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Population Dynamics of the Andean Lizard *Anolis heterodermus*: Fast-slow Demographic Strategies in Fragmented Scrubland Landscapes

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ABSTRACT

Habitat fragmentation and loss affect population stability and demographic processes, increasing the extinction risk of species. We studied *Anolis heterodermus* populations inhabiting large and small Andean scrubland patches in three fragmented landscapes in the Sabana de Bogotá (Colombia) to determine the effect of habitat fragmentation and loss on population dynamics. We used the capture-mark-recapture method and multistate models to estimate vital rates for each population. We estimated growth population rate and the most important processes that affect λ by elasticity analysis of vital rates. We tested the effects of habitat fragmentation and loss on vital rates of lizard populations. All six isolated populations showed a positive or an equilibrium growth rate ($\lambda = 1$), and the most important demographic process affecting λ was the growth to first reproduction. Populations from landscapes with less scrubland natural cover showed higher stasis of young adults. Populations in highly fragmented landscapes showed highest juvenile survival and growth population rates. Independent of the landscape's habitat configuration and connectivity, populations from larger scrubland patches showed low adult survivorship, but high transition rates. Populations varied from a slow strategy with low growth and delayed maturation in smaller patches to a fast strategy with high growth and early maturation in large patches. This variation was congruent with the fast-slow continuum hypothesis and has serious implications for Andean lizard conservation and management strategies. We suggest that more stable lizard populations will be maintained if different management strategies are adopted according to patch area and habitat structure.

Abstract in Spanish is available in the online version of this article.

Key words: Capture-recapture; fast-slow continuum; habitat loss and fragmentation; habitat structure; landscape configuration.

THE ANDES ECOREGION IS ONE OF THE GREATEST HOTSPOTS OF SPECIES DIVERSITY IN THE WORLD AND HARBORS A HIGH DEGREE OF ENDEMISM (Olson & Dinerstein 1997, Primack *et al.* 2001). In Colombia, Andean ecosystems are highly deforested, with just 27 percent of the natural habitat remaining (Armenteras *et al.* 2003). Habitat fragmentation is a spatial and temporal process (Schlaepfer & Gavin 2001) that affects landscape-scale habitat patterns through four main processes (Fahrig 2003): (1) habitat loss; (2) increase in the number of habitat patches; (3) decrease in patch size; and (4) increase in isolation distance between habitat patches. In addition to landscape-scale effects, other factors at the patch-level include changes in patch shape (Saunders *et al.* 1991), edge-matrix effects on biodiversity, and their relationships with vegetation structure and environmental variables in tropical montane ecosystems (Isaacs & Urbina-Cardona 2011).

It is well-known that habitat fragmentation, loss, and degradation are the main threats to the persistence of biodiversity (Wilcox & Murphy 1985). The level of habitat transformation and resulting changes in land use and cover affect populations of a species differently, depending on a species' natural history-functional traits (endogenous factors). These differences make some areas more vulnerable than others (exogenous factors; Fahrig 2003). When population stability and their demographic processes are affected, species extinction risk may increase due to changes in population density, size, or structure (Wiegand *et al.* 2005). In addition, habitat fragmentation may decrease reproductive, recruitment, and survival rates due to increased predation, diminished resources, and altered population structure (Schlaepfer & Gavin 2001, Aponte *et al.* 2003, Hokit & Branch 2003b). Finally, habitat fragmentation increases isolation and loss of connectivity, which increases the risk of inbreeding depression (Madsen *et al.* 1996) and changes dispersal patterns (Boudjemadi *et al.* 1999).

Reptiles are key organisms to study the effects of habitat fragmentation and loss at fine spatial scales due to their low dispersion capability. Several observed declines in reptile populations illustrate that their conservation status may be as critical as that of amphibians (Gibbons *et al.* 2000, Reading *et al.* 2010). Nevertheless, reptiles have received weaker support for research, management, and conservation (McGarigal & Cushman 2002, Urbina-Cardona 2008) when compared with other vertebrates, such as birds and mammals (Gardner *et al.* 2007). The main reason is that reptile species usually exhibit natural low abundance, and have cryptic habits and solitary lives (Gibbons *et al.* 2000), making them difficult to study.

Some studies on communities of reptiles have detected changes in structure and composition due to edge effects by habitat fragmentation, resulting in different species assemblages that require different habitat quality and conservation strategies along a pasture-forest edge-forest interior gradient (Schlaepfer & Gavin

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2001, Urbina-Cardona *et al.* 2006). In addition, some lizard species occur at higher densities in forest fragments than in continuous forest; this unexpected pattern may lead us to infer that population parameters may vary with habitat fragmentation and loss (*following* Bell & Donnelly 2006). For example, the reproductive rates of lizards in remnant patches might be reduced due to a decrease in habitat quality and resource availability, thereby restricting the body size of individuals and their reproductive output (Díaz *et al.* 2004). In addition, increased habitat isolation decreases survival rates due to changes in lizard dispersal behavior (Boudjemadi *et al.* 1999), and increased predation rates on eggs and adults, which affects reproductive success, recruitment, and survival rates in lizard populations. All these demographic changes due to the decrease in patch quality could be responsible for the local extinction of lizard populations in small and degraded patches (Díaz *et al.* 2000).

To predict the effect of habitat fragmentation and loss on a particular species, it is necessary to study its population ecology in detail (Simberloff 1988). Recently, some authors used matrix population models to study the variation in lizard demography associated with climatic and geographic gradients, under assumptions of the fast-slow continuum hypothesis of life-history evolution (Blomberg & Shine 2001, Zúñiga-Vega *et al.* 2007, Rojas-González *et al.* 2008, Zúñiga-Vega *et al.* 2008). The fast-slow continuum hypothesis states that adult class mortality is the driving factor of life-history strategies. This hypothesis predicts that organisms with high adult mortality rates will exhibit fast developmental rates, high fecundity, and short life cycles, whereas organisms with low adult mortality rates will exhibit slow developmental rates, low fecundity, and long life cycles (Harvey & Zammuto 1985, Promislow & Harvey 1990, Stearns 1992).

Anolis lizards are good models to study ecological processes (Losos 1994), and *Anolis heterodermus* is especially suited because it has a low dispersal capability and is restricted to natural forested areas (Miyata 1983, Ramírez 1986). We studied *Anolis heterodermus* population dynamics in six Andean scrubland patches at three fragmented landscapes in the Sabana de Bogotá (Colombia). We aimed to answer the following questions: (1) Do population growth and vital rates of *A. heterodermus* change among populations that inhabit scrubland patches with different sizes? (2) How do demographic parameters and processes vary with landscape configuration, patch size and shape, and vegetation structure? And (3) do the demographic strategies of lizard populations differ when comparing large and small patches?

We expect that, independent of landscape fragmentation, populations of *A. heterodermus* inhabiting small scrubland patches will exhibit lower population growth rates than populations from large patches due to changes in vegetation structure. We also expect that populations with high mortality rates in small patches will exhibit a fast strategy, whereas populations from large patches with low mortality rates will exhibit a slow strategy.

METHODS

Species and study area.—*Anolis heterodermus* is an endemic lizard of Colombia restricted to altitudes between 1800 and 3750 m asl (Dunn 1944). This lizard inhabits Andean scrubland and Andean forest (Dunn 1944), and exhibits moderate to high population densities (Miyata 1983). *Anolis heterodermus* is an arboreal lizard with slow movements and a 'sit and wait' foraging strategy (Pianka 1966). Osorno and Osorno (1946) reported that their potential predators are birds in the families Falconidae and Accipitridae, and in the genus *Turdus*. The maximum snout-vent length (SVL) recorded for females was 85 mm and 85.4 mm for males. Miyata (1983) determined that *A. heterodermus* reach sexual maturity at 55 mm SVL, and Ramírez (1986) found that adult females produce two eggs per mo.

This study was carried out in scrubland forest patches in three fragmented landscapes of the municipalities of Madrid, Tabio, and Bogotá D.C., in Cundinamarca state, Colombia (N 4° 45′–4°55′: W 74°4′–74°12′. 2590–2774 m asl). The landscapes are separated from each other by approximately 16 km in a straight line. This region has a semi-dry climate with two defined wet seasons, April to May and October to November, and a mean annual precipitation of 850 mm (Claro-R 1995). Scrubland forest is characterized by a vegetal association of *Myrcianthes leucoxylae-Miconio squamulose* (Cortés *et al.* 1999) with a maximum shrub height of 4 m and no canopy coverage.

Habitat features in landscapes and patches.—Study sites were selected by identifying potential Andean scrubland forests in Quick Bird satellite images from 2008 at a 1:15,000 scale for each of the three landscapes (Bogotá, Madrid, and Tabio). We measured spatial variables using GRASS 6.3.0 software (GRASS Development Team 2008) at both the landscape and patch scale (Table 1) to describe habitat fragmentation and loss and differentiate their effects (*following* Fahrig 2003). Landscape variables reflect habitat fragmentation based on habitat amount and configuration, such as: (1) number of habitat patches; (2) mean habitat patch size; and (3) mean distance between patches. Patch variables reflect habitat loss based on: (1) patch size; and (2) patch shape according to the Patton index (Patton 1975).

At each landscape, we selected two scrubland patches to conduct the lizard surveys. The criterion to select the patches was their size and we chose the largest and smallest patches on each landscape (Table 1). We analyzed the vegetation structure in five plots of 25 m^2 (the plots were measured with a metric tape of 15 m and each plot was delimited using plastic cord) at the interior and the edges of each selected patch. Inside each plot,

TABLE 1. *Habitat configuration and patches sizes for each landscape.*

Habitat configuration/Landscape	Bogotá	Madrid	Tabio
Habitat amount (ha)	157.1	215.4	104.9
Numbers of patches	3	7	11
Mean patch size (ha)	52.3	30.8	9.5
Mean distance between patches (m)	19.02	39.01	65.64
Matrix	Urban	Pastures	Pastures
Largest patch (ha)	125.1	113.4	42.6
Smallest patch (ha)	4.3	8.5	0.9

we measured vegetation coverage of grass (0–0.30 m), herbaceous (0.31–1.5 m), and shrub (>1.5 m) strata. Height of scrub strata was calculated using clinometers.

LIZARD SAMPLING.—Data were collected from April to October 2008. Each patch was sampled on five occasions by three people; individual lizards were captured and marked using the Hero (1989) code. We searched for lizards using a visual encounter survey (Crump & Scott 2001) and examining vegetation between 0 and 3 m in height. The sampling effort was greater at large patches than small ones (*e.g.,* Schoereder *et al.* 2004): Tabio small patch 80 man-hours, Bogotá and Madrid small patches 120 man-hours; large patches: Bogotá 192 man-hours and Madrid and Tabio 240 man-hours each one.

Individual lizards were sexed based on the presence of post cloacae plates in males. We recorded snout-vent and total length using a digital caliper. We defined the population structure based on three size classes, *i.e.*, juvenile class (SVL <55 mm size; based on Miyata (1983), Adults 1 (SVL between 55 mm and 70 mm), and Adults 2 (SVL >70 mm). The size classes of adults were defined based on the statistical mode of SVL measures of 227 adult lizards.

STATISTICAL ANALYSIS.—To determine differences between patches in size and shape, we performed Mann–Whitney U tests, and to detect differences on vegetation structure, we used Student's *t*-test. We also described relationships between habitat configuration and vegetation structure using Spearman correlations. For each of the six patch populations, we estimated survival and transition rates (these rates describe the movements of individuals through their life cycle, probability of survival through time, and maturation or transit between age classes) using multistate models and maximum likelihood procedures with MARK 5.0 software (White & Burnham 1999).

We assumed a base model with different vital rates between size classes. Subsequently, we performed 23 models using linear models to test for the effects of factors (sex, landscape, patch size groups, and matrix type) and covariates (sample effort per patch, time, habitat landscape, patch features, and structure of vegetation) on vital rates of *Anolis heterodermus* populations. The model that best explained the vital rates of *A. heterodermus* was chosen based on Akaike information criterion (White & Burnham 1999) and the adjustment of the data to capture-marking-recapture methods was performed using U-CARE 2.3 (Choquet *et al.* 2005). The survival (S) and transition (Ψ) parameters were determined with posterior distribution after 15,000 simulations using MCMC to fix the parameter estimation in multistate models with several states, which have a propensity to fail in local minimal values (Lebreton & Pradel 2002, Brown *et al.* 2006, Cooch & White 2008).

On the basis of values of transition (Ψ) and survival (S) rates, we calculated stasis (S*[1−Ψ]) and growth (S*Ψ). We estimated 12 eggs per female in the study period based on reproductive data recorded by Ramírez (1986) that show a potential reproductive output of two eggs per mo for species. The fecundity for each adult class was calculated using an equation for a population with continuous reproduction and structured size classes (Caswell 2001).

We used projection matrix elements stasis (S*[1−Ψ]), growth (S*Ψ), and fecundity as elements to build transition matrices (Lefkovitch 1965) to each population and each matrix represented 6 mo (Table 4). By mean of matrix population models, we estimated the intrinsic population growth rate (λ) as a direct measure of the fitness of each population. Confidence intervals of λ were estimated following the analytical approximation suggested by Alvarez-Buylla and Slatkin (1991). To detect the most important demographic processes and size classes affecting λ, we performed an elasticity analysis using PopTools 2.6.2 software (Hood 2004) while elasticity values for vital rates were estimated using the chain-rule approach (Caswell 2001). Elasticity value of each matrix element indicates the relative importance of each element to change λ value (Caswell 2001). The relative importance of each size class to λ was the sum of values per column of the elasticity matrix. The sum of diagonal elements of matrix, the sum of sub-diagonal elements, and the sum of remaining values of elasticity matrix were, respectively, the relative importance values of stasis, growth, and fecundity.

We evaluated the differences between populations in λ and elasticity values graphically. The relationships between habitat configuration and vital rates, λ, or elasticity were analyzed with Spearman and Pearson correlations; prior to these analyses, we verified normality, variance homogeneity, homoscedasticity, and colinearity between the variables. Finally, we revealed differences in demographic strategies using a demographic triangle (Silvertown *et al.*1992).

RESULTS

HABITAT FEATURES FOR LANDSCAPES AND PATCHES.—All patches were totally surrounded and isolated by pastures or urban landscapes, but the amount of habitat varied among the landscapes. The landscape with the least amount of habitat was Tabio, followed by Bogotá and Madrid. Coincidentally, habitat fragmentation in Tabio was also higher than in Madrid and Bogotá (Table 1). At the landscape scale, independent of patch size, edge shrub coverage was positively correlated with habitat amount ($r = 0.90$; $P = 0.03$). Also, when fragmentation increased (more patches, smaller patches, and greater separation between patches), the grass coverage in the forest interior was higher ($r = 0.94$; $P = 0.01$).

At the patch scale, larger patches had greater perimeters ($U = 0.0$; $P = 0.05$), more complex shapes ($U = 0.0$ $P = 0.05$), and higher herbaceous coverage at the forest edge ($t = 5.39$; $P = 0.012$; Table 2) than small patches. Perimeter ($r = 0.94$; $P = 0.01$) and patch shape ($r = 0.88$; $P = 0.05$) were also correlated with patch size. Herbaceous coverage on the forest edge was greater for large patches compared with small ones ($t = 5.39$; $P = 0.01$), and this coverage was positively correlated with both the patch area ($r = 0.80$; $P = 0.04$) and the perimeter ($r = 0.9$; $P = 0.005$). The dominant stratum at the patch interior was shrub (79%), followed by herbaceous (60%), and grass stratum

TABLE 2. *Patch features and vegetal structure. Values in parenthesis are Standard Deviation.*

			Stratum coverage percent					
			Patch edge			Patch interior		
Patch Size	Perimeter (m)	Shape index	Grass	Herbaceous	Shrub	Grassing	Herbaceous	Shrub
Large	7241.8 (1169.6)	2.2 (0.5)	58.2 (11.2)	82.7 (8.8)	52.3 (21.5)	32.7 (10.5)	43.5 (5)	78.7 (19.5)
Small	893.2 (467.9)	1.2 (0.1)	66 (23.3)	25.9 (12.7)	66.8 (22.3)	32 (13.8)	71.7 (38.8)	79.5 (6.9)

(32%); at the patch edges, grass and shrub strata were dominant with 63 and 61 percent, respectively.

VARIATION IN VITAL RATES AND POPULATION DYNAMICS ASSOCIATED WITH PATCHES AND LANDSCAPES.—After 992 man-hours of sampling effort, we captured 458 lizards and recaptured 68 lizards—four lizards four times, seven lizards twice, and 57 lizards once. The captures per sample occasion were 91 (±15) lizards and the recaptures were 13 (±2) lizards. The model that best represented the encounter history was one that incorporated effects of patch by group size (Table S1). The other factors or covariates explained between 1 and 49 percent of capture-recapture data variation when compared with the best model. Covariation of vital rates with sampling effort explains only 30 percent of the variation when compared with the best model (Table S1). Vital rates did not vary with either sex or time (Table S1).

We found the highest juvenile survival rate in the large patch in Tabio, whereas the lowest survival rate was found in the large patch in Madrid (Tables 3 and 4). Different juvenile survival rates between patches were found in Madrid and Tabio (Tables 3 and 4). The highest survival rates of Adults 1 occurred in both patches in Tabio, whereas the lowest survival rate was found in the large patch in Madrid (Tables 3 and 4). The survival rate of the adults 1 between patches was only different in Madrid (Tables 3 and 4). We found both the highest and lowest survival rates for Adults 2 in Bogotá, and only in this landscape were the survival rates for adults 2 different between the patches (Tables 3 and 4).

The highest transition rates from juvenile to Adult 1 were found in large patches from Bogotá and Madrid. Within the same landscapes, the transition rates were different between large and small patches (Tables 3 and 4). The highest and lowest transition rates from Adult 1 to Adult 2 were found in Bogota and Tabio, respectively. In Tabio, the transition rates were different between patches (Tables 3 and 4). The average fecundity of adults was not different between large and small patches (Adults 1: $t = 0.93$, $P = 0.45$; Adults 2: = 2.91, $P = 0.09$; Table 4).

We found that the population growth rate was positive for large patch populations from Bogotá and Tabio, whereas in the other populations, the population growth rate approached equilibrium (Fig. 1). The highest value of λ was found in the large patch population of Tabio and was significantly different from the other populations, whereas the large patch population of Madrid showed the lowest λ value (Fig. 1).

Survival was the most important vital rate (Fig. 2A). In almost all of the *Anolis heterodermus* populations, Adult 1 was the most important size class, and juvenile growth was the most important individual demographic process to λ (Figs. 2B and C). The values of elasticity per demographic processes showed that in the large patches populations from Bogotá and Tabio and both populations from Madrid, the most important process was growth, whereas in the small patch populations from Bogotá and Tabio, the most important process was stasis (Fig. 2B). At lower level parameters, the most important vital rate to λ in *Anolis heterodermus* populations was survival rate (Fig. 2A).

TABLE 3. *Vital rates and capture probability for the populations of* A. heterodermus *per landscape and patch. Values in parenthesis are Standard Deviation.*

	Bogotá		Madrid		Tabio	
Vital rate	Large patch	Small patch	Large patch	Small patch	Large patch	Small patch
Juvenile Survival	0.35 (0.08)	0.32 (0.04)	0.25 (0.01)	0.57 (0.07)	0.87 (0.03)	0.37 (0.06)
Juvenile Capture Probability	0.26 (0.08)	0.53 (0.08)	0.32 (0.04)	0.33 (0.05)	0.27 (0.05)	0.19 (0.04)
Transition to Adult 1	0.89 (0.04)	0.20 (0.04)	0.38 (0.04)	0.18 (0.03)	0.23 (0.05)	0.16 (0.05)
Adults 1 Survival	0.25 (0.05)	0.43 (0.08)	0.23 (0.01)	0.39 (0.02)	0.84 (0.02)	0.77 (0.06)
Transition to Adult 2	0.29 (0.07)	0.10 (0.03)	0.25 (0.04)	0.25 (0.01)	0.19 (0.02)	0.05 (0.02)
Adults 1 Capture Probability	0.70 (0.08)	0.44 (0.08)	0.37 (0.03)	0.45 (0.04)	0.12 (0.03)	0.21 (0.05)
Adults 1 Fecundity	4.43	4.87	3.72	6.26	10.31	6.48
Adults 2 Survival	0.25 (0.06)	0.73 (0.06)	0.35 (0.05)	0.34 (0.04)	0.39 (0.03)	0.52 (0.09)
Adults 2 Capture Probability	0.18 (0.06)	0.34 (0.08)	0.35 (0.06)	0.37 (0.06)	0.50 (0.05)	0.33 (0.05)
Adults 2 Fecundity	3.73	6.82	3.88	4.99	7.64	8.02

TABLE 4. *Projections matrices rates for the populations of* A. heterodermus *per landscape and patch. Values in bold indicate fecundity, in italic growth, and underlined stasis.*

		Large patch			Small patch		
Landscape	Size class	Juveniles	Adults 1	Adults 2	Juveniles	Adults 1	Adults 2
Bogotá	Juveniles	0.04	**4.43**	**3.73**	0.26	**4.87**	**6.82**
	Adults 1	*0.32*	0.17	0	*0.06*	0.39	0
	Adults 2	0	*0.07*	0.25	0	*0.05*	0.73
Madrid	Juveniles	0.16	**3.72**	**3.88**	0.46	**6.26**	**4.99**
	Adults 1	*0.10*	0.17	0	*0.10*	0.29	0
	Adults 2	0	*0.06*	0.35	0	*0.10*	0.34
Tabio	Juveniles	0.68	**10.31**	**7.64**	0.31	**6.48**	**8.02**
	Adults 1	*0.20*	0.68	0	0.06	0.73	0
	Adults 2	0	*0.16*	0.39	0	*0.04*	0.52

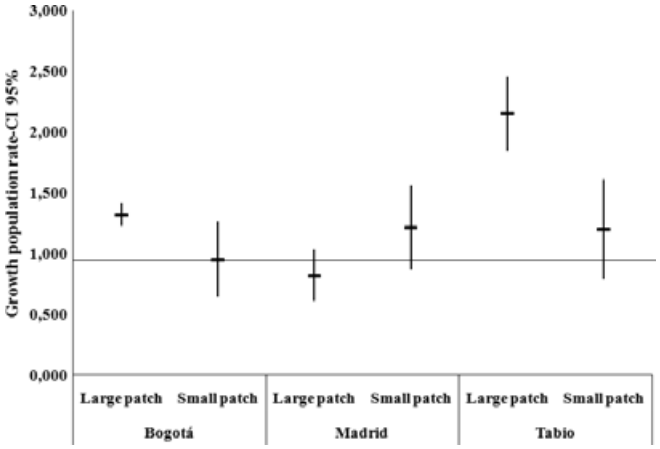

FIGURE 1. Growth population rates of *Anolis heterodermus* populations.

VARIATION IN VITAL RATES AND POPULATION DYNAMICS ASSOCIATED WITH HABITAT FEATURES.—We found a negative correlation of juvenile survival with shrub coverage in the forest interior ($r = -0.94$, $P = 0.005$). In addition, the survival rate of Adults 1 was negatively correlated with habitat amount ($r = -0.84$, $P = 0.004$) and shrub coverage inside the patch ($r = -0.83$, $P = 0.04$). We did not find any relationships between the survival rates of Adults 2 with the habitat features. Both the transition rates of juvenile to Adult 1 and of Adult 1 to Adult 2 were positively correlated with patch area ($r = 0.94$, $P = 0.004$) and patch perimeter ($r = 0.88$, $P = 0.01$). The transition rate of juvenile to adult 1 was also positively correlated with herbaceous coverage at the forest's edge ($r = 0.94$, $P = 0.004$). The fecundity of Adults 1 was negatively correlated with interior shrub coverage ($r = -0.94$, $P = 0.004$) and the fecundity of Adults 2 was negatively correlated with patch area ($r = -0.82$, $P = 0.04$). Population growth rates were not correlated with habitat features.

We found no relationship between the elasticity values for each size class with habitat features, elasticity values of Adults 2 were negatively correlated with λ. The growth elasticity value

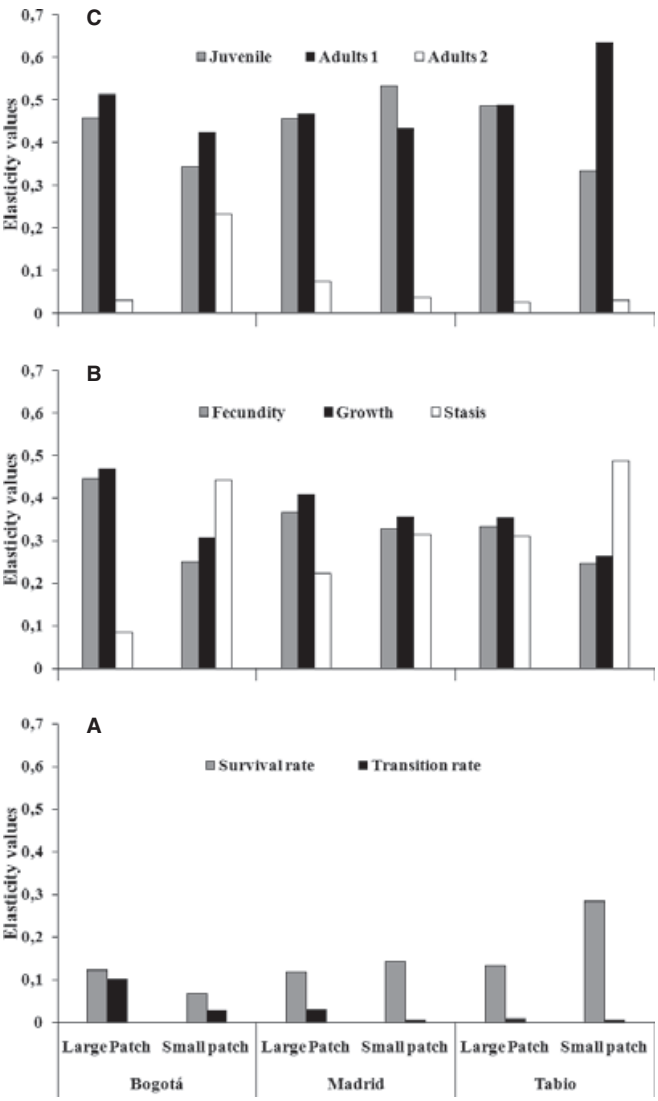

FIGURE 2. Elasticity values of A: Vital rates, B: Matrix elements, and C: Size classes.

was positively correlated with patch area ($r = 0.94$, $P = 0.004$) and with patch perimeter ($r = 0.88$, $P = 0.02$). Stasis was negatively correlated with herbaceous coverage at forest edge ($r = -0.88$, $P = 0.02$) and elasticity of fecundity was positively correlated with patch perimeter ($r = 0.94$, $P = 0.004$) and with the herbaceous coverage at the forest edge ($r = 0.88$, $P = 0.02$). Finally, elasticity of survival rate was positively correlated with grass coverage at interior of patch ($r = 0.94$, $P = 0.004$), whereas elasticity of the transition rate was negatively correlated with the same habitat feature ($r = -0.88$, $P = 0.02$).

Taking into account the relative contribution of each demographic process to *A. heterodermus* population dynamics, we found that populations were distributed across a gradient from low fecundity and stasis to high fecundity and growth (Fig. 3). The distribution of *Anolis heterodermus* populations on growth-stasis-fecundity space was congruent with the variation from the slow demographic strategy in the small patch population to a fast demographic strategy in the large patch population (Fig. 3).

DISCUSSION

CHANGES IN VITAL RATES AND POPULATION DYNAMICS ASSOCIATED WITH LANDSCAPE HABITAT CONFIGURATION.—At the three studied landscapes, habitat transformation occurred along flat lowland areas with easy access for both agricultural and urban activities. This pattern of habitat transformation is consistent with non-random habitat loss, where anthropogenic activities are concentrated in flat areas (Winter *et al.* 1987) with productive soils (Chatelain *et al.*1996) near roads (Laurance *et al.* 2001).

In patches from landscapes with less scrubland, stasis of adults 1 was increased. This finding is relevant because this size class (Adult 1) contributes the most to the population growth rate of *A. heterodermus*. Therefore, if individuals spend more time in this age class, their populations will produce a higher number of offspring than in populations from landscapes with more scrubland habitat. These differences explain the high population growth rates found in the Tabio populations. In addition, population growth rate and Adult 1 growth of Tabio patches were the most different when compared with patches in the other landscapes. This finding adjusts with models that predict that habitat loss is responsible for more than 68 percent of the variation in population size (Wiegand *et al.* 2005) or population densities (Wolff *et al.* 1997). If the reduction in habitat area increases the variation in Adult 1 growth rates, then intrinsic growth population rates and population sizes will be more variable.

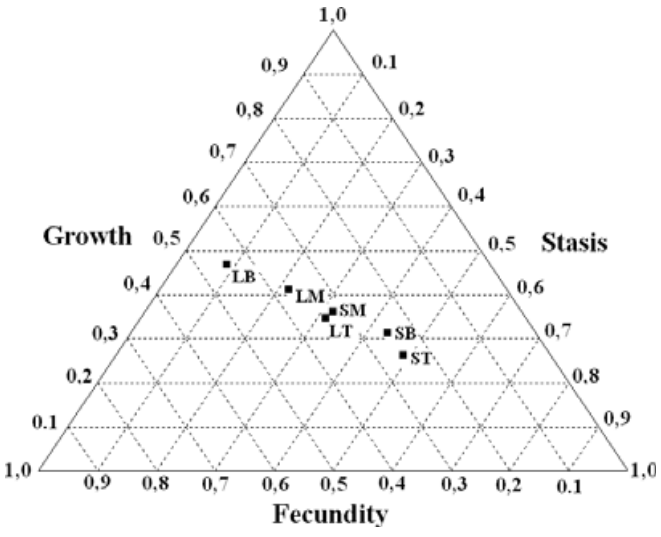

FIGURE 3. Demographic triangle for *A. heterodermus* populations. L: Large patches and S: Small patches; B: Bogotá, M: Madrid and T: Tabio.

Populations in the most fragmented landscape (Tabio) exhibited the highest juvenile survivorship and fecundity rates. Therefore, the highest population growth rates may be associated with hyper-dynamism, a term used to designate the acceleration of rates and processes at different scales due to habitat fragmentation (Laurance 2002). Within populations, a decrease in predation pressure due to either an increase in the distances between patches, or the immigration of individuals from recently degraded areas, may result in hyper-dynamism (Laurance 2002, Burke & Reed 2006).

Nevertheless, the distance between patches may be a poor predictor of increase in lizard survival rates because it is independent of predation by highly mobile predators. The common predators of *A. heterodermus* are birds, such as eagles, falcons, and robins (Osorno & Osorno 1946), which generally cover long distances and use disturbed areas to search for prey between patches. An increase in vegetation coverage at the lower strata (typical in a highly fragmented landscape), however, provides more protection and shelter against potential predators. In addition, more vegetation cover provides more substrate for protecting eggs, resulting in improved juvenile survival.

A rapid increase in population density, such as immigration from adjacent and recently degraded areas, could destabilize a patch population. (Hagan *et al.*1996, Schmiegelow *et al.* 1997). This situation is apparent at more fragmented landscapes (*e.g.*, Tabio), which have higher densities of *A. heterodermus* (0.03–0.06 individuals/m^2) than less fragmented landscapes (*e.g.*, Bogotá with 0.001 individuals/m^2, R. A, Moreno-Arias unpubl. data). This reinforces the idea that lizard populations are denser in fragmented forests than in continuous ones (Bell & Donnelly 2006).

CHANGES IN VITAL RATES AND POPULATION DYNAMICS ASSOCIATED WITH PATCH HABITAT FEATURES.—Throughout our 7-mo survey, we found all recaptured lizards in microhabitats less than 3 m from their original capture site, independent of the landscape or patch size, indicating low mobility and high site fidelity of *A. heterodermus* individuals. Therefore, our estimated survival rates are assumed real and not apparent survival rates, hence the remaining portion of the survival rates estimated represent the mortality rate.

Mortality rates in lizards are shaped by different selective pressures due to several environmental conditions and biotic factors (Aucoin *et al.* 2000, Rojas-González *et al.* 2008). In this sense, it is possible that reduction in patch size generates differential mortality pressures that explain the decrease in adult survivorship and the increase in transition rates related with patch area.

Our result differs from Hokit and Branch (2003a, b), however, who found that the *Sceloporus woodi* lizard survival rate was positively correlated with patch area. This discrepancy among species may be due to their particular ecology, movement patterns, habitat use, or their response to anthropogenic disturbances.

Our finding that adult lizard mortality increases with patch shrub coverage is in agreement with other reported patterns that indicate that predation on lizards is higher in sites with greater vegetation coverage in the upper strata (Shepard 2007). Despite the difficulty of observing predation in nature, by analyzing data such as the activity patterns in lizards in relation to a predator's attacks (Rose 1981, Rojas-González *et al.* 2008) is possible study predation through indirect evidence (Shepard 2007). Like other authors found that more active and exposed lizards are more susceptible to predation (Shepard 2007, Rojas-González *et al.* 2008), we found that *A. heterodermus* adults in large patches showed high mortality were more active in higher vegetation strata (1–2 m from the soil) and used more exposed perches, such as branches and leaves for thermoregulation and foraging activities, than did adults with low mortality from small patches (R.A. Moreno-Arias, unpubl. data).

There is a relationship between the degree of diet specialization and the habitat preference of the species (*e.g.*, patch edge or interior; Laurance & Yensen 1991). Moreover, reptile species have been categorized based on habitat quality associated with physical proximity to the edge of the forest (Urbina-Cardona *et al.* 2006). *Anolis heterodermus* can be categorized as forest species that uses the edge and the interior interchangeably. On the other hand, when the quantity and quality of food resources improve, so does individual growth rate (Vogel 1984, Guyer 1988a, b, Sinervo & Adolph 1989). Thus, by increasing patch size and perimeter, therefore herbaceous coverage also increase at the patch edge. More herbaceous vegetation enhances the food availability and perches to thermoregulation for juvenile lizards. Therefore, greater amount of herbaceous coverage available in large patch perimeters may improve juvenile lizard growth rates in larger patches, which reflects the direct relationship of juvenile–adults transition rates with patch area.

Demographic strategies in fragmented landscapes.—Our demographic results indicate that the six populations showed an increase or stability in their population sizes, which means that in different environmental conditions, population adopt different demographic strategies (Rojas-González *et al.* 2008). Similar environmental conditions in the same habitat could lead to convergent life-history strategies (Ferguson *et al.*1980, Ballinger & Congdon 1981). Thus, the observed pattern in *A. heterodermus* population dynamics fits the scenario where in populations inhabiting larger patches, growth is the most important demographic process, whereas in smaller patches, the predominant process is stasis. These divergent demographic strategies also fit the adult lizard mortality and transition rate trends and suggest that larger and smaller forest fragments require different management strategies to conserve lizard populations.

The fast-slow continuum hypothesis states that adult mortality regimes are the main selective factors in the evolution of life-history strategies (Promislow & Harvey 1990, Charnov 1991, Stearns 1992). In our study, high adult survival rates (*i.e.*, low mortality) and low transitions rates for populations inhabiting smaller patches were associated with slower growth and delayed maturity (slow life cycle), whereas populations inhabiting large patches predominately showed low adult survival (low mortality), but high transition rates associated with fast growth and early maturity (fast life cycle).

As elasticity can be interpreted as the intensity of selection acting on different life stages (Van Tienderen 2000), in fast life cycles, growth and fecundity are important for population fitness; however, in slow cycles, stasis is most important for the population fitness (Benton & Grant 1999). These strategies have also been documented for other taxa, such as plants (Franco & Silvertown 1996), fishes (Letcher *et al.* 2007), birds (Sæther & Bakke 2000), mammals (Heppell *et al.* 2000, Oli & Dobson 2003), and for population of lizards inhabiting different climatic zones (Rojas-González *et al.* 2008) or through time (Zúñiga-Vega *et al.* 2007, 2008). Furthermore, populations with a fast demographic strategy generally maintain their long-term growth rate greater than or equal to one (Andrews 1988, Van Sluys 2000, Wiederhecker *et al.* 2003), whereas in populations with growth rates below one, the slow strategy is favored by reducing growth and delaying reproduction (Blomberg & Shine 2001).

CONCLUSION

Our results are preliminaries and only document 7 mo of the annual population dynamics of six *A. heterodermus* populations in fragmented Andean scrub forest, but show the consequences of habitat transformation on species populations' life history. The elasticity analysis predicts the population behavior when the same vital rates persist over time. It is plausible, however, that demographic pattern changes depending on climatic variation, such as during El Niño Southern Oscillation (ENSO) years, in synergy with anthropogenic disturbance, and deforestation patterns of native forests.

Our results can be interpreted as a warning signal that illustrates the consequences of habitat fragmentation and loss processes on short-term population dynamics because populations in small patches are less resilient due to their demographic strategy, then fluctuation in the number of individuals impact more strongly on these populations. Our results also document how these processes can act alone or synergistically, to the detriment of populations of *A. heterodermus*. In this sense, fragmentation and loss of natural vegetation result in negative changes in critical reproductive categories of these populations. An increase in habitat fragmentation could generate more frequent population fluctuations due to hyper-dynamism in λ, amplifying the probability that density-dependent processes occur in populations from fragmented landscapes. At the same time, if habitat isolation increases the inbreeding depression, then the loss of genetic variability in lizard populations might also increase. In particular, further fragmentation of the scrubland Andean landscape could result in smaller patch sizes that cross critical thresholds, thereby produc-

ing slow demographic strategies in anoles lizard populations that make them more vulnerable to drastic environmental and demographic changes.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Models evaluated to test effect of habitat factors and covariates on vital rates of* A. heterodermus *populations.*

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