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POPULATION DYNAMICS OF THE LIZARD *Riama striata* (SQUAMATA: GYMNOPHTHALMIDAE) IN AN URBAN AREA OF THE COLOMBIAN HIGHLANDS

Dinámica Poblacional del Lagarto *Riama striata* (Squamata: Gymnophthalmidae) en un área urbana de las montañas colombianas

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ABSTRACT

Urbanization causes transformations in wildlife habitat, provoking alterations in the population dynamics which results in declines and local extinctions. However, some studies in Andean gymnophthalmid lizards highlight the occupation of highly transformed habitats, suggesting a possible urban tolerance in some species. Here we show a case study using capture-mark-recapture sampling on two populations of the endemic Colombian lizard *Riama striata*, each facing different anthropic pressures. Despite urbanization, *Riama striata* maintains stable population growth and diverse demographic strategies. Populations differed in survival rates, rate transition from juvenile to adult, and population sizes and densities. The most important size class and demographic processes contributing to λ were adults, and stasis and growth, respectively. Also, in relative terms, stasis was larger than growth in one population, while fecundity was more important to λ in the other population. Our results demonstrate that this species can maintain small but stable populations in urban environments with the presence of artificial refuges. Furthermore, we highlight the importance of grasslands and shelter microhabitats for the population viability of the lizard *R. striata,* and we suggest conducting more studies on other tropical Andean lizards to assess the impacts of human disturbance in urban lizard species.

Keywords: Artificial refuges, Fast-Slow continuum, Human disturbance, Population ecology, Urban ecology.

RESUMEN

La urbanización causa transformaciones en el hábitat de la fauna silvestre que generan alteraciones en la dinámica poblacional, haciéndolas más propensas a declives y extinciones locales. Sin embargo, algunos estudios de lagartijas andinas de la familia Gymnophthalmidae resaltan la capacidad de estas especies para ocupar hábitats altamente transformados, sugiriendo una posible tolerancia a hábitats urbanos. Presentamos un estudio de caso usando el método de captura-marca-recaptura en dos poblaciones de la lagartija *Riama striata* sometidas a diferentes presiones antrópicas. Aunque ambas poblaciones presentaron un crecimiento poblacional estable, mostraron estrategias demográficas diferentes. Las poblaciones difirieron en las tasas de supervivencia, la tasa de transición de juveniles a adultos, y los tamaños y densidades poblacionales. La clase de tamaño más importante y los procesos demográficos que más contribuyeron a λ fueron los adultos, y la permanencia y el crecimiento, respectivamente. Además, en términos relativos, la permanencia fue más importante para λ en una población, y el crecimiento y la fecundidad más importantes para λ en la otra población. Nuestros resultados demuestran que esta especie es capaz de mantener poblaciones pequeñas pero estables, y establecerse con éxito en entornos urbanos donde existan refugios artificiales. Adicionalmente, resaltamos la importancia de los pastizales y microhábitats de refugio para la viabilidad poblacional de *R. striata*, y sugerimos realizar más estudios en otros lagartos andinos tropicales para evaluar los impactos del disturbio humano en especies de lagartijas urbanas.

Palabras clave: Continuo rápido-lento, Disturbio humano, Ecología de poblaciones, Ecología urbana, Refugios artificiales.

INTRODUCTION

Human disturbance has proven to be a significant factor in lizard demography, altering the vital rates of populations living in habitats affected by cover loss, fragmentation, or urbanization-related cover changes (Hokit and Branch, 2003; Moreno-Arias and Urbina-Cardona, 2013; Wolf et al., 2013). Some populations of the green anole *Anolis carolinensis* Voigt 1832 and the legless lizard *Anniella pulchra* Gray 1852 exhibit tolerance to urban landscapes, using human-made structures as new microhabitats. However, in newly urbanized landscapes, their occurrence, reproduction, and survival decrease when compared to populations in non-urban landscapes (Rodewald and Gehrt, 2014). In contrast, there are lizard species, such as the house gecko *Hemidactylus frenatus* Duméril and Bibron 1836, which are urban resource exploiters. They thrive by effectively utilizing resources available in new urban landscapes, leading to higher population densities in urban areas compared to non-urban regions (Rodewald and Gehrt, 2014). On the other hand, lizards like the McCann skink *Oligosoma maccanni* (Hardy, 1977) exhibit consistent survivorship when utilizing artificial retreats (Lettink et al., 2008, 2010).

Population dynamics of lizards from Neotropical highlands are poorly known, but few studies report that some populations show different demographic responses. Previous studies in Central America mountains report considerable interannual fluctuations in population growth where the transition from juvenile to adults, as a vital rate, and small adults, as a size class, contributed the most to the fitness of *Sceloporus mucronatus mucronatus* Cope 1885 (Ortega-León et al., 2007). In contrast, geographically widespread populations of *Sceloporus grammicus* Wiegmann 1828 show demographic stability over time. Adult stasis and large adults contribute significantly to fitness as vital rates and size classes, respectively (Zúñiga-Vega et al., 2008). More recently, Vargas-García et al. (2019) showed that survival of both sexes in *S. torquatus* Wiegmann 1828 decreased during the cold-dry season while no such decline was observed in *S. grammicus* nor *Sceloporus megalepidurus* Smith 1934. During the rainy season, *S. grammicus* showed a high recruitment rate whereas *S. megalepidurus* showed a low rate. Recruitment in *S. torquatus* was high in both dry and rainy seasons.

In the South American mountains, lowland populations of *Anolis mariarum* Barbour 1932 exhibit higher multimodel-average survivorship compared to their high-altitude counterparts, despite the best model indicating no differences between populations. They also show higher male survivorship than females but maintain a stable reproductive output despite the differences in altitude or the contrast between dry and rainy seasons (Bock et al., 2010; Rubio-Rocha et al., 2011). In *Anolis heterodermus* Duméril 1851 and *Anolis richteri* (Dunn, 1944), Moreno-Arias and Urbina-Cardona (2013) have demonstrated how landscape configuration favors changes in demographic strategies: populations inhabiting small habitat patches tend to mature early, while those in larger patches experience delayed maturation. In landscapes with low fragmentation and habitat loss, population dynamics are more stable.

The endemic lizard species, *Riama striata* (Peters, 1863) inhabits the Andean region of Colombia, where it can colonize anthropogenic environments (Méndez-Galeano and Pinto-Erazo, 2018) (Fig. 1a-1c). Recent data on its natural history (Méndez-Galeano, 2020) suggest that this lizard is a good study model to explore the demographic response of lizards across urban-dominated landscapes. Populations of *R. striata* have been found at the campus of the National University of Colombia in Bogotá City (Méndez-Galeano and Pinto-Erazo, 2018), hence, this locality holds significant importance for the conservation and research of this species. Therefore, this study aimed to characterize the population dynamics of the lizard *R. striata* living in two anthropic-transformed sites within Bogotá city.

MATERIALS AND METHODS

STUDY SITE

The study was carried out at the campus of the National University of Colombia in Bogotá city (4°38' N; 74°04' W, 2560 m a.s.l.), department of Cundinamarca, Colombia. The study site is characterized by a bimodal rainfall regime, having rain peaks in April-May and October-November (Moreno-Arias and Urbina-Cardona, 2013), the mean annual rainfall is 901.6 mm, and the mean annual temperature is 14.9 °C (IDEAM, 2019). For this study, a systematic sampling method was used to define the potential distribution of each population in two discrete areas mostly covered by *Cenchrus clandestinum* grass (Hochst ex. Chiov) with each area separated by a main street on the Campus, hereafter referred to as the Agronomy and Cinema populations. In terms

Figure 1. Some individuals of the high-Andean lizard *Riama striata* (Squamata: Gymnophthalmidae). a. a female, b. a male, c. a juvenile. Photos: Daniel Vivas-Barreto

of the capture-recapture sampling, we delimited a sampling quadrat of 900 m2 in each area, based on the locations where the highest lizard abundance was observed (Fig. 2). Both sampling quadrats are separated by an approximate distance of about 700 m, and both have natural refuges, such as rocks and trunks, as well as artificial refuges, including bricks, pieces of concrete, wooden tables and pieces of metal (Fig. 2a-2b). Furthermore, the sampling quadrats showed different anthropic pressures: in the Cinema there was the presence of cattle grazing, a higher number of people walking through the area, the Cinema building and the campus stadium, and many cement bricks, while in Agronomy equine grazing, agricultural activities in greenhouses and some bricks were observed. Additionally, Agronomy experienced occasional flooding, especially during the rainy season.

SAMPLING

In 2016, two researchers (MAM and MAP) actively searched for individuals and captured them by hand, under shelters, or between the grass and walls of buildings (Méndez-Galeano, 2020). We sampled for half an hour per quadrant per day during the diurnal activity period of the species (Méndez-Galeano, 2020). We conducted a capture-mark-recapture (CMR) sampling defined by twelve primary occasions, one associated with each month, with four secondary occasions (sampling days) per month (except for September, which included five secondary occasions). The total sampling effort of 49 hours/per person per quadrant. To mark the specimens, the toe clipping technique was used using a code adapted for all twenty toes of the lizards (Hero,

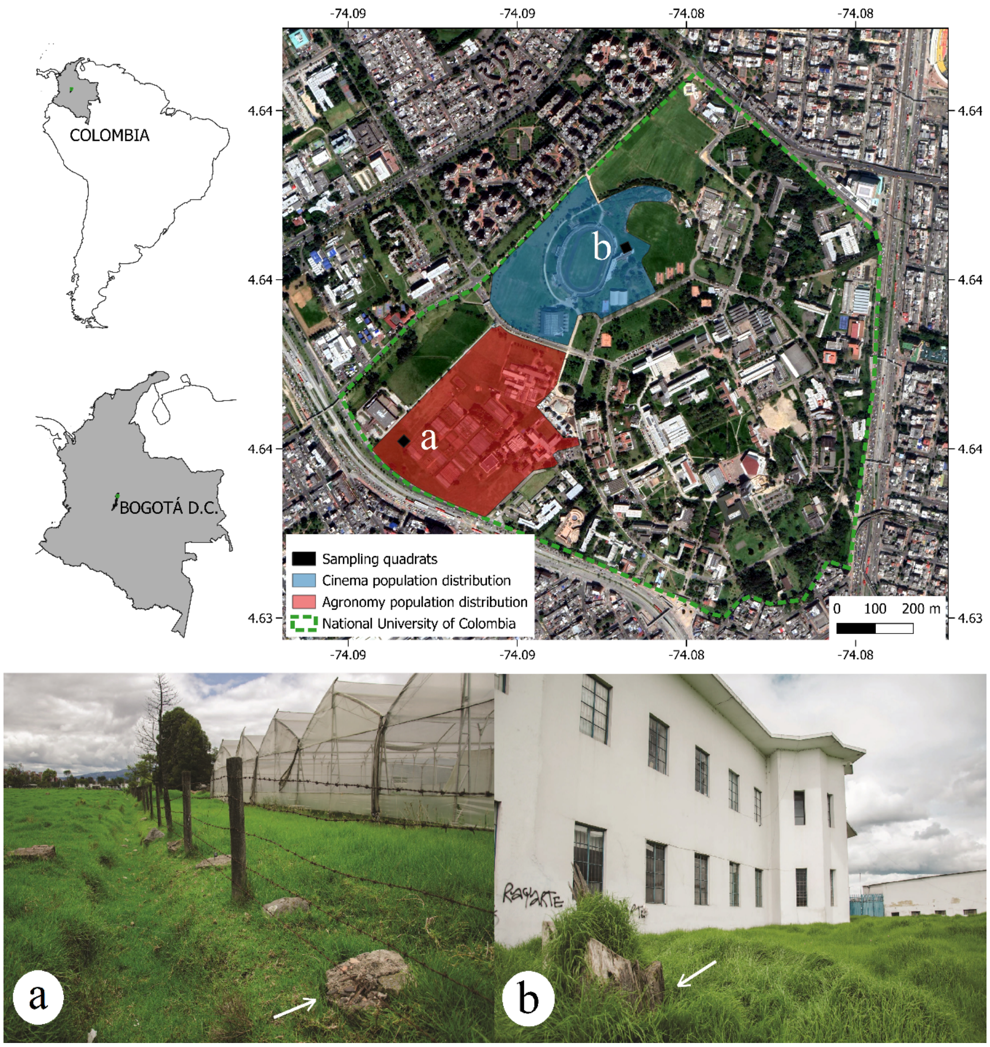

Figure 2. Top. Sampling quadrats and distribution of Agronomy and Cinema R. striata populations at National University Campus. Bottom. Habitats of R. striata populations at National University Campus. Arrows show shelter microhabitats. a. Agronomy, b. Cinema. Photos: MAP; extracted and modified from Méndez-Galeano y Pinto-Erazo (2018).

1989). This method follows the scientific and ethical guidelines required for demographic studies and does not affect the survival of the organisms (Perry et al., 2011). Likewise, no specimen was marked on three or more phalanges, as research has shown that the ectomization of several phalanges can negatively affect individual survival (Olivera-Tlahuel et al., 2017).

We measured snout-vent length (SVL) using a digital caliper (precision 0.05 mm). To establish the population structure, we defined juvenile and adults as size categories based of sexual maturity minimum sizes defined in Méndez-Galeano y Pinto-Erazo (2018), and also determined the sex of adult individuals as follows: adult males were identified as lizards with SVL > 50 mm and five or more femoral pores, while females where those with SVL > 46 mm and less than five femoral pores (Méndez-Galeano and Pinto-Erazo, 2018; Méndez-Galeano, 2020). After data collection, each animal was released, and recaptures were recorded as they occurred.

POPULATION DYNAMICS ANALYSES

To determine whether the population could be assumed as a single or a dual spatially structured population, we tested the degree of connectivity between sites (Cinema and Agronomy). This assessment involved estimating the probability of individual migration between them using a Robust Multistate Model included in MARK 6.2 software (White and Burnham, 1999) with each site corresponding to a state and state transitions (Ψ) representing the movement of individuals between sites. Therefore, we conducted 14 models to illustrate different degrees of transition (Table S1 Supporting information). For all subsequent analyses, we assumed the sampling sites as two independent populations during study period based on multiple lines of evidence: (1) the more supported model indicated no movement of individuals between sites ($\Psi = 0$), (2) no recaptures between sites, (3) the presence of a road between the sites, which based on Strayer et al. (2003), can be defined as a tangible anthropogenic ecological boundary with a finite thickness (10 m) and an extension of around 300 m. This road is characterized by a distinct structure (pavement) that separates the two grassland areas with the species' refuge microhabitats, and (4) the low vagility reported in semifossorial high-Andean gymnophthalmids (Doan et al., 2021).

To determine the population dynamics, we also used the same Robust Multistate approach but instead of transitions between sites we used transitions between size classes (juvenile and adults). We conducted and tested 40 models to estimate the vital rates of each size class covering the hypothesis of variation, constant or variable on time according to the monthly and seasonal precipitation (Dry: months with a rainfall ≤ to annual rainfall average; Wet: months with a rainfall > to annual rainfall average) (Table S2 Supporting information). For CMR both modeling, data adjustment was tested with U-CARE 2.3 (Choquet et al., 2005) and the corrected Akaike information criterion (Burnham and Anderson, 2004) was used to choose the model that best explained the encounter history (White and Burnham, 1999) discarding models with less fit ($\Delta AICc > 2$) compared with the fittest model (minimum AICc value). The parameter values and their variation, estimated by the best model, were determined based on their posterior distribution after 15 000 simulations using MCMC. This procedure is recommended for models that estimate several parameters–such as multistate models, which tend to fail in local minimum values (Lebreton and Pradel Cefe, 2002; Brown et al., 2006; Cooch and White, 2019).

The values of transition and survival rates, stasis ($S^*[1-\Psi]$), growth ($S^*\Psi$), and monthly population size were calculated for each population. The potential reproductive output of 24 eggs per female in the study period was estimated based on: (1) a two-eggs nest size reported for microteiids (Shine and Greer, 1991), (2) a conservative clutch-size trend in lizards (Kratochvíl and Kubička, 2007), and (3) on the monthly nesting behavior by females, as observed in other Andean Gymnophthalmidae and Alopoglossidae species (Ramos-Pallares et al., 2010; Jerez and Calderón-Espinosa, 2014; Ramos-Pallares et al., 2015; Calderón-Espinosa et al., 2018). Therefore, the fecundity value was calculated with the equation for populations with continuous reproduction and structured size classes (Caswell, 2001).

The fitness value of each population was measured via the population growth rate (λ), which was estimated through matrix population models. The stasis, growth, and fecundity values were extracted from the projection matrix to construct a one-year transition matrix (Lefkovitch, 1965) for each population. Confidence intervals of λ were estimated following the analytical procedure suggested by Alvarez-Buylla and Slatkin (1994). Since the elasticity values, ranging from zero to one (indicating less important to more importance) for each matrix element reflect the relative importance of each element influencing the λ value (Caswell, 2001), an elasticity analysis was carried out using PopTools 2.3 software (Hood, 2019) to detect the most important demographic processes (growth, stasis, and fecundity) and size classes affecting λ. Finally, differences in demographic strategies were identified graphically using a demographic triangle (Silvertown et al., 1992) and lifecycle graphs for each population.

RESULTS

A total of 108 individuals were captured (11.5 ± 2.7 per primary occasion), and 31 individuals were recaptured (0.8 ± 1.1 per primary occasion). In the Cinema population, 40 individuals were registered, while 68 were found in the Agronomy population. In Cinema, 31 individuals were captured once, six individuals twice, and three individuals three or more times. In Agronomy, 56 individuals were captured once, ten individuals twice, and two individuals three or more times. Relative abundance in Cinema ranged from 0.03 ind/m2 (in August and October) to 0.33 ind/m2 (in May), and for Agronomy ranged from 0.1 ind/m2 (in February) to 0.5 ind/m2 (in November). The adult proportion was higher than the juvenile proportion in both populations (Cinema: 0.62, Agronomy: 0.53) but the size structure was not significantly different between populations ($X2 = 0.9261$, df = 1, $p = 0.33$). The sex ratio was consistent between populations ($X2 = 0.0058$, df = 1, $p = 0.94$) with a ratio of 1.6 female/male.

The model that best represented the migration between sites, based on the encounter history, showed the same overall recapture probability and the same adult and juvenile capture probabilities between populations. However, it differed across juvenile and adult survivals, as well as the transition from juvenile to adult (Table 1). Additionally, adult and juvenile survival varied between populations (only slightly in juvenile survival) and survival varied between juveniles and adults (Table 1). Furthermore, the estimated population size was higher in Agronomy (155 ± 46 individuals, 50 ± 7 juveniles, and 105 ± 39 adults) than in Cinema (93 ± 33 individuals, 21 ± 4 juvenile, and 73 ± 29 adults). Likewise, the population density was also higher in Agronomy (6.7 + 0.3 lizards) than in Cinema (4.1 + 0.2 lizards).

Changes in population size throughout the year were similar for both populations, with an increase from February to May followed by a decrease until July, and a second increase up to November. However, Agronomy showed a faster increase than Cinema in the second part of the year (Fig. 3). Nevertheless, we did not find any seasonal or monthly (precipitation effect) variations in adult or juvenile survival, or size class transition between populations.

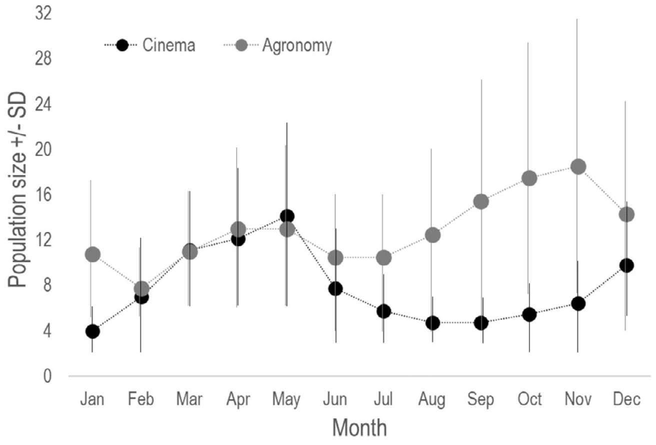

Figure 3. Annual dynamic of Riama striata populations from National University Campus.

Table 1. Vital rates and capture/recapture probabilities for both populations of *Riama striata* (Peters 1963). Standard Deviation values in parentheses.

Parameter	Cinema	Agronomy
Juvenile Survival	0.21 (0.03)	0.28 (0.04)
Adults Survival	0.67 (0.01)	0.43 (0.01)
Transition from juvenile to adult	0.54 (0.10)	0.26 (0.07)
Juvenile capture probability	0.32 (0.002)	
Adults capture probability	0.11 (0.001)	
Recapture probability	0.05 (0.007)	

The results shown in (Fig. 4) indicate that adults' stasis value was higher in Cinema compared to Agronomy. Additionally, adults' stasis values were higher for both localities when compared to juvenile stasis values. Also, fecundity and growth values were higher in Cinema than in Agronomy.

Importantly, the growth population rate λ was different between populations, where λ in Cinema has a growth (1.26), while in Agronomy has a negative growth (0.91). Nevertheless, the 95 % CI in both populations suggested growth at equilibrium (Agronomy: 0.41 – 1.41; Cinema: 0.82–1.69). The most important size class and demographic processes affecting λ were the Adults, and Stasis and Growth in both populations, respectively (Fig. 4). However, in relative terms, Stasis was larger than Growth in Cinema compared to Agronomy, and Fecundity was more important to λ in Agronomy compared with Cinema (Fig. 4). Despite the differences mentioned above, both populations suggested a stable structure with a larger proportion of juveniles (0.8) compared to adults (0.2).

DISCUSSION

Studies in demography and population dynamics of lizards living in urban-disturbed habitats, as well as species from Neotropical highlands have increased in the last decade, especially for *Sceloporus* and *Anolis* genera (Ballinger and Congdon, 1981; Gomez and Acosta, 2001; Endriss et al., 2007; Bock et al., 2010; Moreno-Arias and Urbina-Cardona, 2013; Wolf et al., 2013; Pérez-Mendoza and Zúñiga-Vega, 2014; Pérez-Mendoza et al., 2014; Rodewald and Gehrt, 2014; Bock et al., 2016; Vargas-García et al., 2019). In this context, our study makes several noteworthy contributions with demographic data of *Riama striata,* a species that is becoming a good model species to evaluate ecological traits and population parameters in human-modified landscapes. The population viability of this species is achieved through two different demographic strategies, with 1) growth and 2) stasis as the most important processes affecting each population's fitness.

Fitness value for both populations was similar, with stasis and growth as the most important demographic processes, and adults as the most important size class influencing the population growth rate (λ). However, stasis and fecundity elasticity values, as well as survival rates, were different between populations. The observed demographic pattern of *R. striata* aligns with the Fast-slow continuum hypothesis, which posits that adult mortality has a strong influence on life history traits, in which populations with high mortality present low stasis and high fecundity (fast strategy), whereas populations with low mortality the opposite (slow strategy) (Promislow and Harvey, 1990). In this sense, the Agronomy population tends to lean towards the fast side, while the Cinema population leans towards the slow side of the demographic strategies continuum. For this reason, if both populations are under similar conditions of habitat disturbance, it is important to identify the potential factors that could change vital rates and produce divergent demographic strategies between populations.

Previous studies suggested that at high latitudes, or elevations, lizard populations will tend to adopt a slow strategy (in which survival and stasis increase, and fecundity and growth decrease) due to constraints on lizard's activity and reproduction caused by high seasonal variability in rainfall and humidity (Ballinger and Congdon, 1981; Jones et al., 2008). Current data on lizards fail to provide evidence for any ubiquitous trend in the population dynamics of highland species. Instead, a plethora of demographic responses have been found in several studies, depending on the studied species and localities in which they are found (e. g. Ortega-León et al., 2007; Zúñiga-Vega et al., 2008; Bock et al., 2010; Rubio-Rocha et al., 2011; Vargas-García et al., 2019). Our results are consistent with the idea that population dynamics could be more correlated with habitat conditions or ecological interactions at local scales than with conditions at historical and geographical scales, as previously documented (Moreno-Arias and Urbina-Cardona, 2013).

In this sense, our data do not support statistical seasonal or monthly variation (or precipitation effect) in the vital rates of *R. striata* studied populations. However, a growth trend in the population sizes was observed in the rainy seasons, with Agronomy growing faster in the second rainy season, and

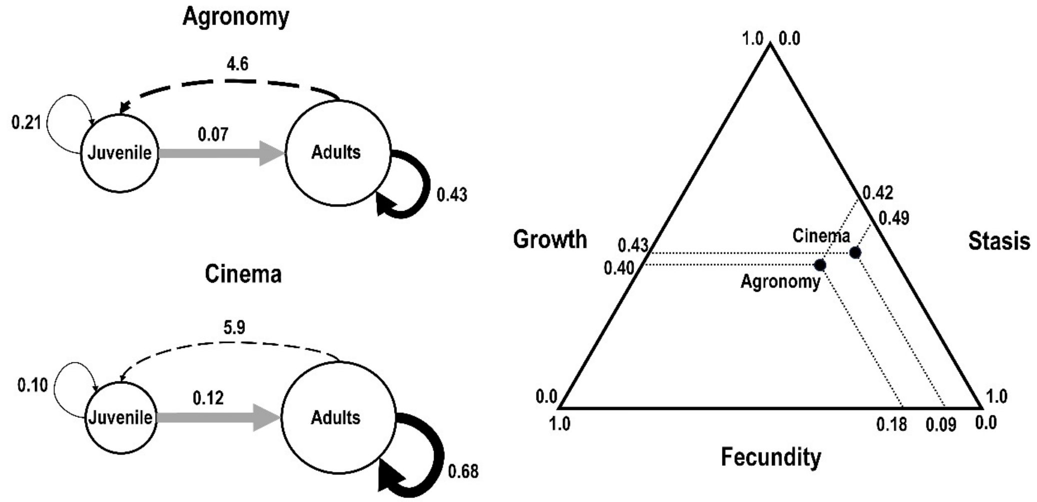

Figure 4. Lifecycle graphs (left) and position on the demographic triangle (right) of each R. striata population. Black solid arrows indicate stasis, grey solid arrows indicate growth and dotted lines indicate fecundity. The size of ovals and arrows indicates the relative importance for each size class and demographic process for λ. The numbers above arrows indicate the estimated value of each transition in the life cycle. Elasticity values are indicated in the demographic triangle.

this difference could be related to humidity conditions (e.g. soil moisture) of both sites (Cinema and Agronomy). This scenario could be the local analog of the reported effects of altitude and latitude on humidity and their impact on lizard demography (Ballinger and Congdon, 1981; Jones et al., 2008). This "local humidity" hypothesis warrants further investigation in future terrestrial, fossorial, and semifossorial lizard studies. Additionally, rainfall and wet seasons can also influence food abundance, by increasing arthropod availability and subsequently affecting growth (Vogel, 1984; Barrows, 2006), which was faster in Agronomy in the second rainy season.

On the other hand, habitat loss and fragmentation (Berglind, 2000; Hokit and Branch, 2003; Wiegand et al., 2005; Moreno-Arias and Urbina-Cardona, 2013; Walkup et al., 2017), including cover replacement by urbanization (Wolf et al., 2013; Walkup et al., 2017) can modify vital rates, demographic strategies, and population sizes, leading in some cases to local extinctions. In this context, *R. striata* is a low-mobility lizard with a high shelter fidelity (Méndez-Galeano, 2020) that seems to be an urban-tolerant species (Rodewald and Gehrt, 2014). Moreover, studied populations inhabit very restricted areas that offer both natural and artificial shelter microhabitats (Méndez-Galeano, 2020). These shelters provide protection against grazing and may also offer other resources, such as thermal niches, reproductive sites, or food sources (Gomez and Acosta, 2001; Méndez-Galeano, 2020).

However, the population with the greatest urbanization and human presence (Cinema) has the smallest population size and the slowest growth during the second rainy season, which aligns with predictions related to habitat fragmentation (Wiegand et al., 2005). A population with a small size and slow growth may be ill-equipped to face high-intensity disturbances, potentially increasing its susceptibility to local extinction (Moreno-Arias and Urbina-Cardona, 2013). Importantly, the urban tolerance and demographic plasticity of the studied populations of *R. striata*, which manage to keep their population growth rates (λ) at equilibrium, should not be confused with attributes of urban-exploiters species (Pérez-Mendoza et al., 2014; Rodewald and Gehrt, 2014). The loss of grasslands or removal of shelter microhabitats in these populations may lead to their extirpation (Berglind, 2000; Méndez-Galeano, 2020).

Conservation strategies are urgently needed to preserve these unique lizard populations within Bogotá city, as well as other adjacent or outlying *R. striata* populations. These efforts should start with the protection of shelter microhabitats and maintenance of grassland cover, especially in sites with high human activity, such as Cinema (Méndez-Galeano, 2020). Additionally, demographic studies of other high-elevation gymnophthalmids, such as the co-distributed vulnerable species *Anadia bogotensis* (Peters 1863) (Jerez and Calderón-Espinosa, 2014; Calderón-Espinosa et al., 2018), will improve our understanding about the population dynamics of high-Andean lizards.

CONCLUSIONS

This study demonstrates that the gymnophthalmid lizard *Riama striata* can maintain small but stable populations in urban environments, despite exhibiting different demographic strategies, for example, in terms of vital rates, as well as processes contributing to λ. We hypothesized that local variations in humidity levels across seasons, rather than elevational or latitudinal differences in humidity, could be influencing the population dynamics of this and other highland lizard species. Moreover, habitat loss and fragmentation may also impact the observed population traits. Finally, grasslands with shelter microhabitats seem to be crucial for the population viability of *R. striata* populations. Further studies on the populations of this and other Andean lizards are necessary to assess the effects of human disturbance on highland urban lizard species.

AUTHOR CONTRIBUTION

MAM, RAM, MAP conception, design, data acquisition, analysis, and writing manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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MATERIAL SUPLEMENTARIO / SUPPLEMENTARY MATERIAL

SUPPLEMENTARY MATERIAL ARTICLE: POPULATION DYNAMICS OF THE LIZARD *Riama striata* (SQUAMATA: GYMNOPHTHALMIDAE) IN AN URBAN AREA OF THE COLOMBIAN HIGHLANDS

Material suplementario artículo: Dinámica Poblacional del Lagarto *Riama striata* (Squamata: Gymnophthalmidae) en un área urbana de las montañas colombianas

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Table S1. Assessed models to estimate migration between the study sites. S = survival rate. Ψ = transition probability between sites. Pent = - probability of entry onto the study area at time *t*. Phi = probability of remaining on the study area *s* at time *t*, given that the animal had previously entered the study area. p = capture probability given that the animal is on the study area at time *t*.

Model	AICc	Delta AICc	AICc Weight	Likeli-hood	Para-meters	2 Log (L)
S_{Cinema} (.) S_{Agronomy} (.) $\Psi_{\text{Cinema to Agronomy}} = \Psi_{\text{Agronomy to Cinema}}$ (0) $\text{Pent}_{\text{Cinema}}$ (.) $\text{Pent}_{\text{Agronomy}}$ (.) $\text{Phi}_{\text{Cinema}}$ (.) $\text{Phi}_{\text{Agronomy}}$ (.) $p_{\text{Cinema}} = p_{\text{Agronomy}}$ (.)	654.9	0.0	0.33	1.00	7	640.1
S_{Cinema} (.) S_{Agronomy} (.) $\Psi_{\text{Cinema to Agronomy}} = \Psi_{\text{Agronomy to Cinema}}$ (0.001) $\text{Pent}_{\text{Cinema}}$ (.) $\text{Pent}_{\text{Agronomy}}$ (.) $\text{Phi}_{\text{Cinema}}$ (.) $\text{Phi}_{\text{Agronomy}}$ (.) $p_{\text{Cinema}} = p_{\text{Agronomy}}$ (.)	655.0	0.1	0.31	0.95	7	640.2
S_{Cinema} (.) S_{Agronomy} (.) $\Psi_{\text{Cinema to Agronomy}} = \Psi_{\text{Agronomy to Cinema}}$ (0.01) $\text{Pent}_{\text{Cinema}}$ (.) $\text{Pent}_{\text{Agronomy}}$ (.) $\text{Phi}_{\text{Cinema}}$ (.) $\text{Phi}_{\text{Agronomy}}$ (.) $p_{\text{Cinema}} = p_{\text{Agronomy}}$ (.)	655.9	0.9	0.20	0.62	7	641.1
S_{Cinema} (.) S_{Agronomy} (.) $\Psi_{\text{Cinema to Agronomy}} = \Psi_{\text{Agronomy to Cinema}}$ (.) $\text{Pent}_{\text{Cinema}}$ (.) $\text{Pent}_{\text{Agronomy}}$ (.) $\text{Phi}_{\text{Cinema}}$ (.) $\text{Phi}_{\text{Agronomy}}$ (.) $p_{\text{Cinema}} = p_{\text{Agronomy}}$ (.)	657.2	2.2	0.11	0.33	8	640.1
S_{Cinema} (.) S_{Agronomy} (.) $\Psi_{\text{Cinema to Agronomy}} = \Psi_{\text{Agronomy to Cinema}}$ (.) $\text{Pent}_{\text{Cinema}}$ (.) $\text{Pent}_{\text{Agronomy}}$ (.) $\text{Phi}_{\text{Cinema}}$ (.) $\text{Phi}_{\text{Agronomy}}$ (.) p_{Cinema} (.) p_{Agronomy} (.)	659.4	4.5	0.03	0.11	9	640.1
S_{Cinema} (.) S_{Agronomy} (.) $\Psi_{\text{Cinema to Agronomy}}$ (.) $\Psi_{\text{Agronomy to Cinema}}$ (.) $\text{Pent}_{\text{Cinema}}$ (.) $\text{Pent}_{\text{Agronomy}}$ (.) $\text{Phi}_{\text{Cinema}}$ (.) $\text{Phi}_{\text{Agronomy}}$ (.) p_{Cinema} (.) p_{Agronomy} (.)	661.7	6.8	0.01	0.03	10	640.1
S_{Cinema} (.) S_{Agronomy} (.) $\Psi_{\text{Cinema to Agronomy}} = \Psi_{\text{Agronomy to Cinema}}$ 0.1 $\text{Pent}_{\text{Cinema}}$ (.) $\text{Pent}_{\text{Agronomy}}$ (.) $\text{Phi}_{\text{Cinema}}$ (.) $\text{Phi}_{\text{Agronomy}}$ (.) $p_{\text{Cinema}} = p_{\text{Agronomy}}$ (.)	663.5	8.6	0.00	0.01	7	648.7
S_{Cinema} (.) S_{Agronomy} (.) $\Psi_{\text{Cinema to Agronomy}} = \Psi_{\text{Agronomy to Cinema}}$ (0.2) $\text{Pent}_{\text{Cinema}}$ (.) $\text{Pent}_{\text{Agronomy}}$ (.) $\text{Phi}_{\text{Cinema}}$ (.) $\text{Phi}_{\text{Agronomy}}$ (.) $p_{\text{Cinema}} = p_{\text{Agronomy}}$ (.)	670.2	15.3	0.00	0.00	7	655.4
S_{Cinema} (.) S_{Agronomy} (.) $\Psi_{\text{Cinema to Agronomy}} = \Psi_{\text{Agronomy to Cinema}}$ (0.5) $\text{Pent}_{\text{Cinema}}$ (.) $\text{Pent}_{\text{Agronomy}}$ (.) $\text{Phi}_{\text{Cinema}}$ (.) $\text{Phi}_{\text{Agronomy}}$ (.) $p_{\text{Cinema}} = p_{\text{Agronomy}}$ (.)	684.9	30.0	0.00	0.00	7	670.1
S_{Cinema} (.) S_{Agronomy} (.) $\Psi_{\text{Cinema to Agronomy}}$ (.) $\Psi_{\text{Agronomy to Cinema}}$ (.) $\text{Pent}_{\text{Cinema}}$ (.) $\text{Pent}_{\text{Agronomy}}$ (.) $\text{Phi}_{\text{Cinema}}$ (.) $\text{Phi}_{\text{Agronomy}}$ (.) $p_{\text{Cinema*session}}$ (.) p_{Agronomy} (session)	691.2	36.3	0.00	0.00	32	608.8
S_{Cinema} (.) S_{Agronomy} (.) $\Psi_{\text{Cinema to Agronomy}}$ (.) $\Psi_{\text{Agronomy to Cinema}}$ (.) $\text{Pent}_{\text{Cinema}}$ (.) $\text{Pent}_{\text{Agronomy}}$ (.) $\text{Phi}_{\text{Cinema}}$ (session) $\text{Phi}_{\text{Agronomy}}$ (session) p_{Cinema} (session) (.) p_{Agronomy} (session)	744.2	89.2	0.00	0.00	54	572.3
S_{Cinema} (.) S_{Agronomy} (.) $\Psi_{\text{Cinema to Agronomy}}$ (.) $\Psi_{\text{Agronomy to Cinema}}$ (.) $\text{Pent}_{\text{Cinema}}$ (session) $\text{Pent}_{\text{Agronomy}}$ (session) $\text{Phi}_{\text{Cinema}}$ (.) $\text{Phi}_{\text{Agronomy}}$ (.) p_{Cinema} (session) p_{Agronomy} (session)	756.1	101.2	0.00	0.00	54	584.3
S_{Cinema} (.) S_{Agronomy} (.) $\Psi_{\text{Cinema to Agronomy}}$ (.) $\Psi_{\text{Agronomy to Cinema}}$ (.) $\text{Pent}_{\text{Cinema}}$ (session*.) $\text{Pent}_{\text{Agronomy}}$ (session) $\text{Phi}_{\text{Cinema}}$ (session) $\text{Phi}_{\text{Agronomy}}$ (session) p_{Cinema} (session) p_{Agronomy} (session)	872.7	217.8	0.00	0.00	76	555.9
S_{Cinema} (.) S_{Agronomy} (.) $\Psi_{\text{Cinema to Agronomy}} = \Psi_{\text{Agronomy to Cinema}}$ (1.0) $\text{Pent}_{\text{Cinema}}$ (.) $\text{Pent}_{\text{Agronomy}}$ (.) $\text{Phi}_{\text{Cinema}}$ (*.) $\text{Phi}_{\text{Agronomy}}$ (*.) $p_{\text{Cinema}} = p_{\text{Agronomy}}$ (.)	18866.7	18211.8	0.00	0.00	8	18849.7

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Table S2. Assessed models to estimate migration between the study sites. S = survival rate. Ψ = transition probability between age classes. p = capture probability. c = recapture probability. f = number of animals in the population that were never captured

Model	AICc	Delta AICc	AICc Weights	Model Likeli-hood	Num. Par	-2log(L)
S (site*age) Ψ Juvenile to Adult (site) p (age) c (.) f (site*age*season)	610.4	0.0	0.20	1.00	29	538
S Cinema Juvenile (precipitation) S Cinema Adults (.) S Agronomy (age) Ψ Juvenile to Adult (site) p (age) c (.) f (site*age*season)	611.0	0.6	0.15	0.74	30	535
S (site*age) Ψ Juvenile to Adult (site) p (age) c Juvenile (.) Adults (c=p) f (site*age*season)	611.9	1.5	0.10	0.47	29	539
S Cinema Juvenile (.) S Cinema Adults (precipitation) S Agronomy (age) Ψ Juvenile to Adult (site) p (age) c (.) f (site*age*season)	611.9	1.5	0.10	0.47	30	536
S Cinema (age*precipitation) S Agronomy (age) Ψ Juvenile to Adult (site) p (age) c (.) f (site*age*season)	612.4	2.0	0.07	0.36	31	533
S Cinema (age*precipitation) S Agronomy (age) Ψ Juvenile to Adult (site) p (age) c (.) f (site*age*season)	612.4	2.0	0.07	0.36	31	533
S Cinema (age) S Agronomy Juvenile (.) Agronomy Adults (precipitation) Ψ Juvenile to Adult (site) p (age) c (.) f (site*age*season)	612.5	2.0	0.07	0.36	30	537
S Cinema (age) S Agronomy Juvenile (precipitation) Agronomy Adults (.) Ψ Juvenile to Adult (site) p (age) c (.) f (site*age*season)	612.7	2.3	0.06	0.31	30	537
S Juvenile (site*precipitation) S Adults (site) Ψ Juvenile to Adult (site) p (age) c (.) f (site*age*season)	613.4	3.0	0.05	0.23	31	534
S (site*age) S Ψ Juvenile to Adult (site) p (age) c (age) f (site*age*season)	613.5	3.0	0.04	0.22	30	538
S Juvenile (site) S Adults (site*precipitation) Ψ Juvenile to Adult (site) p (age) c (.) f (site*age*season)	614.1	3.7	0.03	0.16	31	535
S Cinema (age) S Agronomy (age*precipitation) Ψ Juvenile to Adult (site) p (age) c (.) f (site*age*season)	614.8	4.4	0.02	0.11	31	536
S (site*age*precipitation) Ψ Juvenile to Adult (site) p (age) c (.) f (site*age*season)	617.1	6.7	0.01	0.04	33	531
S Cinema (age) S Agronomy (.) Ψ Juvenile to Adult (site) p (.) c (.) f (site*season)	625.2	14.8	0.00	0.00	17	586
S Cinema (age) S Agronomy (.) Ψ Juvenile to Adult (site) p (age) c (age) f (site*season)	630.3	19.9	0.00	0.00	19	586
S (site*season) Ψ Juvenile to Adult (site) p (age) c (age) f (site*season)	641.0	30.6	0.00	0.00	26	577
S Cinema (age) S Agronomy (.) Ψ Juvenile to Adult (site) p (.) c (.) f (site*age*season)	642.5	32.1	0.00	0.00	27	576
S (site*age*precipitation) Ψ Juvenile to Adult (site) p (.) c (.) f (site*age*season)	651.7	41.3	0.00	0.00	32	569
S (site*age*season) Ψ Juvenile to Adult (site) p (age) c (.) f (site*age*season)	654.5	44.1	0.00	0.00	45	524
S (site*age*season) Ψ Juvenile to Adult (site) p (age) c (age) f (site*age*season)	658.6	48.2	0.00	0.00	46	524
S (site*age*season) Ψ Juvenile to Adult (site) p (age) c (age) f (site*season)	665.2	54.8	0.00	0.00	36	569
S Juvenile (site*month) S Adults (site) Ψ Juvenile to Adult (site) p (age) c (.) f (site*age*season)	671.6	61.2	0.00	0.00	49	524
S Cinema (age*month) S Agronomy (age) Ψ Juvenile to Adult (site) p (age) c (.) f (site*age*season)	672.7	62.3	0.00	0.00	49	525
S Cinema (age) S Agronomy (age*month) Ψ Juvenile to Adult (site) p (age) c (.) f (site*age*season)	673.3	62.9	0.00	0.00	49	525
S Juvenile (site) S Adults (site*month) Ψ Juvenile to Adult (site) p (age) c (.) f (site*age*season)	674.5	64.1	0.00	0.00	49	526
S (site*age) Ψ Juvenile to Adult (site) p (age) c (.) f (site*age*month)	711.7	101.3	0.00	0.00	57	524
S Cinema (age) S Agronomy (.) Ψ Juvenile to Adult (site) p (age) c (age) f (site*age*month)	713.1	102.6	0.00	0.00	57	526

Model	AICc	Delta AICc	AICc Weights	Model Likeli-hood	Num. Par	-2log(L)
S Cinema (age*precipitation) S Agronomy (age) Ψ Juvenile to Adult (site) p (age) c (.) f (site*age*month)	718.5	108.1	0.00	0.00	59	520
S (site*age) Ψ Juvenile to Adult (site) p=c (site) f (site*age*month)	741.4	131.0	0.00	0.00	56	559
S (site*season) Ψ Juvenile to Adult (site) p (age) c (age) f (site*age*month)	746.8	136.3	0.00	0.00	64	519
S (site*age) Ψ Juvenile to Adult (site) p=c (site*age) f (site*age*month)	747.5	137.1	0.00	0.00	58	555
S (site*age) Ψ Juvenile to Adult (site) p (site) c(site) f (site*age*month)	752.2	141.8	0.00	0.00	58	559
S (site*age*month) Ψ Juvenile to Adult (site) p (age) c (.) f (site*age*season)	774.3	163.8	0.00	0.00	69	512
S (site*age*season) Ψ Juvenile to Adult (site) p (age) c (.) f (site*age*month)	802.7	192.3	0.00	0.00	73	511
S (site*age*month) Ψ Juvenile to Adult (site) p (.) c (.) f (site*age*season)	804.7	194.2	0.00	0.00	68	550
S Cinema (age) S Agronomy (age*month) Ψ Juvenile to Adult (site) p=c (site) f (site*age*month)	862.0	251.6	0.00	0.00	76	545
S Juvenile (site*month) S Adults (site) Ψ Juvenile to Adult (site) p=c (site) f (site*age*month)	865.5	255.0	0.00	0.00	76	549
S (site*age*month) Ψ Juvenile to Adult (site) p (age) c (.) f (site*age*month)	1073.8	463.4	0.00	0.00	97	500
S (site*age*month) Ψ Juvenile to Adult (site) p=c (site) f (site*age*month)	1092.4	482.0	0.00	0.00	96	535
S (site*age) Ψ Juvenile to Adult (site) p=c (site*age*month) f (site*age*month)	1186.1	575.7	0.00	0.00	102	515