BEHAVIORAL ASSESSMENT REVEALS SOCIAL AGGREGATIONS IN *PETROSAURUS THALASSINUS*

EVALUACIÓN DE COMPORTAMIENTO REVELA AGREGACIONES SOCIALES EN P*ETROSAURUS THALASSINUS*

Ingrid C. Morales-Méndez[1], Makenna M. Orton[2], Janey B. Haddock[1,2], Lorena Siles-Cervantes[1], Marcia Y. Valenzuela-Molina[3], Maria A. Eifler[2], María de L. Ruiz-Gomez[1] & Douglas A. Eifler[2]

[1]*Ecology and Behavior Lab, Autonomous University of the State of México, Toluca Estado de México, 50000, México.*

[2]*Erell Institute, 2808 Meadow Drive, Lawrence, Kansas, 66047, USA.*

[3]*Instituto Tecnológico de Sonora, Antonio Caso 2266, Villa ITSON, 85130, Ciudad Obregón Sonora, México.*

*Correspondence: mdruizg@uaemex.mx

Resumen.— En un breve estudio de la lagartija endémica *Petrosaurus thalassinus*, en el Cañón de la Zorra, en la Reserva de la Biosfera Sierra La Laguna en México, a lo largo de siete días buscamos obtener un panorama preliminar de su estructura social al evaluar su comportamiento, morfología y uso de hábitat. Capturamos, marcamos y medimos 28 adultos y realizamos 19.4 horas de observaciones focales en 47 adultos marcados y no marcados en campo. Los machos tuvieron una longitud hocico-cloaca mayor a la de hembras, pero las hembras presentaron una mayor masa que los machos. Las lagartijas realizaron 30 conductas diferentes que se organizaron en ocho categorías. Los resultados resaltan la agregación de individuos en grupos de dos a cinco lagartijas, las cuales permanecían muy cerca (separados por < 1m) y en contacto visual frecuente (25/47 observaciones, 53.2%) mientras termorregulaban en rocas, o compartían espacios en grietas. Si bien las lagartijas agregadas exhibieron altos niveles de tolerancia mutua y despliegue de señales, también mostraron poca o ninguna agresión. Los individuos más grandes usaron las rocas más altas y ocuparon posiciones más altas sobre estas, pero no hubo diferencia entre sexos. Además, observamos interacciones interespecíficas de *P. thalassinus* con *Sceloporus hunsakeri* y con *Ctenosaura hemilopha*. Nuestros resultados indican que *P. thalassinus* podría tener un sistema social más complejo que el reportado en la mayoría de las lagartijas, lo que justifica una mayor investigación.

Palabras clave.— Agregaciones, lagartijas, estructura del hábitat, etograma.

Abstract.— In a brief study on the endemic lizard, *Petrosaurus thalassinus*, in the Cañon de la Zorra region of Sierra La Laguna Biosphere Reserve in Mexico, over seven days we aimed to gain a preliminary insight into their social structure by examining their behavior, morphology, and habitat use. We captured, marked, and measured 28 adults, and conducted 19.4 hours of focal observations on 47 marked and unmarked adults in the field. Males had longer snout-vent lengths than females, but females had greater mass than males of the same snout-vent length. Lizards exhibited 30 behaviors organized into eight categories. Most notably, while basking on rocks or sharing crevices they aggregated in groups of two to five individuals (< 1m apart) and in frequent visual contact (25/47 observations, 53.2%) while basking on rocks or sharing crevices. Although aggregated lizards showed high levels of mutual tolerance and signaling behavior, they exhibited little to no aggression. Larger lizards used taller rocks and took higher positions on them, but there was no difference between sexes. Furthermore, we observed *P. thalassinus* in interspecific interactions with *Sceloporus hunsakeri* and with *Ctenosaura hemilopha*. Our results indicate that *P. thalassinus* could have a more complex social system than reported for most lizards, which warrants further investigation.

Keywords.— Aggregations, ethogram, habitat structure, lizards.

INTRODUCTION

Cataloging and documenting the natural behavior of a species is imperative to providing an accurate baseline of normal behavioral expressions, as animals in captivity can exhibit behavioral alterations and anomalies (Kitchen & Martin, 1996; Morgan & Tromborg, 2007). For many species, their behavioral repertoire has been well-documented with functions and mechanisms associated with each behavior that can promote an understanding of their ecology, as well as an ability to assess sociality.

Most studies on behavior and its drivers have been carried out on birds, mammals, and insects, whereas reptile behavior studies tend to focus on the role of habitat and space use in life history. Habitat can shape the morphology and behavior of lizards (Williams, 1983; Losos et al., 1998; Goodman et al., 2008; Tulli et al., 2009), with rock-dwelling lizards tending to have flat bodies, flat heads, and short limbs (Herrel et al., 2002; Pelegrin et al., 2017). Changes in habitat structure can in turn influence and modify behavioral plasticity in lizards (e.g., Ramos & Peters, 2017).

Social behavior, which for lizards often consists of ecological aggregations, can be affected by biotic components of the habitat in combination with resource availability, as individuals that are attracted to the same environmental features are more likely to interact (Graves & Duvall, 1995; Mouton et al., 1999; Kearney et al., 2001; Mouton, 2011; Eifler & Eifler, 2014). In the wild, lizards that tend to aggregate usually share crevices, shelters, or basking and feeding sites (Mouton et al., 1999; Nieuwoudt et al., 2003; Bishop & Echternacht, 2004; Barry et al., 2014; Eifler & Eifler, 2014). When shelters and food are experimentally provided so they are not limiting resources, some individuals avoid conspecifics (Schutz et al., 2007), while others maintain aggregations (Gardner et al., 2016). Viviparous lineages of lizards are more likely to aggregate (Gardner et al., 2016; Halliwell, et al., 2017), perhaps due to delayed juvenile dispersal (Davis et al., 2011), although longevity, monogamy, and investment in chemical signaling also enhance tendencies to aggregate (Gardner et al., 2016; Baeckens & Whiting, 2021).

Proximity among individuals that facilitate aggregation also arises from mutual attraction, direct benefits (e.g., predator defense (Downes & Hoefer, 2004; Mouton, 2011), enhanced vigilance (Mouton et al., 1999), or thermoregulation (Shah et al., 2003)). More complex forms of sociality, such as parental care (Qi et al., 2012), cooperative burrow construction (McAlpin et al., 2011), or protection against infanticide (O'Connor & Shine, 2004)

can occur in lizards when the social composition of a group includes both sexes or juveniles. Nevertheless, fully interacting social groups in lizards have only rarely been observed, with true sociality documented in less than 1% of all lizard species (Gardner et al., 2016).

Petrosaurus thalassinus (Cope), the San Lucan Rock lizard, is a large, oviparous species in the family Phrynosomatidae that is endemic to rocky areas in the southern half of the Baja California peninsula. Although an iconic reptile, little is known about the species. Some insights into their reproduction, parasitic loads, thermoregulation, and genetic variability are available (Aguilars-S. et al., 1988; Jiménez & Palacios, 1999; Goldberg & Beaman, 2004; Bursey & Goldberg, 2007; Cardona-Botero et al., 2020), but their behavior in their natural environment is largely unknown. They are omnivorous and probably sit-and-wait foragers like the closely related *P. mearnsi* (De Lisle, 1991; Ardura, 2021). Adult males are generally larger than females, with body size ranging from 87 – 175 mm Snout – Vent Length (SVL) and their banded tail sometimes nearly twice as long as their body (Goldberg & Beaman, 2004). We aimed to develop a comprehensive catalog of the behavior of *P. thalassinus* based on field observations, and to gain preliminary insight into their social structure by examining the relationship between behavior, morphology, and habitat.

MATERIALS AND METHODS

Study site

During seven days (12th – 19th March 2022) we studied *P. thalassinus* in the Cañón de la Zorra, in the Sierra La Laguna. This area, located in Baja California Sur, Mexico (23.498339° N, 109.793504° W; WGS84 datum) was designated by the Mexican Government as a Protected Area (CONANP, 1994) and later, as a Global Biosphere Reserve (designated by UNESCO, 2003) (Fig. 1). Our study site (90,000 m²) was adjacent to Arroyo San Juanito, a small shallow river in a valley strewn with numerous large boulders, vegetation, and sand banks. The Sierra La Laguna is primarily a San Lucan xeric scrub ecoregion, with open forests of *Quercus tuberculata* and short shrubs of *Mimosa xanti*, *Acacia brandegeeana*, *Dodonaea viscosa*, *Tephrosia cana*, and *Bernardia lagunensis*. The climate is a tropical and subtropical desert climate (i.e., BWh) (Peel et al., 2007; Gonzalez-Abraham et al., 2010). We recorded air temperature every 300 s (from 08:30 – 14:30 h) with a temperature data logger (Tempo Disc ™ BlueMaestro) placed on a rock in full sun at the edge of the river (recorded temperature range = 12.2° – 47.8° C). We observed little cloud cover and no precipitation for the duration of the study.
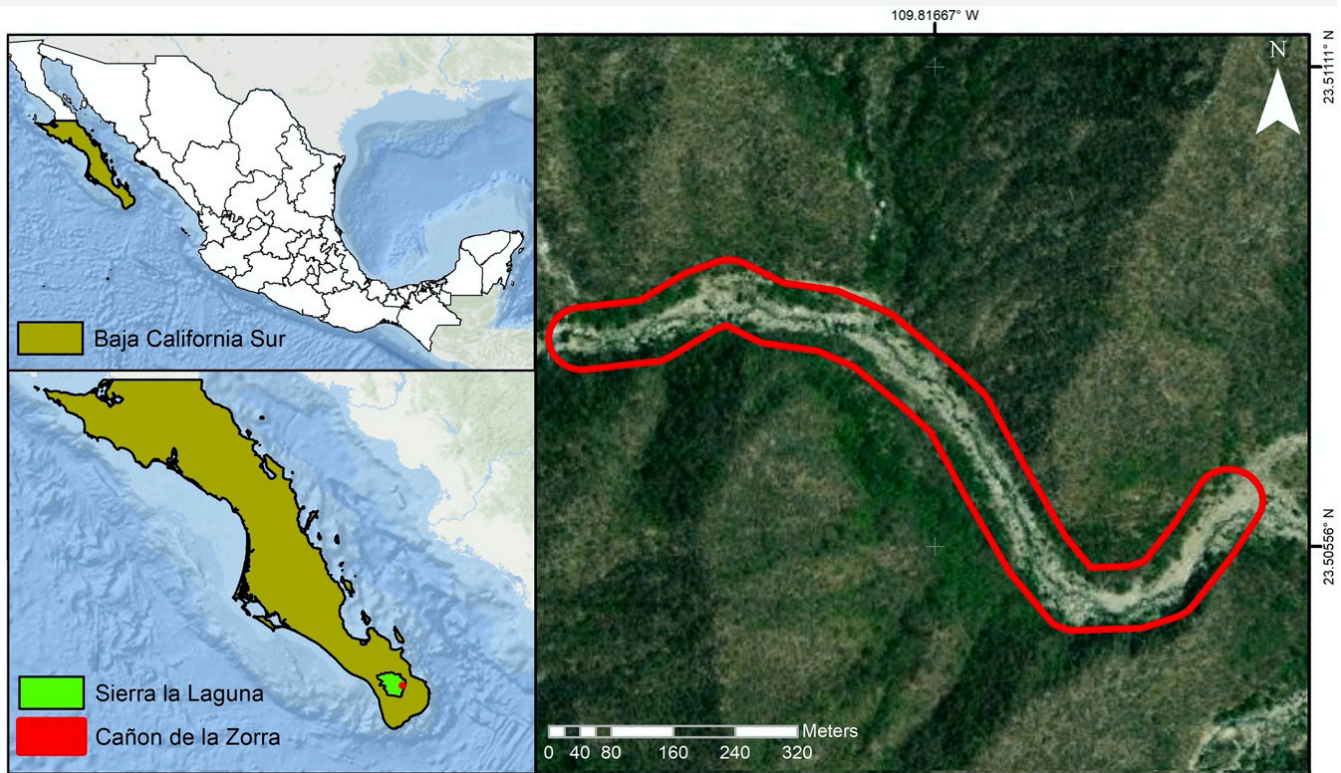
Figura 1. Área de estudio Cañón de la Zorra, localizada en el área natural protegida Sierra La Laguna, Baja California Sur, México.

Figure 1. Study Area Cañón de la Zorra (Fox Canyon), located in the Sierra La Laguna natural protected area in Baja California Sur, Mexico.

Animal capture and habitat data

We captured lizards using a small lasso attached to an extendable pole, recorded the location of their initial sighting with a hand-held GPS (Garmin Oregon 500) and marked the capture site to characterize the habitat in the afternoon of the same day. We measured all captured animals (Snout-Vent-Lenght, SVL, tail length, and mass), sexed them by probing, and uniquely marked each with nontoxic paint at the base of their tail to avoid recapture and to allow identification during behavioral observations. We always captured lizards and recorded their behavior on the rocks, almost never sighting them off rocks. After each capture, we recorded information relative to where the lizard was initially sighted: the height of the rock (= rock height; an assessment of the maximum vertical position available to lizards), the vertical position of the lizard on the rock (= height on rock; an assessment of the lizard's position relative to available vertical locations), the presence of crevices, and whether the lizard was initially sighted on a local high point.

We defined a local high point as a location from which movement in any direction resulted in a lower height on the rock. All lizards were released at their initial sighting location

within 3 – 6 h after capture and were not observed for 24 h after release. We also observed some lizards that we were unable to capture, for which we could not assign sex or assess body size. We marked areas where we first sighted lizards and did not make any additional observations of unmarked lizards in the area to avoid recording information for the same individual more than once.

Ethogram and behavioral observations

Prior to conducting focal observations, we spent several days observing animals throughout the study area to generate an ethogram. Lizards were observed with binoculars from a distance of ca. 10 – > 50 m. In addition to defining behaviors, we designated behaviors as events (by counting their occurrence) or as states (by timing their occurrence) and grouped behaviors into categories. Subsequently, from 08:30 – 14:30 h, teams of two people conducted 30-min focal observations. We conducted a total of 1165 min of focal observations on 47 lizards, 13 of which were previously marked (see above, 27.7%; n = 8 males, 5 females). We observed each lizard only once, halting observations prior to 30 min when the animal moved out of sight for > 2 min. During observations, one team member watched the focal animal
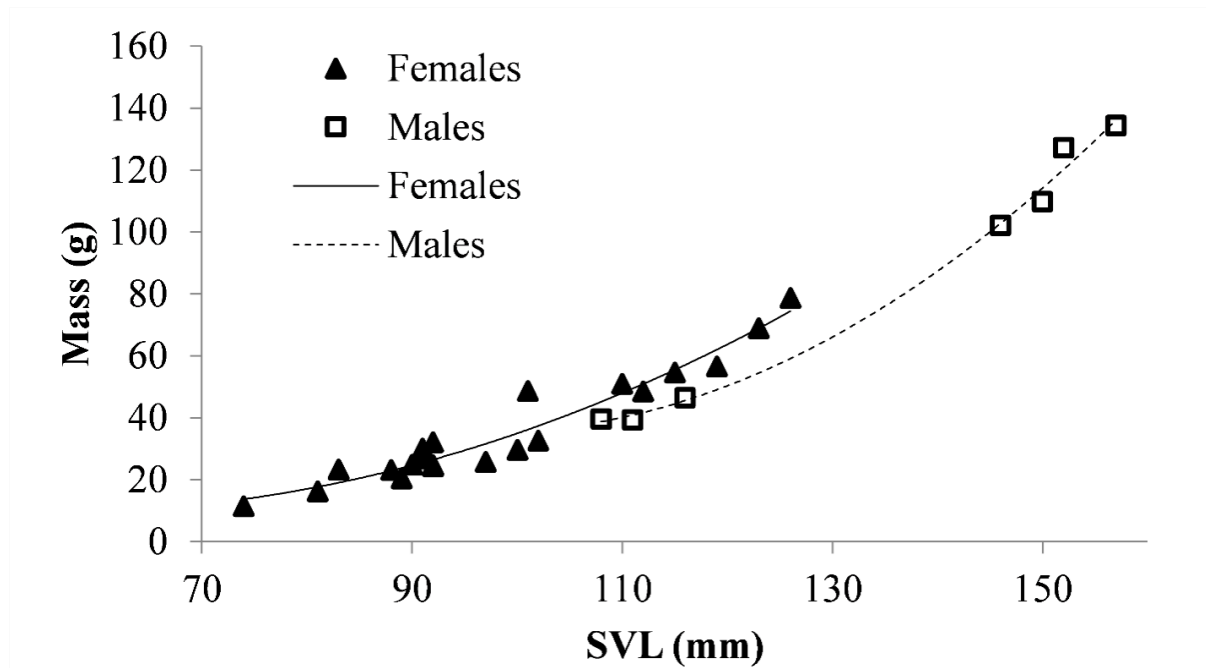
Figura 2. Relación entre masa y LHC de machos y hembras de *Petrosaurus thalassinus*. **/Figure 2.** Relationship between mass and SVL of male and female *Petrosaurus thalassinus*.

and dictated its behavior to the second team member who recorded behaviors and used a stopwatch to time the duration of behavioral states. We also noted other *P. thalassinus* within 1 m of the focal lizard (i.e., group size) and recorded details of interspecific interactions. Interactions with other species were recorded opportunistically outside of observation periods.

Statistical Analyses

We used general linear models to examine the scaling relationship for log-transformed body size (mass and SVL) by sex and to examine the relationship between rock height, height on rock, and body size (square root-transformed SVL). For general linear models, we employed stepwise selection, where SVL, sex and their interaction were considered with a threshold of $P = 0.15$ for removal. For analyses, we converted behaviors that were counted (i.e., events) into rates (per h), and behaviors that were timed (i.e., states) to percentages relative to the total observation period. We analyzed the interrelationship between the behavioral categories of movement, signals, and environmental monitoring, as well as their relationship with temperature using Pearson correlations. We tested for behavioral differences between the sexes, as well as individual lizards and those in groups using Mann-Whitney tests, considering differences significant when $P<0.05$. We used Minitab 19 (College Park, PA) for statistical analysis.

RESULTS

Body size and perch use

We captured, marked, and measured 28 adult *P. thalassinus* (21 females and 7 males). Males had longer SVLs than females (GLM, $P < 0.05$, Fig. 2). Body mass was significantly related to both SVL and sex (GLM: SVL: $F_{1,25} = 431.5$, $P < 0.001$; Sex: $F_{1,25} = 5.63$, $P = 0.026$), with females being heavier than males of similar SVL (Fig. 2). Lizards with longer SVLs perched higher on taller rocks (rock height: $F_{1,26} = 6.16$, $P = 0.02$; height on rock: $F_{1,26} = 4.39$, $P = 0.046$); neither height on rock nor rock height was related to sex. Of the 28 captured lizards, 93% (n = 26) were found on rocks with crevices, 96% (n = 27) were positioned under the canopy, and 39% (n = 11) were initially observed on a local high point. We observed 30 behaviors, which we organized into eight behavioral categories (Table 1). We observed lizards eating on a few occasions but were unable to determine the food consumed. Digging behavior was only observed in one individual, which repeatedly jumped from a rock and then dug in the same sandy location. The digging did not lead to eating, and after several iterations the lizard left the area.

The behavioral category of movement was positively correlated with the category of signals ($r = 0.243$, $P = 0.046$) and of environmental evaluation ($r = 0.642$, $P < 0.001$). None of those three categories were correlated with temperature (movement: r

Tabla 1. Etograma de los comportamientos expresados por *Petrosaurus thalassinus*, durante 1165 min de observación directa en el área natural protegida Sierra La Laguna, Baja California Sur, México. Los comportamientos separados por "/" indican pares de comportamientos que ocurrieron juntos durante una interacción.

Table 1. Ethogram of behaviors expressed by *Petrosaurus thalassinus*, obtained during 1165 min of direct observation in Sierra La Laguna natural protected area, Baja California Sur, Mexico. Behaviors separated by "/" indicate pairs of behaviors that occurred together during an interaction.

Behavioral category	Specific behavior	Definition
Agonistic	Avoidance	Lizard one turns away at the presence of lizard two
	Chase/Flee	Lizard one quickly moves towards lizard two. Lizard two moves away quickly. Lizard one pursues, following any directional changes of lizard two.
	Displacement	Lizard one moves towards lizard two. Lizard two avoids lizard one by relinquishing its location to lizard one (i.e., is displaced). Lizard one takes the position of lizard two.
Environmental Monitoring	Head turns	The head is moved (up, down, left, or right) while the body remains still.
	Head tilt	The head is rotated longitudinally while the body remains still.
	Substrate touch	The lizard touches the ground with its mouth or tongue or drags its face along the ground before returning its head to a neutral position.
Miscellaneous	Biting	The mouth is opened and then closed around a non-food object (agonistic or environmental monitoring, depending on object).
	Dig	The anterior legs scratch at the substrate creating a depression.
Feeding	Biting	The lizard consumes a food item: opening and closing its mouth repeatedly, then swallowing the food item.
Movement	Jump	Movement in which the lizard displaces its body while all four feet are off the ground.
	Moves	A shift in location of the whole body.
Postural	Back-arch	The middle of the back is raised upwards while the feet are on the ground and the head and chest are lowered to make a curved arc.
	Body dangle	The anterior portion of the lizard's body extends off the edge of a surface, such as a rock, while the posterior portion stays in contact with the surface.
	Body tilt	With its feet remaining in contact with the substrate, the lizard rolls its body along the longitudinal axis, exposing its ventral area.
	Compressed posture	The lizard lowers its body so that the ventral surface touches the substrate, giving the lizard a flattened appearance.
	Eye lick	The lizard touches their own eye with their tongue.
	Eyes closed	The eyelids are closed for more than a blink.
	Survey posture	The lizard raises the anterior part of the body and lifts the head while the posterior part of the body stays close to the ground.
	Tail move	A wave of or adjustment to the position of the tail.
	Toes-up	The lizard raises their toes off the ground while the rest of the foot remains on the ground.
	Yawn	The lizard fully opens then closes its mouth; could be a signal but unclear from context.

Tabla 1 (cont.). Etograma de los comportamientos expresados por *Petrosaurus thalassinus*, durante 1165 min de observación directa en el área natural protegida Sierra La Laguna, Baja California Sur, México. Los comportamientos separados por "/" indican pares de comportamientos que ocurrieron juntos durante una interacción.

Table 1 (cont.). Ethogram of behaviors expressed by *Petrosaurus thalassinus*, obtained during 1165 min of direct observation in Sierra La Laguna natural protected area, Baja California Sur, Mexico. Behaviors separated by "/" indicate pairs of behaviors that occurred together during an interaction.

Behavioral category	Specific behavior	Definition
Signals	Exposed throat	The lizard raises and tilts its head upwards, displaying its throat.
	Head bobs	The alternate raising and lowering of the head in a continuous motion that can be counted.
	Head shudder	A very rapid series of head bobs that are too quick to be individually counted.
	Head sway	The lizard deliberately moves its head along the horizontal plane in a fluid motion.
	Push-up	The raising and lowering of the anterior part of the body while the posterior of the body remains on the substrate and still.
	Throat expansion	The lizard inflates and then deflates the gular region. The inflation & deflation can be fast, or the inflation can last for a few s.
Social tolerancel	Crevice sharing	≥ two lizards positioned in the same rock crevice at the same time.
	Mutual tolerance	≥ two lizards are positioned within 30 cm of each other for > 30 s.
	Non-aggressive contact	≥ two lizards touch each other's bodies without force or biting.

= −0.035, P = 0.817; signals: r = −0.286, P = 0.051; environmental evaluation: r = −0.225, P = 0.128). We observed nearly all focal individuals (46/47, 98%) engaging in environmental evaluation (i.e., head turns, head tilts, and substrate touches). Head tilts (i.e., visual evaluation; n = 35/47 lizards, 74%) were positively correlated with substrate touches (i.e., chemical evaluation; n = 11/47 lizards, 23%; r = 0.520, P < 0.001). Among signaling behaviors, head bobs were especially common (n = 37/47 lizards, 79%), with one animal performing head bobs at a rate of 249.6/h (Table 2). The only behavior that differed significantly between the sexes was throat expansion, which was only seen in males (n = 5 of 8 males (63%); U = 6, P = 0.018), although we observed throat expansions in 10 lizards that we were unable to capture so were of unknown sex (n = 18; 5.89 ± 2.42 (SE), range: 0 – 46, median = 4.0). The only behaviors where individual lizards and those in groups differed were chases and nonaggressive contact, both of which can only occur for lizards in groups. Individuals spent most of their time in survey posture (= 57.5%; Table 2). When we compared single lizards to individuals in groups, we found no significant differences for any behavior (Mann-Whitney tests).

Slightly more than half of the lizards we observed (n = 25; 53%) were found interacting in conspecific groups (i.e., with individuals < 1 m apart). Of those, 52 % (n = 13) were observed interacting in pairs, 32 % (n = 8) interacted in groups of three, and 16 % (n = 4) were found in groups of four (Figs. 3 – 6). Conspecific interactions were influenced by ambient temperature, with the number of group members (r = 0.314, P = 0.032) and the percentage of time spent in a state of mutual tolerance (r = 0.287, P = 0.050) being positively, while frequency of avoidance (r = −0.301, P = 0.040) and head tilts (r = -0.376, P = 0.009) were negatively correlated with temperature. On three occasions we observed adult *P. thalassinus* involved in interspecific interactions with adult lizards of other species: 1) one *P. thalassinus* avoided one *Ctenosaura hemilopha* (Fig. 7); 2) one *P. thalassinus* shared a rock for ca. 5 min with one *C. hemilopha*, with the two ca. 60 cm apart and apparently in visual contact. During the interaction, the *P. thalassinus* did push-ups and head bobs; and 3) one *P. thalassinus* shared a rock with one *Sceloporus hunsakeri* (Fig. 8), with the two ca. 80 cm apart for ca. 2 min before both moved to a local high point on a different rock that they also shared, remaining ca. 60 cm apart for ca. 5 min.

Figure 3 (up). Dos ejemplares de *Petrosaurus thalassinus* en tolerancia mutua en una grieta. Fotografía de Marcia Valenzuela.

Figura 3 (arriba). Two *Petrosaurus thalassinus* showing mutual tolerance in a crevice. Photo by Marcia Valenzuela.

Figure 4 (right). Secuencia de la interacción entre dos hembras marcadas y un individuo de tamaño grande sin marcar de *Petrosaurus thalassinus*. a) un individuo sin marcar en la postura de vigilancia, posado en una posición más alta sobre una roca en comparación con dos hembras marcadas ubicadas más abajo en la misma roca. b) el individuo sin marcar bajó y se mantuvo cercano a las dos hembras marcadas. Fotografía de Marcia Valenzuela.

Figura 4 (derecha). Sequence of the interaction between two marked females and a larger unmarked individual of *Petrosaurus thalassinus*. a) an unmarked individual in survey posture, perched higher on a rock compared to two marked females located lower on the rock. b) the unmarked individual ran down and stayed in close proximity to the two marked females. Photo by Marcia Valenzuela.

Figura 5. Área rocosa donde se observaron cinco *Petrosaurus thalassinus* próximos, cuatro de los cuales se muestran en la foto. La agrupación no se identificó durante las observaciones focales y los individuos no cumplieron con nuestra distancia de interacción, por lo que el grupo no se incluyó en los análisis. Fotografía de Marcia Valenzuela.

Figure 5. Rocky area where we noted five proximate *Petrosaurus thalassinus,* with four pictured. The assemblage did not occur during focal observations and individuals did not meet our interaction distance, so the aggregation was not included in analyses. Photo by Marcia Valenzuela.

Figura 6. *Petrosaurus thalassinus* (izquierda) en una grieta (i.e., evitando), en respuesta a la presencia de un *Ctenosaura hemilopha* (derecha). Fotografía de Marcia Valenzuela.

Figure 6. *Petrosaurus thalassinus* (left) in a crevice (i.e., in avoidance) in response to the presence of a *Ctenosaura hemilopha* (right). Photo by Marcia Valenzuela.

DISCUSSION

Ethogram

Our study provides baseline information on the behavior and natural history of *P. thalassinus*. A small subset of the behaviors defined in our ethogram (Table 1), primarily from the categories of movement, signaling, or environmental monitoring, accounted for most of the activity we observed during our study, possibly as individuals evaluated and responded to their social environment and habitat (Watters, 2009; Steinberg et al., 2014). Other behaviors occurred infrequently, probably due to the short duration of our study as well as the nature of *P. thalassinus* foraging, as sit-and-wait lizards are generally inactive (Huey & Pianka, 1981). Additionally, adult phrynosomatids are only rarely observed foraging and most frequently are immobile, with the main behaviors recorded for other species falling into our postural or signal categories (Watters, 2009).

Sex differences

We found no measurable differences in behavior between the sexes, except in incidents of throat expansion, although our conclusions are limited by the small number of animals that we were able to capture and sex. Nevertheless, we were able to document differences between males and females in body size and basic habitat use. Males of *P. thalassinus* were longer than females, but females were heavier than males of the same length (Fig. 2).

Similar mixed body-size differences between the sexes have been found in other lizard species, possible due to phylogeny or to reproduction (Cox et al., 2007). Gravid females can be heavier than males due to the presence of eggs (Cox et al., 2007; López Juri et al., 2018); our study corresponded with the reproductive season for *P. thalassinus* (Goldberg & Beaman, 2004), which could account for our mixed body-size measurements. Body mass and SVL measurements are needed at other times of the year to verify whether the trend we found continues outside the breeding season and to interpret sexual size dimorphism in the species. Although we did not detect sex differences in habitat use, body size was related to both the size of rocks on which we found lizards (i.e., rock height) and the position of the lizards on the rocks (i.e., height on rock). A similar pattern in *Anolis*

Figura 7. Interacción interespecífica (tolerancia mutua) entre *Petrosaurus thalassinus* (izquierda) y *Sceloporus hunsakeri* (derecha). Fotografía de Marcia Valenzuela.

Figure 7. Interspecific interaction (mutual tolerance) between a *Petrosaurus thalassinus* (left) and a *Sceloporus hunsakeri* (right). Photo by Marcia Valenzuela.

homolechis was attributed to urbanization and to the presence of predators (Vidal et al., 2023). Although Cañón de la Zorra is not urbanized, the site is frequented by eco-tourists. Vigilance from high perching sites could help individuals monitor the environment better and make them less prone to predatory attacks or human disturbance (Vidal et al., 2023).

Tabla 2. Tasas (media± SE), rangos y medianas de los comportamientos específicos más frecuentes observados en *Petrosaurus thalassinus* en Sierra La Laguna. Debido a que no se observaron diferencias entre sexos, se muestran los datos para todos los animales (n = 47).

Table 2. Rates (mean ± SE), ranges, and medians of the most frequent specific behaviors observed in *Petrosaurus thalassinus* in Sierra La Laguna. Because there were no differences between the sexes in behavior, data are combined for all animals (n = 47).

Variable	Mean ± SE	Range	Median
Head bobs h−1	30.4 ± 6.6	0.0, 249.6	15.9
Head shudder h−1	3.5 ± 1.3	0.0, 47.3	0.0
Head tilt h−1	10.3 ± 1.5	0.0, 33.5	6.0
Head turn h−1	50.9 ± 4.8	0.0, 159.6	42.0
Jumps h−1	4.9 ± 0.9	0.0, 25.1	2.8
Moves h−1	39.8 ± 5.8	0.0, 169.3	28.0
Push up h−1	15.6 ± 3.4	0.0, 116.3	6.0
Substrate touch h−1	1.5 ± 0.5	0.0, 16.2	0.0
Survey posture (%)	57.5 ± 4.5	0.0, 100.0	58.1

AGGREGATIONS

Intraspecific interactions

The behaviors we observed and recorded indicate that *P. thalassinus* individuals are more social than previously realized, similar to what has been found in *P. mearnsi* (De Lisle, 1991). We recorded interactions, most of them non-aggressive, frequently seeing individuals in aggregations and positioned close to each other. In addition, we repeatedly found the same sets of marked individuals sharing crevices and observed some of the marked lizards interacting repeatedly (Figs. 3 – 5). We observed infrequent displacements, which are indicators of a dominance hierarchy, and we did not observe individuals defending an area, reducing the likelihood that *P. thalassinus* is a territorial species (Effenberger & Mouton, 2007). However, because we captured, sexed, and marked relatively few individuals in the population, we cannot speak definitively to their space use or social system. Besides the possibility of social attraction, the aggregations we observed could be due to resource limitation or habitat structure.

The preferred habitat of *P. thalassinus* contained tall rocks with crevices, which seemed to be unevenly distributed and limited in availability. Both the distribution of resources and a reliance on concentrated but limited resources can contribute to animal aggregations (Gardner et al., 2016; Garrison et al., 2016). When habitats contain limited numbers of appropriate rocks with crevices, groups can form when individuals congregate in suitable refugia (Chapple, 2003; Michael et al., 2010). As for other lizard species, sharing habitat resources by living in groups would be beneficial for *P. thalassinus* (Effenberger & Mouton, 2007; Whiting & While, 2017).

Diet, predator pressure, ontogenetic stage, temperature, and season also could contribute to their tendency to form non-aggressive aggregations (Lemos-Espinal et al., 1997; Ruby, 1997; Chapple, 2003; Watters, 2009; Steinberg et al., 2014; Johnston et al., 2020). More detailed studies of the habitat structure, resource distribution and availability, and social connectedness in *P. thalassinus* in Sierra La Laguna are needed to understand the nature of their social relationships and to determine the causes underlying their aggregations. Social animals can use multimodal signals to convey information (Hews & Martins, 2013); for *P. thalassinus*, we determined that behaviors allowing visual evaluation of the environment (i.e., head tilts) were related to behaviors that allow chemical evaluation of the habitat.

Further studies thoroughly evaluating the social components of communication are also merited. In terms of sampling design, our distance metric to define animals aggregating into a group was 1 m. Distance between individuals considered proximate is rarely reported, with the occurrence of aggregations based on an observer's subjective assessment and often defined as crevice sharing, shelter sharing, or basking together (Halliwell et al., 2017). Given that we observed individuals signaling to each other or responding to disturbance from people at distances >1 m (e.g., Fig. 6), individual *P. thalassinus* were likely to be aware of each other's presence at greater distances than our conservative metric of 1 m. If individuals are aware of and respond to each other at distances > 1 m, future studies should consider a broader definition of proximity to better understand the extent of social aggregations.

Interspecific interactions

Interactions between *P. thalassinus*, *Ctenosaura hemilopha* and *Sceloporus hunsakeri* (Figs. 7 & 8) could occur as a result of limited resources in their shared habitat (Sillero & Gomes, 2016), as all three species prefer rocky habitats and both *C. hemilopha* and *P. thalassinus* perch high on rocks, close to refuges such as holes or crevices (Blízquez & Rodríguez-Estrella, 1997; Grismer, 2002; present study). We observed both avoidance and mutual tolerance among the three species, but a more thorough evaluation of interspecific interactions and the extent to which they partition habitat resources is merited.

CONCLUSIONS

The array of behavioral traits we recorded included social signals, movements, and environmental evaluation (Table 1). In combination with their tendency for intra- and interspecific social tolerance in the form of sharing rocks and crevices, indications are that *P. thalassinus* might be more social and behaviorally complex than previously thought. Future, large-scale studies focused on the role of habitat structure and food resources in group formation and maintenance, as well as a thorough social analysis of *P. thalassinus*, would shed light on a potentially nuanced and intricate social system in lizards.

CITED LITERATURE

Aguilars-S, M.A., J.W. Sites Jr. & R.W. Murphy. 1988. Genetic variability and population structure in the lizard genus *Petrosaurus*. Journal of Herpetology 22:135-145.

Ardura, A.C. 2021. New visual records of plants consumed by 10 lizard species on islands of the Gulf of California, and implications for the insular ecology and trophic webs. Revista Latinoamericana de Herpetología 4:23-52.

Baeckens, S. & M.J. Whiting. 2021. Investment in chemical signaling glands facilitates the evolution of sociality in lizards. Proceedings of the Royal Society B: Biological Sciences 288:20202438.

Barry, M., U. Shanas & D.H. Brunton. 2014. Year-round mixed-age shelter aggregations in Duvaucel's geckos (*Hoplodactylus duvaucelii*). Herpetologica 70:395-406.

Bishop, D.C & A.C. Echternacht. 2004. Emergence behavior and movements of winter-aggregated green anoles (*Anolis carolinensis*) and the thermal characteristics of their crevices in Tennessee. Herpetologica 60:168-177.

Blízquez, M.C. & R. Rodríguez-Estrella. 1997. Factors influencing the selection of basking perches on cardon cacti by spiny-tailed iguanas (*Ctenosaura hemilopha*). Biotropica 29:344-348.

Bursey, C.R. & S.R. Goldberg. 2007. New species of *Parapharyngodon* (Nematoda: Pharyngodonidae) and other helminths in *Petrosaurus repens* and *P. thalassinus* (Squamata: Phrynosomatidae) from Baja California Del Sur, Mexico. The Southwestern Naturalist 52:243-250.

Cardona-Botero, V.E., R.A. Lara-Resendiz & P. Galina-Tessaro. 2020. Field and selected body temperatures of the San Lucan rock lizard (*Petrosaurus thalassinus*) in Baja California, Mexico. Herpetology Notes 13:485-486.

Chapple, D.G. 2003. Ecology, life-history, and behavior in the Australian scincid genus *Egernia*, with comments on the evolution of complex sociality in lizards. Herpetological Monographs 17:145-180.

Cox, R.M., M.A. Butler & H.B. John-Alder. 2007. The evolution of sexual size dimorphism in reptiles. Pp. 38–49. In Fairbairn, D.J., W.U. Blanckenhorn & T. Székely (Eds.), Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford University Press. New York, New York, USA.

Davis, A.R., A. Corl, Y. Surget-Groba & B. Sinervo. 2011. Convergent evolution of kin-based sociality in a lizard. Proceedings of the Royal Society B: Biological Sciences 278:1507-1514.

De Lisle, H.F. 1991. Behavioral ecology of the banded rock lizard (*Petrosaurus mearnsi*). Bulletin, Southern California Academy of Sciences 90:102-117.

Downes, S. & A.M. Hoefer. 2004. Antipredatory behaviour in lizards: interactions between group size and predation risk. Animal Behaviour 67:485-492.

Effenberger E. & P. Le FN Mouton. 2007. Space use in a multi-male group of the group-living lizard. Journal of Zoology 272:202-208.

Eifler, D.A. & M.A. Eifler. 2014. Social foraging in the lizard Ameiva corax. Behavioral Ecology 25:1347-1352.

Gardner, M.G., S.K. Pearson, G.R. Johnston & M.P. Schwarz. 2016. Group living in squamate reptiles: a review of evidence for stable aggregations. Biological Reviews 91:925-36.

Garrison, G., M. Phillips, M. Eifler & D. Eifler. 2016. Intraspecific variation in opportunistic use of trophic resources by the lizard *Ameiva corax* (Squamata: Teiidae). Amphibia-Reptilia 37:331-334.

Goldberg, S.R. & K.R. Beaman. 2004. Reproduction in the San Lucan banded rock lizard, *Petrosaurus thalassinus* (Phrynosomatidae) from Baja California Sur, Mexico. Bulletin, Southern California Academy of Sciences 103:147-150.

González-Abraham, C. E., P. Garcillán, & E. Ezcurra. 2010. Ecorregiones de la península de Baja California: una síntesis. Boletín de la Sociedad Botánica de México. 87: 69-82.

Goodman, B.A., D.B. Miles & L. Schwarzkopf. 2008. Life on the rocks: habitat use drives morphological and performance evolution in lizards. Ecology 89:3462-3471.

Graves, B.M. & D. Duvall. 1995. Aggregation of squamate reptiles associated with gestation, oviposition, and parturition. Herpetological Monographs 9:102-119.

Grismer, L.L. 2002. Amphibians and reptiles of Baja California, Including its Pacific Islands and the Islands of the Sea of Cortés. University of California Press, Berkeley, California, USA.

Halliwell, B., T. Uller, B.R. Holland & G.M. While. 2017. Live

bearing promotes the evolution of sociality in reptiles. Nature Communications 8:2030.

Herrel, A., J.J. Meyers & B. Vanhooydonck. 2002. Relations between microhabitat use and limb shape in Phrynosomatid lizards. Biological Journal of the Linnean Society 77:149-163.

Hews, D.K. & E.P. Martins. 2013. Visual and chemical signals of social communication: providing the link to habitat and environment. Pp. 111-141. In Lutterschmidt, W. (Ed.), Reptiles in Research: Investigations of Ecology, Physiology, and Behavior from Desert to Sea. Nova Science Publishers, Inc., Hauppauge, New York, USA.

Huey, R.B. & E.R. Pianka. 1981. Ecological consequences of foraging mode. Ecology 62:991-999.

Jiménez, M.L. & C. Palacios. 1999. Incidencia de la chinche piedrera (*Dipetalogaster maximus*) (Hemiptera: Heteroptera: Reduviidae) vector de *Tripanosoma cruzi* en zonas urbanas de La Paz, Baja California Sur, México. Anales del Instituto de Biología Serie Zoología 70:215-221.

Johnston, G. R., E. J. Lanham, & C. M. Bull. 2020. United in adversity: Aridity and cold influence aggregation behaviour in social lizard, *Egernia stokesii*. Austral Ecology 45:418-425.

Kearney, M., R. Shine, S. Comber & D. Pearson. 2001. Why do geckos group? An analysis of "social" aggregations in two species of Australian lizards. Herpetologica 57:411-422.

Kitchen, A.M. & A.A. Martin. 1996. The effects of cage size and complexity on the behaviour of captive common marmosets, *Callithrix jacchus jacchus*. Laboratory Animals 30:317-326.

Lemos-Espinal, J. A., R. E. Ballinger, S. S. Sarabia, & G. R. Smith. 1997. Aggregation behavior of the lizard *Sceloporus mucronatus mucronatus* in Sierra del Ajusco, México. Herpetological Review 28: 126-127.

López-Juri, G., M. Chiaraviglio & G. Cardozo. 2018. Macroevolution of sexual size dimorphism and reproduction related phenotypic traits in lizards of the Chaco Domain. BMC Evolutionary Biology 18:186.

Losos J.B., T.R. Jackman, A. Larson, K. de Queiroz & L. Rodríguez-Schettino. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. Science 279:2115-2118.

McAlpin, S., P. Duckett & A. Stow. 2011. Lizards cooperatively tunnel to construct a long-term home for family members. PloS One 6:e19041.

Michael, D.R., R.B. Cunningham & D.B. Lindenmayer. 2010. The social elite: habitat heterogeneity, complexity and quality in granite inselbergs influence patterns of aggregation in *Egernia striolata* (Lygosominae: Scincidae). Austral Ecology 35:862-870.

Morgan K.N. & C.T. Tromborg. 2007. Sources of stress in captivity. Applied Animal Behaviour Science 102:262-302.

Mouton, P. Le FN., A.F. Flemming & E.M. Kanga. 1999. Grouping behaviour, tail-biting behaviour and sexual dimorphism in the armadillo lizard (*Cordylus cataphractus*) from South Africa. Journal of Zoology 249(1):1-10.

Mouton, P. Le FN. 2011. Aggregation behaviour of lizards in the arid western regions of South Africa. African Journal of Herpetology 60:155-170.

Nieuwoudt, C., P. Le FN Mouton & A. Flemming. 2003. Aggregation behaviour and movement patterns in the large-scaled girdled lizard, *Cordylus macropholis*. Amphibia-Reptilia 24:345-357.

O'Connor, D.E. & R. Shine. 2004. Parental care protects against infanticide in the lizard *Egernia saxatilis* (Scincidae). Animal Behaviour 68:1361-1369.

Peel, M.C., B.L. Finlayson & T.A. McMahon. 2007. Updated world map of the Köppen-Geiger climate classification. Hydrology and Earth System Sciences 11:1633-1644.

Pelegrin, N.A., D.O. Mesquita, P.A. Albinati, F.L.S. Caldas, L.B. de Queiroga Cavalcanti, T.B. Costa, D.A. Falico, J.Y.A. Galdino, D.B. Tucker & A.A. Garda. 2017. Extreme specialization to rocky habitats in *Tropidurus* lizards from Brazil: Trade-offs between a fitted ecomorph and autoecology in a harsh environment. Austral Ecology 42:677-689.

Qi, Y., D.W. Noble, J. Fu & M.J. Whiting. 2012. Spatial and social organization in a burrow-dwelling lizard (*Phrynocephalus vlangalii*) from China. PLoS One 7:e41130.

Ramos, J. A. & R. A. Peters. 2017. Habitat-dependent variation in motion signal structure between allopatric populations of lizards. Animal Behaviour 126:69-78.

Ruby, D. E. 1997. Winter Activity in Yarrow's Spiny Lizard, *Sceloporus jarrovi*. Herpetologica. 33:322-333.

Schutz, L., D. Stuart-Fox & M.J. Whiting. 2007. Does the lizard *Platysaurus broadleyi* aggregate because of social factors? Journal of Herpetology 41:354-359.

Shah, B., R. Shine, S. Hudson & M. Kearny. 2003. Sociality in lizards: why do thick-tailed geckos, *Nephrurus milii*, aggregate? Behaviour 140:1039-1052.

Sillero, N. & V. Gomes. 2016. Living in clusters: the local spatial segregation of a lizard community. Basic and Applied Herpetology 30:61-75.

Steinberg, D.S., J.B. Losos, T.W. Schoener, D.A. Spiller, J.J. Kolbe & M. Leal. 2014. Predation-associated modulation of movement-based signals by a Bahamian lizard. Proceedings of the National Academy of Sciences 111:9187-9192.

Tulli, M.J., F.B. Cruz, A. Herrel, B. Vanhooydonck & V. Abdala. 2009. The interplay between claw morphology and microhabitat use in neotropical iguanian lizards. Zoology 112:379-392.

Vidal, A., R. Pradel & F. Cézilly. 2023. Do suburban populations of lizards behave differently from forest ones? An analysis of perch height, time budget, and display rate in the Cuban endemic *Anolis homolechis*. Diversity 15:261.

Watters, J.L. 2009. Daily activity budgets for neonate and adult *Sceloporus jarrovii* and adult *Sceloporus virgatus* in southeastern Arizona. Journal of Herpetology 43:665-675.

Whiting, M.J & G.M. While. 2017. Sociality in lizards. Pp. 390–426. In D.R. Rubenstein & P. Abbot (Eds.), Comparative Social Evolution. Cambridge University Press, Cambridge, UK.

Williams, E.E. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of Anolis. Pp. 326–370. In R.B. Huey, E.R. Pianka & T.W. Schoener (Eds.), Lizard Ecology: Studies of a Model Organism. Harvard University Press, Cambridge, Massachusetts, USA.