (more aggressive and/or larger) over conspecific morphs in some other species (e.g., *Ctenophorus pictus* and *C. decresii*; Olsson et al., 2007; Teasdale et al., 2013; Yewers et al., 2016). However, this is not always the case, since in some other species the dominant morph is of another color (e.g., *Sceloporus grammicus*, Bastiaans et al., 2013; *Urosaurus ornatus*, Thompson & Moore, 1991, 1992).

In non-avian reptiles, many mate choice studies have been conducted under field conditions, which makes it difficult to identify the existence or effect of intra- or intersexual selection (Olsson & Madsen, 1998). For example, in territorial lizards, contests between males frequently determine the size and quality of male territories. Consequently, demonstrating female mate choice on the basis of male traits can be difficult, since female preference for male traits must be distinguished from the choice that females may make on the basis of male resources, such as territory quality (LeBas & Marshall, 2000). Likewise, most studies of mate choice in lizards have focused on a single male feature (LeBas & Marshall, 2000; Tokarz, 2002), even though multiple male phenotypic features may contribute to female mating decisions (Hamilton & Sullivan, 2005). In contrast, studies of aggressive behavior in males have generally consisted of placing two males in an arena in the laboratory, and quantifying behavior patterns exhibited during ensuing contests to identify dominant and subordinate individuals (Bastiaans et al., 2013; Sacchi et al., 2009). Body size, level of aggression, and previous experience are the variables that best predict contest outcome (Olsson, 1992; Sacchi et al., 2009; Tokarz, 1995; Zucker & Murray, 1996), although these results may vary depending on the conditions in which the experiments are performed (Bastiaans et al., 2013).

Most lizards exhibit sexual dimorphism in body size and/or coloration, traits that commonly serve as the basis of mate selection in other taxa, including *U. ornatus (Hamilton & Sullivan*., 2005) and *S. grammicus (Bastiaans et al*., 2014). In addition, they often show conspicuous behaviors, providing information on the signaler's phenotype in which the choice of partner could be based (Censky, 1997; Hamilton & Sullivan, 2005) or that reveal relative dominance status (e.g., *U. ornatus*: Thompson & Moore, 1992; *U. stansburiana*: Sinervo & Lively, 1996; *S. grammicus*: Bastiaans et al., 2013). In this light, it is surprising that few studies have been carried out on mate choice and aggressive behavior in lizards, since many representatives of this group seem to be ideal models for this type of research (Pérez i de Lanuza et al., 2013; Trivers, 1976; Vercken et al., 2006). The phrynosomatid lizard *Sceloporus minor* is a polymorphic species endemic to Mexico, and which has been relatively well studied in certain aspects of its biology (García-Rosales et al., 2017, García-Rosales,

Cruz-Elizalde, et al. 2019; Ramírez-Bautista et al., 2008, 2014; Stephenson, 2010; Stephenson & Ramírez-Bautista, 2012; Wiens et al., 1999). Morphological studies have shown that this species exhibits marked intra- and intersexual phenotypic variation (sexual dimorphism and polymorphism) in body size and color patterns (García-Rosales et al., 2017; Stephenson & Ramírez-Bautista, 2012; Wiens et al., 1999), traits that can indicate the quality of the male and, in turn, provide an advantage in female choice or agonistic encounters (Bastiaans et al., 2013, 2014; Borja, 2002; Hamilton & Sullivan, 2005; Senar, 1994). This offers an excellent opportunity to evaluate the relationship of intraspecific phenotypic variation in morphometry, color patterns, and behavior with the ability of males to attract mates and/or to win contests with other males. Therefore, the objective of this study was to experimentally evaluate the importance of morphometric traits, body coloration, and behavioral attributes of male *S. minor* from a population in central Mexico in order to 1) determine whether there is female choice, and if so, on which features females are choosing, and 2) identify the phenotypic features that predict dominance status in dominant and subordinate males.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

Research was carried out at a study site in El Enzuelado (20°35′N, 98°37′W) in the municipality of San Agustín Metzquititlán, Hidalgo, Mexico. Ecological parameters of this study site have been previously described (Ramírez-Bautista et al., 2014).

### 2.2 | Subjects

We collected sexually mature males ($N = 91$) and females ($N = 45$) at the end of August and early September 2017, a period corresponding to the beginning of the mating season. Adults were identified on the basis of previously reported estimates for minimum body size (SVL) at sexual maturity (Ramírez-Bautista et al., 2014). For each lizard, we collected data on each of the following morphometric characters: snout-vent length (SVL; distance from the tip of the rostral scale to the cloaca), tail length (TLL; distance from the vent to the tip of the tail), jaw length (JL; distance from the tip of the rostral scale to the point of maximum width of the left side of the mandible), jaw width (JW; the maximum distance between the left and right sides of the mandible), head length (HL; distance from the anterior tip of the rostral scale to the posterior margin of the left ear), head width (HW; maximum width of the head, measured as the distance between the posterior margin of the left and right ears), head height (HH; the maximum distance between the dorsal and ventral sides of the head), tibia length (TL; distance from the knee to the pad of the foot), femur length (FL; distance from the angle of the groin to the knee), forearm length (FOL; distance from the elbow to the pad of the foot), and ventral patch length (VPL; the maximum longitudinal distance of dark edge), with the aid of a Mitutoyo digital caliper (±0.01 mm). In addition, body mass (BM) was measured using a Pesola spring scale (±0.01 g), and the status of the tail (complete or regenerated) was recorded. Lizards that showed no sign of tail mutilation or regeneration were scored as having a complete tail, whereas those that exhibited either a mutilated tail or showed evidence of tail regeneration were scored as having a regenerated tail. In addition, no lizard lost any part of its tail during handling or experimental procedures. Finally, we recorded the dorsal and ventral patch color of each individual based on a color catalogue for field work (Köhler, 2012); dorsal color variation in male morphs from El Enzuelado was previously described (see García-Rosales et al., 2017). During fieldwork, it was observed that in mornings or on cold days, the color of males was relatively dark, suggesting a temperature effect on integumentary coloration. Therefore, prior to scoring color, each lizard was exposed to the sun for approximately 15 min in an effort to raise body temperature, and so facilitate the expression of coloration more characteristic of active males (see Stephenson et al., 2017). Following this warming period, lizards were scored for color in an outdoor location with access to natural light. All color measurements were recorded in the morning (9:00–10:00 h) on warm and sunny days. Assessments of color for each lizard were corroborated by at least two observers.

Subsequently, each lizard was placed individually into a transparent plastic container (40 cm × 30 cm × 25 cm) marked with a number to confirm the identity of the lizard inside; as a result, we did not need to mark lizards themselves, avoiding potential problems associated with marking on lizard behavior (Baird et al., 1997; Hamilton & Sullivan, 2005; Husak & Fox, 2003). Lizards in their containers were placed inside a closed room (located near the site where lizards were collected), where they remained until experiments were conducted (Bastiaans et al., 2013, 2014). The room had large windows open (just during the day) to ambient air, permitting lizards' exposure to natural photoperiod and UV light during captivity. We placed soil and small rocks (collected from the same site as the lizards) into each container for substrate. Visual contact between lizards was prevented by placing pieces of paper, cloth, or wood on each side of each container facing containers holding other lizards (Sacchi et al., 2009); however, no more than three sides of each container were covered. Each lizard was provided a wild-caught cricket and small beetle collected at the study site; once a lizard consumed a prey item, it was provided with another of the same category. During the first weeks of captivity, it was observed that each lizard consumed 6–10 insects per week. Therefore, during weeks in which experiments were carried out, eight insects were given to each lizard per week. Water in a bowl was provided throughout the captivity period (Baird et al., 1997; Hamilton & Sullivan, 2005; Sacchi et al., 2009). Containers were cleaned once per week; prey that were not eaten were exchanged for new prey, and water was replaced. All individuals were held in captivity for at least three weeks before use in any trial (Sacchi et al., 2009). All tests were carried out at the same site lizards were collected; consequently, temperature, humidity, light intensity, and other abiotic factors were similar to field conditions, and unlikely

to explain any differences in lizard behavior (Sacchi et al., 2009). However, to limit variation in environmental conditions during experiments, all tests were conducted on warm, sunny days (20–28°C) during periods of peak daily activity for lizards (10:00–17:00 h).

## 2.3 | Female choice

Trials were performed outdoors in a square-shaped arena (1.6 m wide × 1.6 m long × 0.5 m high; Figure 1), placed directly on the natural soil of the study area. This arena was intermediate in size to that used in studies of some other (albeit somewhat smaller) phrynosomatid lizards (*U. ornatus*, Hamilton & Sullivan, 2005; *S. grammicus*, Bastiaans et al., 2014). Before the start of each trial, a single female was placed in a space ("female zone") occupying half of the total arena size. At the other end, two randomly selected adult males were placed in equal-sized spaces ("male zones") and prevented from seeing each other by way of a fixed wooden partition; thus, male behavior was directed exclusively toward the female (Kwiatkowski & Sullivan, 2002). Each male was tethered to a wooden pole by way of transparent monofilament (approx. 0.8 m in length) tied around the waist and placed in sand at a central point opposite to the female zone. Each male could move freely within the limits of its tether, but could not enter either the female zone or the other male zone. In contrast, the female was not tethered and could move freely throughout available arena space, including both male zones. Trials began once a second wooden partition in the middle of the arena was lifted, revealing both males simultaneously to the female. Trials ended when the female made a choice, which we defined as the first instance of a female either (a) approaching a male to within approximately 5–10 cm, (b) rubbing her tail on the male's body, or (c) allowing a male to copulate with her (Hamilton & Sullivan, 2005). To exclude the possibility that female decisions were random, each trial was repeated at least twice by switching the male zone into which each male was placed, providing confirmation as to whether the female was exhibiting choice for a certain male. In all trials, the time it took for the female to choose a male was recorded. The two males used in a single pair of trials were used in either two or three more trial pairs, but were not paired with the same male again; females were used in one pair of trials only (Baird et al., 1997; Hamilton & Sullivan, 2005; Kwiatkowski & Sullivan, 2002).

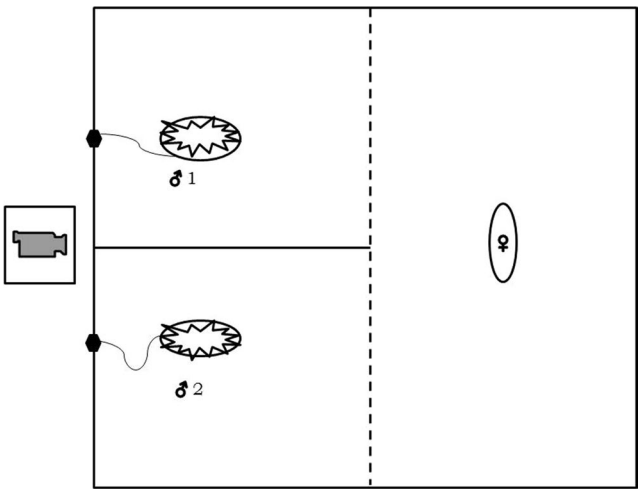


**FIGURE 1** Diagram of the experimental arena used for mate choice trials. Ovals indicate the position of male and female lizards at the start of each trial. The thin solid line between the two males indicates the position of a fixed wooden partition, and the dotted line indicates the position of a removable wooden partition. The box outside the arena shows where the video camera was placed

## 2.4 | Aggressive behavior between males

Tests were performed outdoors in a rectangular-shaped arena (0.8 m wide × 1.6 m long × 0.5 m high; Figure 2), placed directly on the natural soil of the study area. As before, given that there is no standard rule for arena size, we used an arena slightly larger than that used by Bastiaans et al. (2013) with *S. grammicus*, given that adult male *S. minor* are somewhat larger than adult male *S. grammicus* (García-Rosales, Ramírez-Bautista, & Stephenson, 2019; Ramírez-Bautista et al., 2009). The sand was divided into two halves by a vertical wooden partition positioned at the midpoint; each trial began when this partition was removed. Two males were chosen at random for use in each trial, with the condition that each male in a pair was collected from a site (i.e., its territory) at least 50 m away from that of their opponent; this helped avoid possible "dear enemy" effects on behavior (Husak & Fox, 2003; Sacchi et al., 2009). Each trial started when the partition separating the two lizards was removed, allowing lizards to interact and move throughout the arena. For each trial, all behavioral patterns exhibited by each male were recorded. First, we scored each behavior as to whether it was aggressive or not (see Table 1); for those behaviors scored as aggressive, we then assessed whether the aggressive behavior was passive or active. In passive behavior, a given response to an intruder involved no direct physical contact (García-Rosales et al., 2021), for example, performing push-ups with lateral compression ("full show") and revealing the colors of the belly and gular area (Table 1). In active behavior, a given response involved either direct physical contact (e.g., a fight) or one male rushing toward another (García-Rosales et al., 2021; Table 1). Each trial ended when one of the opponents either became inactive (i.e., no movement observed for approximately 5 min) or showed some form of submissive behavior (Table 1). Likewise, whenever one male came into direct physical contact with the other (e.g., biting), the trial was ended immediately, and the lizard that initiated the attack was determined to be the winner (Sacchi et al., 2009). Some males were used in two additional trials, but were never paired with the same opponent male again.

In both experiments, trials were recorded using a Canon Powershot SX530 camera positioned outside of the arena. The camera was supported by a tripod at a height of 150 cm, permitting a complete view of each arena (Figures 1, 2). Prior to the start of each trial, each lizard was placed into an individual chamber (Baird et al., 1997) and allowed approximately 20 min to acclimate itself to the testing space (Hamilton

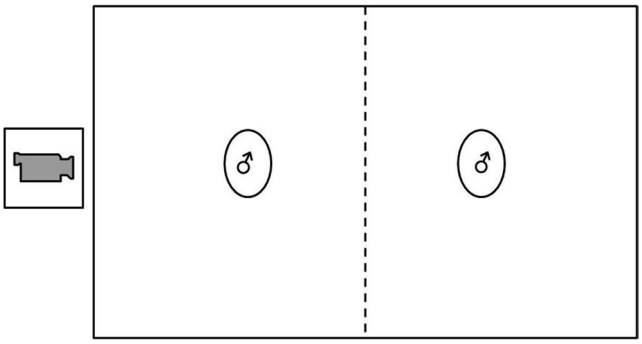

FIGURE 2 Diagram of the experimental arena used for male–male aggression trials. Ovals indicate the position of each male at the start of each trial. The dotted line indicates the position of a wooden partition that was removed at the start of each trial. The box outside the arena indicates where the video camera was placed

& Sullivan, 2005; Sacchi et al., 2009). The floor of the arena was covered with a 2-cm deep layer of sand; this sand was changed between trials in order to prevent any chemicals deposited by subjects from influencing lizard behavior in subsequent trials. Immediately after each trial ended, body temperature (BT) of each male was recorded with a Miller–Weber rapid reading thermometer (±0.2°C). After all tests were completed, each male was permanently marked via phalangeal ectomization and released at its respective site of capture. Although initially we did not intend to mark males, this was performed as part of data collection for other projects taking place at the same time. We used this permanent marking technique since multiple studies have shown that phalangeal ectomization does not affect the physiology, locomotor performance, climbing ability, reproduction, and/or survival of other lizards (Lettink & Hare, 2016; Perry et al., 2011). We also note that the study site was revisited five months later, and 80% of previously marked lizards used in this work were recaptured. All lizards used in experiments were captured within two weeks and kept in captivity for the same time (approximately two months), controlling for any effect of captivity time on experimental outcomes. All animals used were approved under collecting permit SGPA/DGVS/06183/17 issued by the Secretaría del Medio Ambiente y Recursos Naturales (SEMARNAT) of the Government of Mexico.

## 2.5 | Statistical analysis

In female choice trials, we classified males as either "chosen" or "not chosen." Differences between these groups of males were evaluated initially with a generalized discriminant function analysis (GDFA); as

TABLE 1 Ethogram of the behavior patterns observed in *Sceloporus minor* at El Enzuelado

| Behavior | Description | Category |
|---|---|---|
| Full show | A series of short hops accompanied by both lateral compressions of the body that expose the blue abdominal patches, and extensions of the throat (dewlap). Often immediately preceded by 1–4 rapid movements of the tail from one side of the body to the other | Aggression[a] |
| Push-up | Rapid movement of the body up and down due to repeated bending and straightening of the front legs. Cannot be performed while walking | Aggression[a] |
| Touch | Touching the body of the opponent with the tip of the snout | Aggression[b] |
| Aggressive bite | Grasping of the opponent with the jaws. Usually accompanied by shaking of the head from side to side | Aggression[b] |
| Approach | Movement toward an opponent while looking at the opponent | Aggression[b] |
| Chase[c] | Sprinting toward an opponent that results in displacement of the opponent | Aggression[b] |
| Escape scratches | Scratching of the walls of the chamber with the forelimbs, while facing away from the opponent | Submission |
| Retreat | Sprinting away from the opponent | Submission |
| Dorso-ventral flattening | Flattening of the body such that the ventral abdomen, throat, and limbs are all in contact with the ground | Submission or inactivity |
| Without aggression | Male shows none of the aforementioned aggression behaviors, and may even be in direct physical contact with the opponent while exhibiting no obvious aggression behavior | Without aggression |

[a]Passive aggression behavior.

[b]Active aggression behavior.

[c]Definition is that given in Stephenson and Ramírez-Bautista (2012).

these results were not significant, we analyzed the nominal variables (ventral patch coloration, dorsal coloration, and tail state) and continuous variables (all 11 morphometric variables, body mass, and body temperature) separately. The nominal variables were analyzed with a correspondence test, while the continuous variables were evaluated using factor analysis with standardized VARIMAX rotation, considering only eigenvalues greater than 1 (Budaev, 2010). For tests of male aggressive behavior, we classified each male as either a winner (= dominant), loser (= subordinate), or non-aggressive (i.e., a male that did not show any type of aggressive behavior during the trial). Similar to the first experiment, we used a correspondence test to analyze the nominal variables (ventral patch coloration, dorsal coloration, tail state, and aggressive behavior) and factor analysis to analyze the continuous variables (Budaev, 2010). We then used all variables that were highly correlated with any of the factors generated by this last analysis to subsequently perform a discriminant function analysis (DFA). Tests were considered significant if $p \leq .05$. All statistical analyzes were performed using Statistica 7.0 (StatSoft, Inc.). Means are presented as $\overline{X} \pm$ standard deviation.

## 3 | RESULTS

### 3.1 | Female choice

A total of 102 trials were performed (using 43 males and 45 females), representing 45 combinations of trial participants. Of these combinations, 31 trials were repeated only once because the female chose the same male on both occasions (i.e., 62 total trials). Twelve trials were repeated twice, since the female chose a different male in the second trial, necessitating a third trial as a tiebreaker (i.e., 36 total trials). Two trials with their respective repetitions (i.e., four total trials) were discarded; in both trial pairs, the tested female never approached either male. Therefore, analyses were restricted to the remaining 43 trial combinations, with 98 total trials. In these 98 trials, each female was scored as making a choice (latency to choice: $\overline{X} = 29.2 \pm 14.3$ min; range = 10–83 min). However, females never approached a male in a straight line; instead, they typically moved around the female zone first, before entering one or both male zones. Of the three nominal variables analyzed, only ventral patch color differed between males ($\chi^2 = 18.86$, $p = .042$). Specifically, females more frequently chose males with ventral patches of Spectrum Blue or True Blue (Figure 3), whereas males that were not chosen by females exhibited ventral patches of Smalt Blue, Ultramarine, or Dark Venetian Blue (Figure 3). On the other hand, factor analysis showed that none of the 11 morphometric variables, body mass, or body temperature differed between males (Table 2, Figure 4).

### 3.2 | Aggressive behavior between males

We conducted 43 trials using 48 males separate from those used in the female choice trials. In 21 of 43 trials (49%), a winner and loser were clearly identified based on dominant and subordinate behavior. In 20 trials (46%), neither male exhibited any type of aggressive behavior, and in two trials (5%), aggressive behavior was exhibited by both males, but a winner could not be clearly distinguished; therefore, these last two trials were removed from subsequent analyses. Of the four nominal variables analyzed among subjects of the remaining 41 trials, only aggressive behavior differed among the three groups ($\chi^2 = 139.7$, $p < .001$; Figure 5). Specifically, in trials where a winner and loser were clearly identified (21 trials), winner males more frequently showed some form of aggressive behavior (passive behavior: 14/21 trials, 66.6%; active behavior: 7/21 trials, 33.4%) as compared to losing males (passive behavior: 4/21 trials, 19%; active behavior (0/21 trials, 0%). In addition, winner males never showed submissive behavior (0/21 trials, 0%), whereas most loser males did (17/21 trials, 81%). For DFA, we used only seven morphological variables (BM, SVL, HL, HW, JL, JW, and FL) that had an association of at least 90% with one of two factors generated by the prior factor analysis (Table 3). The DFA showed that there were significant differences among the three groups analyzed (Wilks' $\lambda = 0.64$, $F_{(14,146)} = 2.55$, $p = .0026$). However, only SVL was different between groups (Wilks' $\lambda = 0.71$, $F = 4.05$, $p = .021$; Table 4). Specifically, winner males were larger ($\overline{X} = 78.5 \pm 4.6$ mm) than loser males ($\overline{X} = 74.2 \pm 6.0$ mm), and loser males were, in turn, larger than males that showed no aggression at all ($\overline{X} = 69.0 \pm 7.5$ mm; Table 3). The other six variables analyzed with DFA showed no significant differences among winners, losers, and non-aggressive males (Table 4).

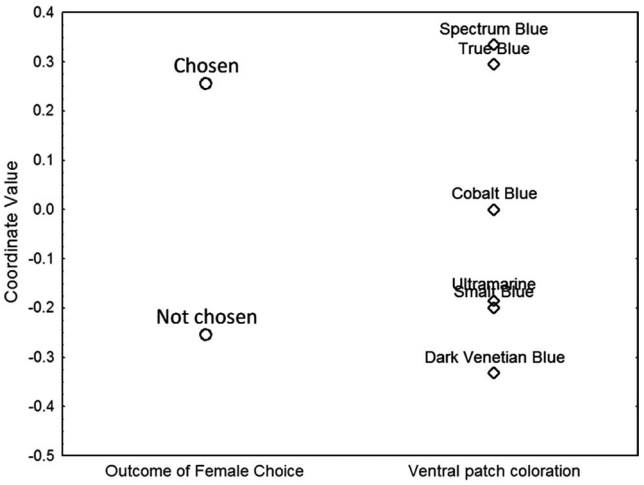


**FIGURE 3** Variation in ventral patch color of male *Sceloporus minor* in the female choice experiment and its relationship to female choice

## 4 | DISCUSSION

Many species of diurnal lizards use visual signals in social contexts; such signals typically include both postural adjustments and movements, as well as displays of conspicuous color patterns and features. Intrasexual variation in male color features often correlates

**TABLE 2** Descriptive statistics (mean ± standard deviation) of morphometric traits (SVL-VPL: mm), body mass (BM: g), and body temperature (BT: °C) used to assess differences between male *Sceloporus minor* in female choice trials, as well as the relationship between these variables and Factors 1 (EV: 9.34, Exp. Var: 71.88%) and 2 (EV: 1.25, Exp. Var: 9.6%) generated from factor analysis

| Variable | Chosen | Not chosen | Factor 1 | Factor 2 |
|---|---|---|---|---|
| SVL | 66.0 ± 8.1 | 68.1 ± 8.2 | 0.1002 | 0.0310 |
| TLL | 97.9 ± 21.5 | 98.2 ± 21.9 | −0.0355 | 0.3858 |
| HL | 15.8 ± 1.8 | 16.2 ± 1.8 | 0.1004 | 0.0266 |
| HW | 14.3 ± 1.9 | 14.8 ± 2.0 | 0.1063 | −0.0076 |
| HH | 8.6 ± 1.3 | 9.1 ± 1.3 | 0.1092 | −0.0477 |
| JL | 11.1 ± 1.1 | 11.5 ± 1.1 | 0.0981 | 0.0096 |
| JW | 12.5 ± 1.4 | 12.8 ± 1.5 | 0.1058 | 0.0031 |
| FL | 14.2 ± 1.9 | 14.9 ± 2.0 | 0.1012 | 0.0010 |
| TL | 12.3 ± 1.7 | 12.1 ± 1.1 | 0.1294 | −0.4209 |
| FOL | 9.7 ± 1.1 | 10.1 ± 1.0 | 0.0835 | 0.0680 |
| VPL | 32.4 ± 5.6 | 33.8 ± 5.5 | 0.0918 | 0.0381 |
| BM | 11.9 ± 4.4 | 12.9 ± 4.6 | 0.1066 | −0.0024 |
| BT | 28.2 ± 3.4 | 27.6 ± 2.5 | 0.0853 | −0.6673 |

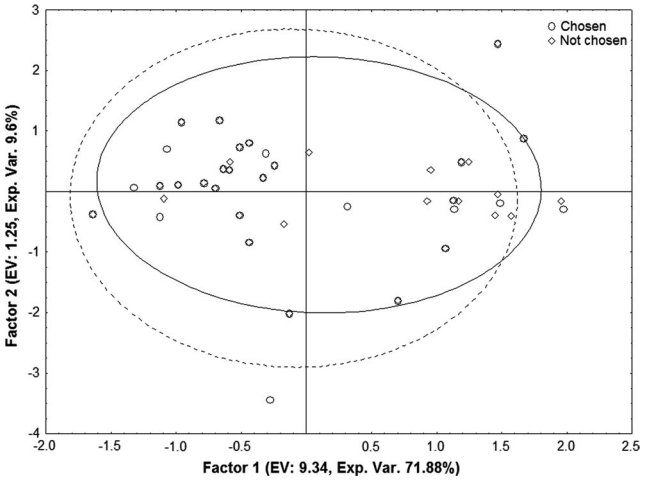


**FIGURE 4** Variation in traits following factor analysis among male *Sceloporus minor* used in the mate choice experiment. Circles = chosen males; diamonds = not chosen males

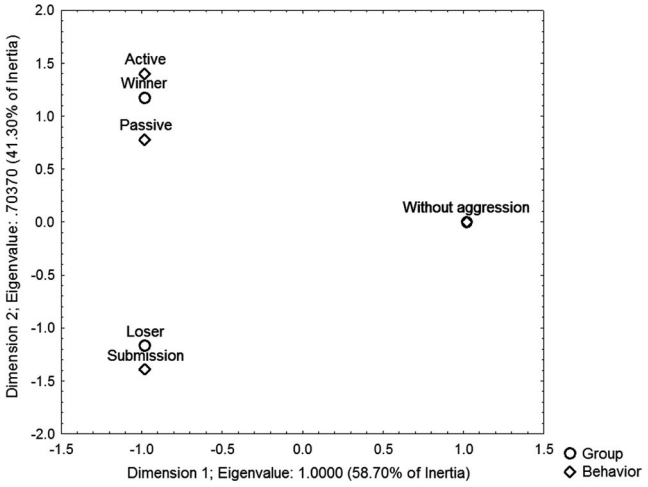


**FIGURE 5** Behavioral patterns shown by *Sceloporus minor* males and their relationship with the results of aggressive behavior experiments

with reproductive status, fighting ability, health state, and/or reproductive success (Bajer et al., 2011; Molnár et al., 2013; Olsson, 1994; Thompson & Moore, 1991). In general, males of a given species with more conspicuous coloration tend to have greater social rank, larger or higher quality territories, and/or access to a greater number of females (Fleishman et al., 2011; Font, 2002; Font et al., 2010). Variation in animal coloration can arise as the result of selection pressures of opposite sign; that is, in interactions with predators and prey, cryptic coloration is often favored, while intraspecific communication favors the expression of more conspicuous colors (Stuart-Fox & Ord, 2004). In support, many lizards show cryptic and or disruptive dorsal coloration that resembles the color features of the substrate when viewed from above, while the ventral and/or ventro-lateral region exhibits conspicuous colors revealed only during social interactions (LeBas & Marshall, 2000). In many species of the genus *Sceloporus* including *S. minor*, as well as members of closely related genera (e.g., *Urosaurus*), males express blue color on the throat and ventral abdominal patches, suggesting that blue coloration is an important characteristic of communication in these species (Wiens et al., 1999). Therefore, ventral patch coloration in *S. minor* (and other species of lizards) is likely to be important in intraspecific communication, since the presentation of these color features during relevant social interactions is often highly conspicuous, especially when coupled with postural adjustments (Cooper & Burns, 1987; Font et al., 2010). In contrast, the possible function of polymorphic male dorsal coloration in *S. minor* remains unresolved (García-Rosales et al., 2017; Stephenson, 2010). Previous studies have argued that maintenance of the color polymorphism in this population is probably not due to niche partitioning (García-Rosales, Ramírez-Bautista, & Stephenson, 2019; García-Rosales et al., 2021); furthermore, in this study, we found no effect of the polymorphism on female choice or degree of male aggressiveness. Therefore, field-based studies of reproductive physiology and behavior are needed to evaluate the proportion of morphs over a longer period of time, since the polymorphism in this population could be explained by at least two hypotheses: (1) the morphs are maintained by their different reproductive qualities, and each morph is evolutionarily stable, or (2) 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 (Pryke et al., 2007; Sinervo & Lively, 1996).

## 4.1 | Female choice

Female choice is a relatively poorly studied topic in non-avian reptiles (Bastiaans et al., 2014; Hamilton & Sullivan, 2005; LeBas & Marshall,

| Variable | Winner | Loser | Without aggression | Factor 1 | Factor 2 |
|---|---|---|---|---|---|
| SVL | 78.5 ± 4.6 | 74.2 ± 6.0 | 69.0 ± 7.5 | 0.9471 | 0.0486 |
| TLL | 98.2 ± 32.5 | 101.9 ± 28.5 | 96.6 ± 26.1 | 0.2656 | 0.4505 |
| HL | 18.1 ± 1.2 | 17.6 ± 1.4 | 16.5 ± 1.9 | 0.9462 | −0.0102 |
| HW | 16.6 ± 1.2 | 16.0 ± 1.8 | 15.1 ± 1.9 | 0.9401 | 0.1009 |
| HH | 10.1 ± 0.9 | 9.7 ± 1.3 | 9.3 ± 1.6 | 0.8823 | −0.1710 |
| JL | 12.6 ± 0.8 | 12.2 ± 1.0 | 11.6 ± 1.1 | 0.9153 | 0.0602 |
| JW | 14.5 ± 0.9 | 14.0 ± 1.1 | 13.1 ± 1.5 | 0.9839 | 0.0193 |
| FL | 17.0 ± 1.3 | 16.2 ± 1.4 | 15.2 ± 2.0 | 0.9264 | 0.1127 |
| TL | 13.0 ± 0.6 | 12.7 ± 1.2 | 12.1 ± 1.3 | 0.8826 | −0.0030 |
| FOL | 11.1 ± 0.8 | 11.0 ± 0.8 | 10.4 ± 1.2 | 0.8938 | −0.2062 |
| VPL | 39.3 ± 3.3 | 37.2 ± 3.8 | 34.5 ± 4.0 | 0.7982 | 0.1560 |
| BM | 18.2 ± 2.6 | 16.5 ± 3.6 | 13.8 ± 4.5 | 0.9741 | 0.0340 |
| BT | 28.4 ± 2.6 | 28.4 ± 2.3 | 27.9 ± 2.3 | −0.2913 | 0.8376 |

**TABLE 3** Descriptive statistics (mean ± standard deviation) of morphometric traits (SVL-VPL: mm), body mass (BM: g), and body temperature (BT: °C) used to assess the behavior of winner, loser, and non-aggressive *Sceloporus minor* males, as well as the relationship between these variables and Factors 1 (EV: 9.43, Exp. Var: 72.60%) and 2 (EV: 1.03, Exp. Var: 7.93%) generated by factor analysis

**TABLE 4** Summary statistics from the discriminant function analysis using the seven variables that were highly correlated in the factor analysis

| Variable | Wilks' λ | *F* | *p* |
|---|---|---|---|
| BM | 0.652 | 0.439 | .646 |
| SVL | 0.716 | 4.054 | .021 |
| HL | 0.652 | 0.409 | .665 |
| HW | 0.659 | 0.795 | .455 |
| JL | 0.646 | 0.065 | .937 |
| JW | 0.646 | 0.086 | .917 |
| FL | 0.649 | 0.270 | .763 |

2000; Olsson & Madsen, 1995; Tokarz, 1995), and it has been argued that the phenomenon may be rare in this vertebrate group (LeBas & Marshall, 2000; Tokarz, 1995). Indeed, overall results are mixed; evidence of female choice has been found in some studies (Bastiaans et al., 2014; Hamilton & Sullivan, 2005), but not in others (LeBas & Marshall, 2001; Olsson, 2001). Notably, in studies where female choice was found, the authors evaluated multiple traits that could be under selection, whereas studies that did not find evidence of choice generally evaluated only a single trait (Bastiaans et al., 2014; Hamilton & Sullivan, 2005; LeBas & Marshall, 2000, 2001; Olsson, 2001; Olsson & Madsen, 1995). Therefore, given both the limited number of studies on female choice in lizards overall, and of those evaluating the role of multiple potential traits simultaneously in particular, the conclusion that female choice in lizards is rare may be premature (Hamilton & Sullivan, 2005). In this study, we found that females of *S. minor* show a preference for males based on ventral patch color; specifically, females chose males with ventral patches of Spectrum Blue or True Blue (Köhler, 2012; Figure 3) over males with ventral patches of other blue hues. Hamilton and Sullivan (2005) showed that female tree lizards (*Urosaurus ornatus*) chose males on the basis of multiple morphological (head size and body mass) and coloration features (tail color and ventral patch size), and that female choice was only evident when assessing all traits simultaneously. In contrast, we only observed a difference between chosen and non-chosen males in a single character (ventral patch color) when analyzing each variable separately; when performing a combined analysis of all variables, no differences were found.

Multiple methods have been proposed for assessing female choice in lizards (Hamilton & Sullivan, 2005; Healey et al., 2008; LeBas & Marshall, 2001). However, each has important drawbacks, and there is no single most-accepted approach to analyze such data; consequently, the results of this study should also be taken with some caution.

## 4.2 | Aggressive behavior between males

In an agonistic interaction, an animal attacks its opponent (Huntingford, 2013); the purpose of this aggression was to force the opponent to leave and, in turn, permitting the winner to obtain or retain a resource (Senar, 1994). Several studies of aggressive behavior among males have shown that residence, body size, and levels of aggressiveness can determine the outcome of agonistic interactions (Bastiaans et al., 2013; Sacchi et al., 2009; Senar, 1994). Our results showed that winner males exhibited more aggressive behaviors and were larger in body size than subordinate (i.e., loser) males. Similarly, Borja (2002) demonstrated that in males of the lizard *Gallotia galloti*, winners more frequently showed aggressive deployments and were larger in body size or heavier than loser males. This same pattern was reported by Sacchi et al. (2009), who noted that body size and residence are better predictors of the outcome of a contest. Body size generally correlates with strength, endurance, and the ability to produce lesions (McEvoy et al., 2013). In addition, large body size can confer an advantage in disputes by virtue of simple size asymmetry, reducing the need for participants to extend to potentially expensive physical encounters, especially when the difference in size between contestants is relatively large (Sacchi et al., 2009; Senar, 1994).

In this study, losing males were generally small-sized individuals, which in most cases showed submission behaviors or no aggressive behavior at all. The submission behaviors shown by these smaller males can help to reduce the cost of agonistic encounters (i.e., injury or mortality during a contest, or increased risk of predation afterward; Sacchi et al., 2009; Senar, 1994). Also, those males classified as non-aggressive were smaller than winner and loser males (Table 3). A lack of aggression could be related to age; in other species, young but sexually mature males normally show lower levels of testosterone in the blood than older adult males (Pryke, 2009), which may, in turn, result in reduced aggressiveness by these younger individuals (Olsson et al., 2007; Sinervo & Lively, 1996; Teasdale et al., 2013). Other studies show that agonistic encounters in males are influenced by resource holding potential (fighting ability), as well as the value of the contested resource, such as females (Olsson, 1992; Sacchi et al., 2009; Senar, 1994). In the experiment described here, no detectable agonistic behavior was exhibited by either male in almost half of the trials. While the reasons for a lack of aggression are unclear, there are multiple possible factors. For one, we may not have provided a stimulus adequate to induce some form of aggressive behavior in all male contestants (Martin & Bateson, 2007; Senar, 1994), that is, a resource worth fighting for, such as a female, prey, or high-quality territory (Sacchi et al., 2009; Senar, 1994). Another possibility is related to male body size; non-aggressive males were relatively small (though sexually mature), and generally, smaller body size is related to lower levels of testosterone and therefore reduced aggressiveness (Pryke, 2009).

In polymorphic lizards, morphs often differ in levels of aggression and body size (Olsson et al., 2007; Sinervo & Lively, 1996; Teasdale et al., 2013; Yewers et al., 2016), and variation in these features confers advantages during agonistic encounters. It has been suggested that a blue dorsal color phenotype in *S. minor* may have evolved, at least in part, by exploitation of a preexisting sensory bias for the color blue (Wiens et al., 1999). In a test of this idea, no support was found for blue dorsal color affecting male aggressive behavior (Stephenson & Ramírez-Bautista, 2012). Similarly, we found no evidence that male dorsal coloration in *S. minor* predicted female choice or male contest outcomes; consequently, we conclude that dorsal color polymorphism in this species does not signal fighting ability, at least in the absence of females as a disputed resource. Likewise, Sacchi et al. (2009) found no relationship between ventral and throat coloration in the polymorphic wall lizard *Podarcis muralis* and male aggressive behavior or contest outcomes, suggesting that the polymorphism in *P. muralis* is not maintained by alternative territorial and/or reproductive strategies (Sacchi et al., 2009). However, behavioral experiments carried out in the field, laboratory, and semi-natural enclosures have shown contrasting results in different polymorphic species (Bastiaans et al., 2013; Olsson et al., 2007; Sinervo & lively, 1996; Thompson & Moore, 1992). For example, Bastiaans et al. (2013) noted that in studies of lizards with discrete red or orange morphs, field experiments have found increased aggression in these color morphs as compared to others (Olsson et al., 2007; Sinervo & Lively, 1996), whereas studies conducted in the laboratory or semi-natural enclosures have found that individuals with orange coloration show a decrease in aggressiveness (Bastiaans et al., 2013). However, earlier work evaluating aggressive behavior of male *S. minor* in the field showed greater aggressiveness of the yellow morph as compared to the red morph (García-Rosales et al., 2021), in contrast to the pattern reported by Bastiaans et al. (2013) in *S. grammicus*. Furthermore, in the present study, morphs from the same population as that used by García-Rosales et al. (2021) but under different conditions (semi-natural enclosures) did not exhibit differences in aggressiveness that could define agonistic encounters. Therefore, standardizing experimental methods and conditions will be necessary to generate results that can be compared across studies more robustly. Finally, the results of this study showed evidence of female choice as well as male-male competition, suggesting that in this population, males exhibit intrasexual interactions to compete for resources such as territories, and produce displays that serve in part to attract females. However, additional field observations will be needed to determine more conclusively what characters predict male territory acquisition, and what mechanisms facilitate mate attraction.

In conclusion, we found that females of *S. minor* prefer males that exhibit ventral patches with certain shades of blue (Spectrum Blue or True Blue), but found no evidence of choice based on other morphological characters examined. In addition, larger and more aggressive males were dominant over smaller and less aggressive conspecifics; however, male dorsal and ventral coloration did not predict contest outcomes. Given the variety of experimental and analytical techniques used in studies of female choice and male-male competition experiments in lizards, adoption of standardized ethological approaches should generate data that can be compared across studies more rigorously (Bastiaans et al., 2013; Hamilton & Sullivan, 2005; Healey et al., 2008).

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## CONFLICTS OF INTEREST

The authors declare that they have no conflicts of interest.

## AUTHOR CONTRIBUTIONS

All authors contributed to the study conception, design, material, preparation, and statistical analyses. Aaron García-Rosales wrote the first draft of the manuscript. Barry P. Stephenson, Aurelio Ramírez-Bautista, Javier Manjarrez, and Numa P. Pavón contributed to manuscript editing and further re-writes.

## CONSENT TO PARTICIPATE

All authors agreed to participate in this project.

## CONSENT FOR PUBLICATION

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