TASK 4 A & B

A POPULATION VIABILITY ANALYSIS OF THE PLATEAU (HOLBROOKIA LACERATA) AND TAMAULIPAN (HOBROOKIA SUBCAUDALIS) SPOT-TAILED EARLESS LIZARDS

ABSTRACT: The historical range of Spot-tailed Earless Lizard populations have declined substantially over the last 70 years. Despite a decade of research, much uncertainty remains about which factors are driving this decline. Consequently, conservation planning is often difficult because of the uncertainty as to which actions will successfully reduce species declines and curtail extinction risks. Here, we used a hybrid theoretical-empirical model framework to perform quantitative population analyses via the modeling software, VORTEX, for both the Plateau (*Holbrookia lacerata)* and Tamaulipan (*Holbrookia subcaudalis*) Spot-tailed Earless Lizards (STEL). The underlying objectives of these models were to identify which parameters of demography drive population growth, to evaluate the impacts of catastrophic events (e.g., drought) and habitat loss on the long-term viability of the species, and to compare the efficacy of potential management and conservation strategies, such as supplementation of captive-reared individuals and habitat restoration. Elasticity analysis of the baseline simulation and manual perturbation analysis of changes in different demographic parameters demonstrated that changes in the mortality rates of hatchlings (age class of 0–1) had the strongest effect (+) on population growth rates and extinction risk. Other important variables that also exhibited high sensitivities to change are the age of first reproduction (-), the percentage of females breeding within a population (-), female sex ratios at birth (+), and clutch size (-). The pressures of a severe drought event can dramatically affect the reproduction of STEL, which in turn lead to population

decline due to low rates of juvenile recruitment. Simulations of anthropogenic impacts showed that small increases in habitat loss (e.g., 2%) can exacerbate extinction risk even for stable populations. Furthermore, the evaluation of four management scenarios revealed that the combination of habitat restoration efforts with supplementation of captive bred individuals yielded the highest population growth as well as genetic diversity. Results from this study emphasize the need for management practices to be aimed at increasing recruitment of individuals into the breeding pool (i.e., decreasing hatchling mortality) and promoting the conservation of suitable STEL habitat.

INTRODUCTION

The Spot-tailed Earless Lizards (Plateau, *Holbrookia lacerata*; Tamaulipan, *Holbrookia subcaudalis*; hereafter both are referred as STEL) are small, enigmatic reptiles native to Texas. Previously, they were recognized as two subspecies, Plateau STEL (*Holbrookia lacerata lacerata*) and Tamaulipan STEL (*Holbrookia lacerata subcaudalis*), but recent investigations of their nucleic and mitochondrial DNA have elevated them to two distinct species (Hibbitts et al. 2019, Roelke et al. 2018). Although small in size, STEL are important ecological contributors in Texas ecosystems because they fill a critical role both as a predator for insects and pests and as prey for mammalian, avian, and larger reptile species (Walkup et al. 2018; Neuharth et al. 2018; Rangel et al. 2023a, 2023b). As of 2011, these species have gained the attention of government wildlife agencies (e.g., US Fish and Wildlife Service (USFWS) and Texas Parks and Wildlife Department (TPWD)) due to allegations of both species experiencing a critical population decline across Texas (DOI 2011). Historically, STEL were present across 75 counties with Plateau STEL existing throughout West Central Texas, and the Tamaulipan STEL occurring throughout South Texas and into parts of the Mexican States of Coahuila, Nuevo Leon, and Tamaulipas (Axtell 1956, 1968; Duran and Axell 2010).

The observed population declines of STEL are believed to be the result of habitat loss, agricultural practices and pesticide use (Axtell 1998; Gibbins et al. 2000; Hopkins 2000), urbanization (McKinney 2008; Wolf et al. 2013), invasive species (Flanders et al. 2006; Fulbright et al. 2013), climate change (Karl et al. 2009, Laduc et al. 2018), and oil and gas development (Pierre et al. 2017; Wolaver et al. 2018).

The few populations of STEL that are thought to be stable are potentially due to long-term maintenance of habitat management practices that are favorable for STEL population persistence (Duran 2014; Hibbits et al. 2021). The growing concern for the conservation for both species has led to protection efforts under the Endangered Species Act by the US Fish and Wildlife Services (DOI 2011; USFWS 2011). However, the lack of data on STEL makes it difficult to quantify relationships between environmental stressors and population dynamics, which present a challenge for conservation planning and assessment.

Morphology

The genus *Holbrookia* is coined after the American zoologist John Edwards Holbrook (Stejneger 1890, Axtell 1956). *Lacerata* is derived from the Latin word "*lacerare*," meaning to cut, destroy, or mangle (Hibbits et al. 2019). It is believed that the reason behind the name “lacerata: is due to the serrated appearance of the posterior border of the transverse brown bars on the back (Cope 1880; Hibbits et al. 2019). The name *subcaudalis*, which is derived from the latin word “*sub*” meaning under or below and “*cauda*” meaning tail, refers to the dark spots on the underside of the tail in the Tamaulipan STEL (Hibbits et al. 2019).

Plateau STEL can be distinguished by the dark, fused blotches forming two rows of transverse bands on each side of the dorsal vertebral line (Axtell 1956, 1968; Hibbits et al. 2019). The appearance of fused blotches continues down to their hind limbs and resemble distinct bands (Axtell 1968). The average adult snout-vent length (SVL) is 55 mm but can range from 32 mm to 64 mm (Axtell 1968, Hibbits et al. 2019). The sum of all femoral pores equals less than 27, with 12 to 13 femoral pores usually observed on each leg (Axtell 1956, 1968; Hibbits et al. 2019). Some individuals will exhibit up to 4 black lateral spots below the cloacal opening (Axtell 1956, 1968; Hibbits et al. 2019). The species is a tan to caramel color. During the breeding season, female Plateau STEL develop a red-orange pattern coloration on the throat, as well as a vibrant, yellow coloration on each dorsolateral side (Axtell 1956, 1968; Duran 2017; Hibbits et al. 2019).

The Tamaulipan STEL can be distinguished by the unfused body blotches forming two longitudinal rows on each side of the dorsal vertebral line (Axtell 1956, 1968; Hibbits et al. 2019). The dark blotches found on their hind legs are also unfused and circular in shape. The average adult snout-vent length (SVL) is 56 mm, but it ranges from 31mm to 72mm (Axtell 1956, 1968; Hibbits et al. 2019). The sum of all femoral pores is greater than 27, with up to 19 femoral pores present on each leg (Hibbits et al. 2019). Tamaulipan STEL are gray in color and most individuals have 1-5 black lateral spots posterior to the cloacal opening (Axtell 1956, 1968; Hibbits et al. 2019). Unlike the Plateau STEL, female Tamaulipan STEL will not develop a red-orange coloration pattern on their throats but will still exhibit a yellow-green coloration on each dorsolateral side during the breeding season (Axtell 1956, 1968; Hibbits et al. 2019). It has also been documented that Tamaulipan STEL have longer hind limbs and longer tails than Plateau STEL (Hibbits et al. 2019).

Systematics

The *Holbrookia* genus falls under the ‘sand lizard’ lineage within the family *Phrynosomatidae* (Wiens et al. 2010; Roelke 2018), which consists of >120 currently recognized species belonging to 9 different genera: *Uma*, *Uta*, *Callisaurus*, *Cophosaurus*, *Holbrookia*, *Petrosaurus*, *Phrynosoma*, *Sceloporus*, and *Urosaurus* (Clarke 1963). Within the *Holbrookia* genus, there are four recognized species, *H. elegans*, *H. lacerata, H. maculata,* and *H. propinqua*, that can be characterized by the lack of a visible external auditory canal (Roelke et al. 2018). Historically, the single species named the Spot-tailed earless lizard (*Holbrookia lacerata*) had two recognized subspecies: *Holbrookia lacerata lacerata* (northern Spot-tailed Earless

Lizard) and *Holbrookia lacerata subcaudalis* (southern Spot-tailed Earless Lizard), that were distinguished based on allopatric and morphological distinctive criteria (Axtell 1956, 1958). The combined evidence of recent genetic examinations of the patterns in data sequencing derived from two genes, one nuclear (RAG-1) and one mitochondrial (ND2), morphological variation, and geographical distribution concluded these subspecies as distinct (Roelke et al. 2018; Hibbits et al. 2019).

Reproduction And Longevity

Both STEL are oviparous, and egg-laying is documented to occur twice, annually, within the breeding season. The first oviposition occurs between May and June, and the second oviposition occurs between July and August (Axtell 1956; Rangel et al. 2022). STELs reach sexual maturity as early as 6 months to 1 year and have an estimated life expectancy of 5 years (Axtell 1956; Duran 2017). It is projected that female STELs younger than one year will typically deposit approximately 4 to 6 eggs during the initial egg-laying period and 5 to 7 eggs during the subsequent period (Axtell 1956). On the other hand, females two years or older are expected to lay 7 to 12 eggs during each egg-laying cycle (Axtell 1956). The eggs are laid and incubated underground and hatch in approximately five to six weeks (Axtell 1956).

Distribution

Plateau and Tamaulipan STEL exist in allopatry and are geographically divided by the Balcones Escarpment (Axtell 1956, 1968; Hibbits et al. 2019). The Balcones Escarpment limits many other reptile species, notably the Eastern Collard Lizard (*Crotaphytus collaris*) and the Ring-necked snake (*Diadophis punctatus*) whose distributions do not extend south of the Balcones Escarpment in Texas, while the distributions of Central American Indigo Snake (*Drymarchon melanurus*), Texas Tortoise (*Gopherus berlandieri*), and Rose-bellied Lizard

(*Sceloporus variabilis*) do not extend north of the Balcones Escarpment (Smith and Buechner 1947; Dixon 2013; Hibbits et al. 2019). The sister species, Striped Whipsnake (*Masticophis taeniatus*) and Schottt's Whipsnake (*M. schotti*) also diverge at the Balcones Escarpment and do not coexist in the same area (Camper and Dixon 1994; Hibbits et al. 2019). Due to the many examples of species divergence along the Balcones Escarpment, this geographic feature appears to be extremely important relative to the distribution of reptiles in Texas and likely has contributed to the high amount of reptile diversity in the state. The Plateau STEL includes all the populations found on the Edward's Plateau ecoregion, north of the Balcones Escarpment (Axtell 1956). This distribution extends north to the Colorado River, east to the eastern edge of the Balcones Escarpment and west to the Pecos River and southern edge of the Llano Estacado (Axtell 1956; Hibbits et al. 2019). The Tamaulipan STEL includes all the populations that are distributed south of the Balcones Escarpment line in the Tamaulipan biotic province of southern Texas. Their distribution extends to the west of the Sierra Madre Oriental in Coahuila, Nuevo Leon, and Tamaulipas, Mexico (Axtell 1956, Hibbits et al. 2019).

Diet

Plateau and Tamaulipan Spot-tailed Earless Lizards are sit-and-wait predators that consume a variety of small-bodied arthropods (Axtell 1954; Hibbitts and Hibbitts 2015, Laduc et al. 2018; Rangel et al. unpubl.). Dietary records indicate that both species' diet consists of small, flying, or hopping insects (Axtell 1954, Laduc et al. 2018). It has been observed that the movement of prey items is essential for capture (Axtell 1954; Rangel et al. unpubl.). Orthopterans are significant prey items of STEL feeding ecology, and they represent the main source of food by volume (Laduc et al. 2018; Rangel et al. unplub.). Grasshoppers are the largest known diet item for these lizards and are likely the most abundant in their environmental niche (Laduc et al. 2018). Furthermore, orthopterans make up more than a third of the diet of both young and adult lizards, indicating their relevance in lizard population maintenance and growth across time (Laduc et al. 2018). Beetles and spiders are the lizards' next most common prey, followed by caterpillars, ants, and true bugs (Laduc et al. 2018). The presence of prey items, such as bees, wasps, and spiders, which prefer to land and move through vegetation, and grasshoppers, which are cryptic when resting in vegetation, reveals that STELs are versatile foragers (Axtell 1954, Laduc et al. 2018). Spot-tailed Earless Lizards are opportunistic generalists that eat few numbers of individual prey items, but will take advantage of large prey items, such as grasshoppers, if the opportunity arises (Laduc et al. 2018). This likely reflects a preference in the foraging strategy of STELs, where focus is on single large, rather than numerous, prey items.

Behavior

Plateau and Tamaulipan STEL are diurnal with a bimodal activity pattern, depending on the season and weather (Axtell 1956; Roelke et al. 2018). During the winter months, STEL are most likely underground or under vegetation cover in a state of dormancy and will consume little to no food items (Laduc et al. 2018). Burying behavior is well documented within the phrynosomatid sand lizard lineage and is exhibited as a method to avoid extreme temperatures and predation, and to lay eggs (Axtell 1956; Hibbitts and Hibbitts 2015; Neuharth et al. 2018; Rangel et al. 2022). STEL will bury themselves into the substrate by “shimming”, which is described as the act of rapidly wiggling their bodies in a back-and-forth movement (Axtell 1956; Rangel et al. 2022). STEL are documented to be extremely wary and will often seek refuge from potential threats by burying themselves in soil substrate (Axtell 1956), hiding beneath leaf litter (Neuharth et al. 2018), or utilizing the burrows of mammals, such as ground squirrels, when available (Axtell 1954; Duran and Yandell 2014). Burying behavior in STEL also coincides with periods of inactivity that typically occur on cool, overcast, and rainy days (Axtell 1956; Neuharth et al. 2018). When active, STEL have been observed basking in areas of bare ground as well as perched on rocks, dirt clods (Axtell 1956, Neuharth et al. 2018), and elevated surfaces, such as wooden fence posts (Owen et al. 2023).

Habitat

STEL were historically found in a variety of habitats such as prairies, mixed-oak-juniper woodlands, and chaparral shrublands across their range (Axtell 1956, 1968; Wild Earth Guardians 2010). Both subspecies (now species) of STEL don't appear to have an extreme obligation to very specific habitats, though they do retain a habitat preference of desert grasslands, mesquite savannahs, or coast prairies harboring some form of disturbance (Duran and axtell 2010; Duran 2014; Kahl et al. 2022). Studies document STEL occur in grazed grasslands with sparse vegetation, minimal woody encroachment, and flat, clayey loam soils free of ground litter (Axtell, 1954, 1958; Duran, 2017; Hibbitts and Ryberg 2017; Kahl et al. 2022). Soil types range from sandy to clay loams, including non-clay loams, but pure sands are typically absent in the habitats of both STEL (Axtell 1956, 1998). Additionally, STEL are observed inhabiting the plowed fields of heavily disturbed agricultural fields (Hibbitts and Ryberg 2017).

Conservation and Threats

Agriculture and Pesticide Use

For most terrestrial lizards, the plowed soils of agricultural fields are extremely simplified habitats, characterized by only herbaceous vegetation, bare soil and, consequently, by the almost complete lack of shade and shelters, except for deep vertical crevices when the soil dries, which may provide temporary refuges from predators. However, STEL were continuously observed in agricultural fields throughout field surveys (Hibbitts and Ryberg 2017; Roelke et al. 2018). The loose soils of agricultural areas are believed to be utilized by STEL to exploit invertebrates and to retreat into predator cover or thermoregulation activity (Roelke et al. 2018). However, inhabiting agricultural fields may expose STEL to pesticides (Gibbs et al. 2009). Studies regarding the toxicological effects of pesticides on reptiles are scarce (Hopkins, 2000; Campbell and Campbell, 2002), but potentially lethal as well as sub-lethal effects have been reported (Weir et al. 2010, F2015). Toxicological effects encompass a wide array of implications for exposed individuals, ranging from hormonal changes and enzymatic responses, oxidative stress, endocrine disruption, neurotoxic implications, and immunosuppression, to physiological reactions like impairments in fertility, development, and locomotor performance (Amaral et al. 2012a, 2012b, 2012c; Bicho et al. 2013; Hopkins and Winne 2006; DuRant 2006, 2007a, 2007b; Soltanian, 2016, Mingo et al. 2017).

Land Development and Fragmentation

Urbanization has become a critical driver of habitat loss along with fragmentation and isolation, all which threatens biodiversity (Brooks et al. 2002; Dirzo and Raven 2003). Studies of vertebrate and invertebrate communities have shown that individual species respond to landscape fragmentation differently; while some species thrive, others decline (Fahrig 2003; Walkup et al. 2017). Fragmentation isolates populations that can cause population declines in vulnerable species by inhibiting movement and disrupting processes such as dispersal, gene flow, recruitment, and survival (Hokit and Branch 2003, Henle et al. 2004, Mitrovich et al. 2009). As it stands, the remaining STEL populations observed may indicate that the species exists in isolated pockets across their range (Hibbits et al. 2021). Restricted gene flow between fragmented areas facilitates reduced genetic variability within isolated populations, which is critical for the long-term survival of a species (Maldonado et al. 2020). Overall, the conversion of natural habitats into human-modified ecosystems has numerous effects on reptiles. Specifically, habitat conversion is known to affect reptiles by decreasing structural complexity and microhabitat availability, creating shifts in microclimatic conditions resulting from the disturbance, reducing the food resources readily available in the area, establishing a time lag in recolonization of native species, and causing indirect effects by altering interactions between species (Estrada et al. 1993, Blair 1996, Perfecto et al. 1997, Burel et al. 1998). Texas has five of the eleven fastest-growing cities in the United States (USDA Census 2017); thus, land-change is expected to result in continued expansion of urban areas into the historic range of Spot-tailed Earless Lizards (Theobald et al. 2012).

Invasive species

Invasive grasses are widespread in Texas and have continually proliferated and dominated much of the landscape since their introduction in the early 1900s (Gould 1960, 1975; Archer 1989). Buffelgrass (*Pennisetum ciliare*) is one invasive, drought-tolerant grass present over much of South Texas, and it is known to alter fire cycles and vegetation structure in the areas that it invades (Daehler and Goergen 2005; De la Barrera 2008; Stevens and Fehmi 2009); as such, it could change the habitat and therefore present an obstacle to conservation of STEL and other native grassland species. Previous research has also noted that invasive grass negatively affects the survival of most terrestrial lizard populations by creating a dense monoculture in the open ground between shrubs and trees that lizards use for foraging and thermoregulation (Scott 1996). The spread of invasive grasses creates closed canopy brushlands that offer less open space and sunlight availability (LaDuc et el. 2018). STEL, like many terrestrial lizard species, need open spaces with high visibility for foraging as well as predator escape and thermoregulation (Hibbitts and Hibbitts 2015); Therefore, invasive grasses may play a role in the apparent reduction in the distribution of *H. subcaudalis*.

In addition to invasive grasses, the introduction of red imported fire ants (*Solenopsys Invicta*) to Texas in the 1950s (Wojick et al. 2001) has contributed to the decline of several native species including the Houston toad (*Bufo houstonensis*; Brown et al. 2012), Texas horned lizard (*Phrynosoma cornutum*; Goin 1992), and southern hognose snake (*Heterodon simus*; Tuberville et al. 2000). Fire ants attack free-roaming lizards in nature and envenomate them by lifting a scale with their mandibles and inserting their sting shaft into the underlying soft skin (Langkilde 2009). The red imported fire ants' venom has a neuromuscular action (Tschinkel 2006), and a lizard that fails to respond to such an attack will become paralyzed and die. Fire ants also prey on lizard eggs deposited in the soil (Newman et al. 2014). Currently, the range of the fire ant covers the entire current Spot-tailed Earless Lizard range, suggesting encounters between the species may be frequent (Wild Earth Guardians 2010).

Climate warming

The pressing issue of climate change poses an imminent threat to the preservation of global biodiversity and is a perceived threat to the persistence of STEL. Rising temperatures and prolonged droughts combined with anthropogenic development alter and reduce native vegetation composition and support the expansion of invasive species, such as buffelgrass (Marshall et al. 2012), which thrive in the changing climate and pose a threat to STEL survival. Fischlin et al. (2007) proposed that the productivity, structure, and carbon balance of grassland ecosystems are extremely sensitive to climatic shifts. This holds significant implications for STEL, which exhibit strong preferences for short-grass prairies and grassland ecosystems. The anticipated change in range or loss of these ecosystems is predicted to also shift or compress the range and decrease the size of STEL populations in the coming decades as current habitat conditions become unsuitable (Laduc et al. 2018).

Given that STEL are ectothermic, their activity levels are likely to be influenced strongly by climate warming. To counter excessively high temperatures, lizards retreat to cool refuges rather than risk death by overheating. However, spending more time in thermal refuges limits foraging, consequently leading to lower rates of growth, maintenance, and reproduction, thereby undermining population growth rates and raising extinction risks (Sinervo et al. 2010). These cumulative effects of climate change place considerable stress on STEL, jeopardizing their long-term viability.

Population Modeling

Population viability analysis (PVA) models are quantitative analysis methods that incorporate population demographics and stochastic factors to assess the threats of small or declining wildlife populations (Beissinger and McCullough, 2002; Lacy 2019). There are many benefits gained from carrying out a population viability analysis, including the assessment of extinction risk of a population, the determination of life history characteristics that contribute to the species' vulnerability, the identification of key life stages as research or management targets, and the evaluation of management options (Morris et al. 2002). Population viability analyses are critically useful for species with limited life history data, such as STEL, because the tool can facilitate the evaluation of demographic parameter assumptions and it can pinpoint which life history characteristics contribute to the species' vulnerability. As such, population viability analyses are becoming increasingly important in applied management and conservation policy (Reed et al. 2002).

We developed a population viability analysis of STEL via the modeling software package VORTEX (version 10.15). VORTEX is an individual-based modelling program that tracks the fate of each individual independently by simulating their annual life cycle through a series of stochastic events and deterministic forces via Monte Carlo simulations (Lacy and Pollak, 2018). From the several PVA packages available, I selected VORTEX due to its flexible ability to model the effects of demographic rates, environmental variation, catastrophes, and other stochastic events, as well as anthropogenic impacts such as habitat loss and harvesting. VORTEX projects changes in population size, age, sex structure, and genetic variation, while estimating the probabilities and time to extinction and recolonization (Lacy 1993). The population growth rate is calculated by analyzing the average birth and death rates using a standard cohort life table analysis. To incorporate natural and environmental variation, VORTEX samples birth rates, death rates, and carrying capacity from binomial or normal distributions. Additionally, VORTEX can test the effects of different management options on the viability of wildlife populations.

In this study, my aim was to assess the population viability of Plateau and Tamaulipan STEL to provide further evidence of the species' future status that will aid in the determination of whether both species warrant federal protection under the Endangered Species Act. To achieve this goal, my research objectives were to:

1) Identify the life history parameters that characterize a population of STEL.
2) Assess the probability of extinction of STEL over the next 100 years.
3) Determine the primary drivers of STEL population growth through input parameter sensitivity tests.
4) Identify the areas of research and management priority for STEL.

5) Investigate how the threat of catastrophic events and sources of anthropogenic impacts affect STEL population trajectory.

And 6) evaluate the efficiency of conservation and management strategies to promote STEL populations.

The findings of this research demonstrate how PVA simulations can be instrumental in pinpointing crucial demographic and environmental factors necessary for effectively planning conservation measures aimed at ensuring the sustained existence of STEL over the long term.

METHODS

Population Viability Analysis

The process of developing a PVA for STELs involved a thorough review of available STEL literature and data investigation to determine the best baseline demographic rates for a general STEL population and highlight knowledge gaps for the species. All models developed in this current study focus on a solitary, small STEL population to reflect an isolated subpopulation in a fragmented ecosystem or a diminished population within a broader distribution area. While this scenario may accurately depict the current situation for certain STEL populations, the models are employed to access the minimum viable population sizes for the species.

We built a baseline model as a starting point for my analyses (Table 4.1). The baseline model consisted of a closed population with demographic assumptions that may be affecting the population dynamics of both STEL species. All uncertain or assumed input parameters were evaluated further in subsequent sensitivity analyses. Testing uncertain parameters is expected to encourage further studies on the demographic and life history aspects of STELs. In addition, we created a single generalized baseline model to represent both species of STEL because of their overlapping life history traits and overall limited knowledge of life history differences.

Table 4.1. Vital rate estimates and sources used for the baseline model representative of a *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard) population.

SCENARIO PARAMETERS	**Value**	**Source**
Num of iterations	1000	
Num years/timestep	100	
Number of populations	1	
Concordance between environmental variation in reproduction and survival	0.5	Estimated
REPRODUCTIVE SYSTEM		
Breeding System	polygynous	Jones and Ballinger 1987
Age of first offspring	1	Axtell 1956; Jones and Ballinger 1987; Duran 2017
Maximum lifespan	5	Jones and Ballinger 1987; Diane Barber, pers. Comm.
Maximum age of reproduction	5	Jones and Ballinger 1987; Diane Barber, pers. Comm.
Maximum number of clutches per year	2	Axtell 1956; Jones and Ballinger 1987; Duran 2017
Maximum number of progeny per clutch	12	Duran 2017; Rangel et al. 2022
Sex ratio at birth in % males	50	There is no evidence of skewed sex ratios.

Table 4.1. continued

SCENARIO PARAMETERS	**Value**	**Source**
REPRODUCTIVE RATES		
% of adult females breeding	90 ± 10	Estimated
% of breeding females that produce a clutch	70	Estimated
% of breeding females that produce two clutches	30	Assumed parameter
Mean clutch size	10 ± 1	Rangel et al. 2022
MORTALITY RATES (MALES=FEMALES, I.E., EQUIVALENT RATES)		
% mortality from age 0 to 1	80	Jones and Ballinger 1987
SD for above due to environ variability	10	Assumed parameter
% mortality after age 1	50	Jones and Ballinger 1987
SD for above due to environ variability	10	Estimated
INITIAL POPULATION SIZE		
Initial population size	100	
CARRYING CAPACITY		
Carrying Capacity	200	

We established the Vortex baseline PVA for STEL as a population-based model and defined extinction as when only one sex remains living in a population. Baseline scenario settings ran 1000 iterations over 100 years (365-day timesteps). The likelihood for a catastrophe was set as null for the baseline model and had no impact on reproduction or mortality in preliminary evaluations.

The baseline initial population size is set to 100. This is a hypothetical figure designed to be large enough to allow model dynamics to be observed without undue influence from inbreeding and demographic stochasticity. The baseline model was intended to reflect the dynamics of a ‘general’ STEL population in Texas and was not intended to represent a specific population. Therefore, we assumed a single, closed population without the input of individuals through immigration or loss of individuals through emigration. Regarding inbreeding depression, there is no evidence to suggest specific values for the lethal equivalents or the percent of recessive lethal alleles, therefore it was omitted from the PVA.

Environmental variation (EV) is the annual variation in reproduction and survival due to random variation in environmental conditions. These factors can affect reproduction and survival independently or simultaneously. In VORTEX, if this value is set to 0.0, then the environmental variation (EV) in reproduction will be independent of EV in mortality. If this value is set to 1.0, then EV in reproduction and EV in survival will be fully synchronized, signifying good years for reproduction are also good years for survival. We input 0.5 percent for environmental variation (EV) correlation between reproduction and survival to model a moderate relationship between the two.

Baseline scenario settings for reproduction required many inputs. We assumed that STEL generally display a polygynous (not long term) breeding system with 100% of adult males competing for mates. It has been documented that female STEL will lay eggs at one year of age or sooner; thus, we input the age of first offspring for both males and females at one (Axtell 1956). This also falls in accordance with the age of first offspring for other species of the *Holbrookia* genus (Gennaro 1974; Droge et al. 1982; Jones and Ballinger 1987).

Based on the available literature for STEL, the maximum number of clutches per year was set to two, and the maximum number of progeny per clutch was set to 12. Additionally, a mean clutch size of 10.5 ± 1.0 and a mean clutch size of 11.25 ± 0.5 were documented for Tamaulipan and Plateau STEL, respectively (Rangel et al. 2022), thus a mean clutch size of 10 ± 1 was input for the base model.

The oldest known STEL individual was documented to have lived six years in captivity settings (Diane Barber, pers. comm.). Outside of captivity, we assumed a longevity of five years for STEL in their natural environment. If the individual is alive, we assumed it could reproduce (given it is not a juvenile); therefore, the maximum age of reproduction was also five years. Normally, the proportion of breeding females would decrease as the size of the population becomes large. In addition, it is possible to model an Allee effect: a decrease in the proportion of breeding females at low densities, due, for example, to difficulty finding reproductive partners. However, in the case of the STEL populations, there is no evidence that suggests reproduction is density dependent, therefore this component was not included in the modeling efforts. The percentage of adult female STEL that do breed in a population is unknown, but it is estimated that a high percentage of adult females can reproduce due to the number of observations of gravid females being detected at the start of April and the latest being detected in late July (Hibbits and Ryberg 2017). Even so, the percentage of adult female STEL breeding was set to 90% to account for the possibility of a small percentage of females that do not find a mate.

Moreover, it is known that STEL can have a maximum of two clutches annually, but the percentage that do in a given population is unknown. Juveniles have been observed as early as mid-June and as late as September. For the baseline model, we input 70% of females having one clutch and 30% percent having two clutches.

Once the reproductive age is reached, the annual probability of mortality remains constant during the remaining lifespan of the individual and is entered only once in VORTEX. The model data consisted of individuals in two age classes defined as hatchlings at age zero to one, and adults at age one through six. No published quantitative data exists on population size trends and specific mortality rates for STEL. The survival rates of a closely related species, the Common Lesser Earless Lizard (*Holbrookia maculata*), are estimated to be 20, 60, and 40% for 0-1 years old, 1-2 years old, and 2-4 years old, respectively (Jones and Ballinger 1987). Therefore, we input a mortality rate value of 80% for hatchlings and decided on a median of 50% mortality rate for adults. Standard deviation due to environmental variation was set at 10% for all age classes.

VORTEX requires a quantitative carrying capacity (K) to limit maximum population size. The estimation of the carrying capacity for any wildlife population is difficult and does not currently exist for STEL. For this assessment, the value was set at twice the initial population size (K = 200). Also, it is assumed that K was not affected by environmental variation because this is already included in other parameters' values within the model.

Sensitivity Analysis

Sensitivity analyses provide a quantitative approach of assessing a population response (e.g., growth rate or extinction risk) when parameters are varied (Reed et al. 2009). To determine the primary drivers of STEL population growth and identify areas of research or management priority, we undertook sensitivity analysis in two ways: manual perturbation and elasticity analysis.

For manual perturbation, we developed separate model scenarios where we systematically increased or decreased the values of each parameter in proportional increments while holding all other parameters at the baseline value (Table 4.2). This can determine which demographic parameters hold a greater influence in the growth of a STEL population and at which point the vital rates pass the threshold where the probability of extinction rises greatly (Morrison and Reed 2016). For this analysis, we identified the following set of parameters from Table 4.1 whose estimate can be seen as considerably uncertain yet important in the long-term population viability of STELs:

Table 4.2. Demographic input parameters and standard deviations (SDs) due to environmental variation (EV) for sensitivity tests for *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard).

Model Input Parameters	**Tested Parameters**
EV correlation in reproduction and survival	0, 0.5, and 1
Age of first offspring	1,2, and 3
Maximum Age of Reproduction	4, 5, and 6
Number of offspring per clutch	Range 2 to 14; increments of 2
Percent of adult females breeding	Range 0 to 100; increments of 10
Percent of adult females having two clutches	Range 10 to 90; increments of 10
Percent mortality for hatchlings	Range 10 to 90; increments of 10
Percent mortality for adults	Range 10 to 90; increments of 10
Initial population size	25, 50, 75, and 100

Correlation of survival and reproduction

An abundance of resources, such as prey and water availability, was found to be correlated to an increase in reproduction but not in survival for Flat-tailed Horned Lizards (*Phrynosoma mcallii*; Young 2010), thus the relationship between EV in reproduction and survival could be uncorrelated to each other for desert-dwelling lizards. Yet findings from other *Phrynosomatids* indicate that good environmental conditions that support overwinter survival also result to higher reproductive success during the breeding season (Whitford and Creusere 1977). Therefore, we tested 0.5% (baseline), 0% (reproduction is independent from environmental variation (EV) in survival), and 1% (environmental variation in reproduction and survival are directly correlated with one another) to examine the parameter space.

Age of reproduction

The age of reproduction in STEL is size-dependent (Barber, pers. comm.); therefore, the age at which a lizard reaches the length of sexual maturity can vary with climatic conditions (Adolph and Porter 1996) and resource availability (Whitford and Creusere 1970; Dunham 19878). We tested age 1 (baseline value), age 2, and age 3 to examine the effects of delayed maturity due to poor environmental conditions.

Sex Ratio (Male to Female)

The sex ratio between the offspring of a reptile population can vary from year to year. We tested 40, 45, 50 (baseline), 55, and 60 percent of the population being male to determine the impact of a reduction in female population proportion on STEL populations.

Maximum lifespan and age of reproduction

Due to the uncertainty of STEL lifespan in wild populations, we tested the values 4, 5 (baseline), and 6 to determine if a greater longevity increases annual population growth.

Percent of adult females breeding

The percentage of female STEL successfully breeding could be impacted by habitat fragmentation (Ryberg et al. 2015), climate change (Sinervo et al. 2010), disease, or predation (Hathcock and Hill 2019). Therefore, we compared the baseline value of 90% females breeding with a full range of possibilities from 0 to 100% (incrementally raised by 10). For all values tested, the standard deviation due to environmental variation remained at 10%.

Percent of females that double clutch

Similar to the percentage of adult females breeding, the percent of females that are capable of producing two clutches in a season could be influenced by a myriad of factors. Here we compared the baseline value of 30% with a range from 0 to 90% (incrementally increased by 10) to evaluate the parameter space in this model.

Mean clutch size

Rangel et al. (2022) reported the expected mean clutch size is 10 ±1 and 11 ±1 for Plateau and Tamaulipan STEL, respectively. Axtell (1956) estimated that female STELs will lay smaller clutches of 4 to 6 eggs, while older STEL will lay between 7 to 12 eggs. therefore, we tested clutch sizes of 2, 4, 6, 8, 10 (baseline), 12, and 14 to explore the effects of having clutches higher or lower than the expected average.

Percent mortality per age class

It has been postulated that changes to the mortality rates of juvenile and adult STEL could be associated with numerous threats during dispersal (Ryberg et al. 2013; Walkup et al. 2019), due to landscape configuration (Hibbitts et al. 2013; Ryberg et al. 2013; Ryberg et al. 2015), or general predation (Hathcock and Hill 2019). We tested the percent mortality for both age classes ($x < 1$; $x > 1$) from a range of 10 to 90% in increments of 10.

Initial population size

It is estimated that the few known populations of STEL vary from a few dozen to several hundred individuals. We tested the following range of initial population sizes that we hypothesize represent the general estimated sizes of different isolated populations within the distribution of the species: 50, 100, 200, and 300. To maintain consistency, the carrying capacity (K) was set at 50% increase of the scenario's initial population size. In other words, with an initial population size of 50, the carrying capacity (K) is set at 75.

We performed a more conventional elasticity analysis to assess how population growth varies in relation to small changes to vital rates, which would be indicative of parameters in need of research or management priority. We varied the values by +10% and -10% for ten demographic parameters, while holding all other parameters at the baseline value and ran independent VORTEX simulations to determine the new annual population growth rate (λ) associated with the percentage change in that parameter (Table 4.3).

Table 4.3. Changes in key parameter values and the associated change in annual population growth rate (λ).

Parameter	**Parameter values**			**Lambda values**		
Model Parameter	**Minimum (-10%)**	**Baseline**	**Maximum (+10%)**	**-10%**	**Baseline**	**+10%**
Mean Clutch Size	9	10	11	1.38	1.50	1.60
Sex Ratio at Birth	45	50	55	1.40	1.50	1.60
% Females Breeding	81	90	99	1.40	1.50	1.59
SD due to EV on % Females Breeding	9	10	11	1.49	1.50	1.49
% Hatchling Mortality (0 – 1)	72	80	88	2.00	1.50	0.98
% Combined Adult Mortality (1+)	72	80	88	1.56	1.50	1.44
% Female Adult Mortality (1+)	45	50	55	1.56	1.50	1.44
% Male Adult Mortality (1+)	45	50	55	1.50	1.50	1.50
SD due to EV on hatchling mortality	9	10	11	1.53	1.50	1.46
SD due to EV on adult mortality	9	10	11	1.50	1.50	1.49

We then calculated the sensitivity value, which is a measure of the proportional change in a population's intrinsic growth rate given a change in a specific parameter while all other parameters remain constant (Caswell 1989). The proportional sensitivity, S, for each parameter tested was determined through the following equation:

$$\mathbf{S = [(\lambda_{Max} - \lambda_{Min}) / (0.1 * \lambda_{Base})]}$$

Where lambda, λ, is the annual rate of population growth calculated from the simulation and subscripts Max, Min, and Base refer to the simulations that include the lambda value associated with the baseline parameter increased by 10%, the lambda value associated with the baseline parameter decreased by 10%, and the lambda value associated with the baseline parameter, respectively. Using this formula, those parameters with the S values >1 or <-1 show the greatest degree of response in terms of population growth rate to changes in those parameters and, hence, the greatest sensitivity (Cross and Beissinger 2001).

Catastrophe Analysis

Catastrophes are singular, environmental events that are outside the bounds of normal environmental variation affecting reproduction and/or survival. These events are modeled in VORTEX by assigning an annual probability of occurrence and a pair of severity factors describing their impact on mortality (across all age-sex classes) and the proportion of females successfully breeding in a given year. These factors range from 0.0 (maximum or absolute effect) to 1.0 (no effect). The effects of these factors are imposed during the single year of the catastrophe, after which time the demographic rates rebound to their baseline values. Although catastrophes tend to have a major influence on the probability of extinction, these effects are often difficult to estimate (Reed et al. 2003). We concluded that a drought would be an appropriate natural event that could result in catastrophic reductions on a relatively small STEL population with an initial population size of 50 individuals.

To determine the impact of current and future long-term droughts on population viability, we parameterized the frequency of catastrophic droughts by counting the number of drought events with a Palmer Drought Severity Index value above -4 that have occurred on the Edward's Plateau and south-central region simultaneously in a century. We counted nine such events: 1908–1911, 1915–1918, 1924-1925, 1950– 1957, 1961-1967, 1995- 1996, 1999- 2001, 2005-2006, and 2010-2012 that occurred in the Edward's Plateau region (Nielson-Gammon 2011). Accordingly, we used a drought frequency of 9%, or 9 drought events per 100 years.

In the presence of severe droughts, we assumed that the reproductive efforts of female lizards are compromised, as their priorities shift towards survival. Consequently, for my models, drought primarily affected reproduction rather than survival. To investigate the possible effects a drought event can have on STEL population viability, we modeled three severity levels: an optimistic (low), moderate, and worst-case scenario (severe).

For the optimistic scenario, reproduction was affected by 50% and survival was affected by 25%. For the moderate scenario, reproduction was affected by 75% and survival was affected by 50%. For the worst-case scenario, reproduction was completely affected by 50% and survival was affected by 75%. We also created scenarios where we doubled the annual frequency of drought from 9% to 18% to investigate if there is a notable increase in the effects of drought due to climate change (Table 4.4).

Table 4.4. Modeled probability of a drought with different severity levels for a *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard) population initially consisting of 50 individuals. Severity levels are expressed as reduction factors (e.g., a severity level of 1.00 means no influence, and a severity level of 0 reflects the greatest influence).

Type of Catastrophe	**Frequency**	**Severity Level**	**Effect on Reproduction**	**Effect on Survival**
Drought	9%	Low	0.50	0.75
		Moderate	0.25	0.50
		Severe	0.0	0.25
	18%	Low	0.50	0.75
		Moderate	0.25	0.50
		Severe	0.0	0.25

Habitat Loss Analysis

Anthropogenic activities in the historic range of STEL include the Eagle Ford and the Permian Basin provinces, in addition to areas that were converted to agriculture or experienced extensive urbanization. Because Texas has five of the eleven fastest-growing cities in the USA (forecasted 2020–2070 population growth of 70%; Census 2016; Wolaver et al. 2018), land-change is expected to continue around expanding urban areas within the historic range of STEL (Theobald et al. 2012). To assess the effects of habitat loss on a STEL population, simulations were run with an annual decrease rate of 0.25, 0.50, 0.75, 1.00, and 2.00 on the carrying capacity (K) for a STEL population of 20, 50, 100, 200, and 300 individuals. Simulations were run for a total of 100 years.

Management Analysis

We created a series of scenarios to explore the impact of major conservation efforts, such as head-starting and habitat restoration programs, on STEL population dynamics. In each simulation, we used baseline values for all parameters except for hatchling and adult mortality. Scenarios included:

1. No human intervention: There is no supplementation of STEL that were reared in captivity to be released into a population of 50 STEL, and the carrying capacity is neither decreasing or increasing (K = 200) in this scenario. All parameters follow the baseline model values with the exception of the hatchling and adult mortality rates, which were increased by 10% of their baseline value (Mort_H = 88% and Mort_A = 55%).
2. Supplementation program: In this scenario, adult male and female STEL are supplemented in pairs of 10 every other year, beginning on year 1 and ending on year 50 of the simulation. A total of 250 individual STEL would be released into a population

with an initial size of 50 STEL (K= 200) by the end of the supplementation program. All parameters follow the baseline model values with the exception of the hatchling and adult mortality rates, which were increased by 10% of their baseline value ($Mort_H$ = 88% and $Mort_A$ = 55%).

3. Habitat restoration and/or extension: The assumption that populations decline in response to habitat loss leads to the reasonable expectation that habitat restoration will be able to rescue these declining populations. Habitat restoration efforts for STEL can include controlling for nonnative grass invasion, implementing grazing regimes, and/or through the planting and maintenance of more native grass patches. To test the efficacy of this management practice, we created a scenario where the carrying capacity (K= 200) for a STEL population size of 50 individuals was increased by at least 1.00 % annually throughout the first 50 years of the 100-year simulation. We assumed habitat restoration efforts will decrease mortality rates of hatchlings and adults by at least 10% ($Mort_H$ = 80% and $Mort_A$ = 50%).
4. Supplementation program with habitat restoration: We combined the supplementation program described in scenario 2 with the habitat restoration and/or extension efforts described in scenario 3.

To compare management models, we described the results of stochastic r, mean final population size, probability of extinction, and genetic diversity in relation to one another. Specifically, we described the similarities and differences between management models as well as trends. As a result, the model outputs are meant to provide guidance on management approaches that are likely to be successful relative to one another.

RESULTS & DISCUSSION

Baseline Model

In the absence of stochastic variation, the results of the baseline PVA model resulted in positive growth (Figure 4.1). The results demonstrated a population of STEL that has the potential to increase by 51.1% per year (det-r = 0.5111, $\lambda = 1.6672$). The average number of female offspring produced per breeding female (R_0) was 2.27, which indicates that each generation can replace itself in the population ($R_0 > 1.00$), and the mean generation time for the STEL population was 1.60 years (Table 4.5).

A distribution of ages according to an initial population of 100 STEL demonstrated that the majority of the population is composed of yearlings (70%) and only 2% of the population reached a maximum life expectancy of four years (Figure 4.2). NMy results exhibited similar patterns to what was observed by Hibbits and Ryberg (2017) from STEL distribution surveys conducted for three consecutive years (2015 – 2017), wherein there was a low recapture rate of individuals across all surveyed population units each year, but new unmarked individuals and juveniles were frequently encountered.

Table 4.5. Deterministic results of the baseline model for *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard).

Parameter	**Estimate**
Deterministic growth rate (Det-r)	0.51
Finite growth rate of increase (λ)	1.67
Net reproductive rate (R_o)	2.27
Generation time (T)	1.60

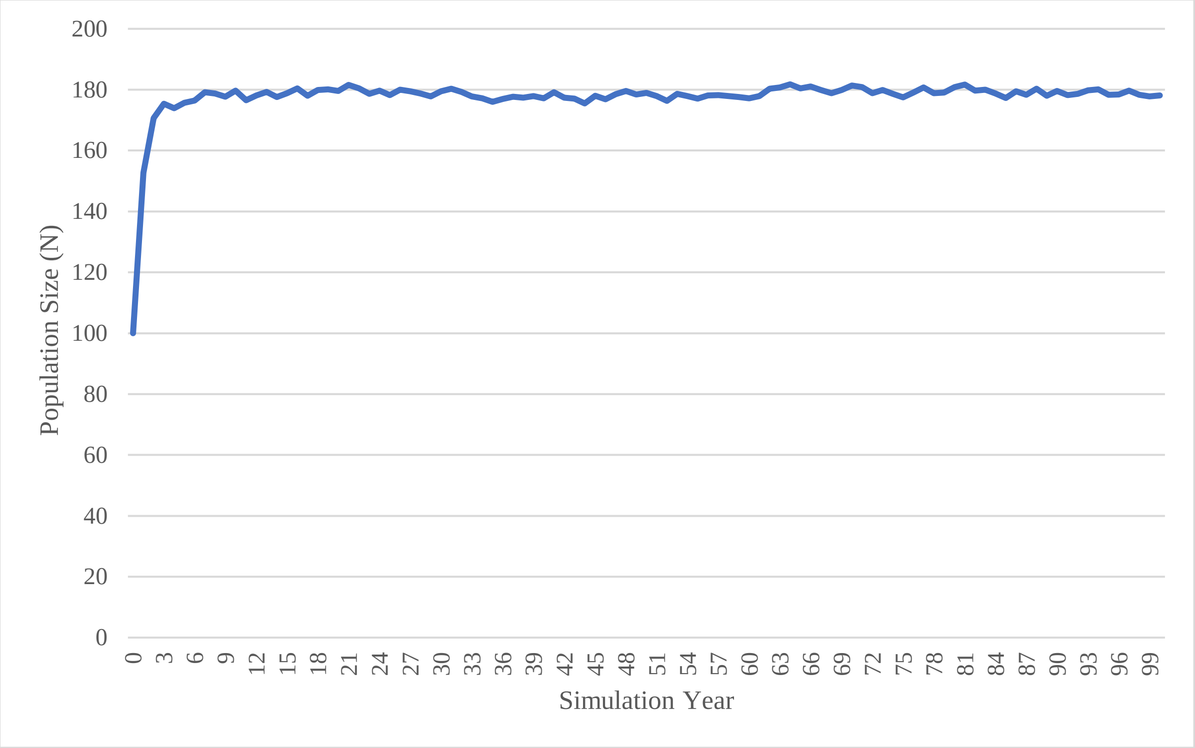

Figure 4.1. The projected population trend of *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard) following the baseline model parameter values. Initial population size is 100 individuals with a carrying capacity of 200.

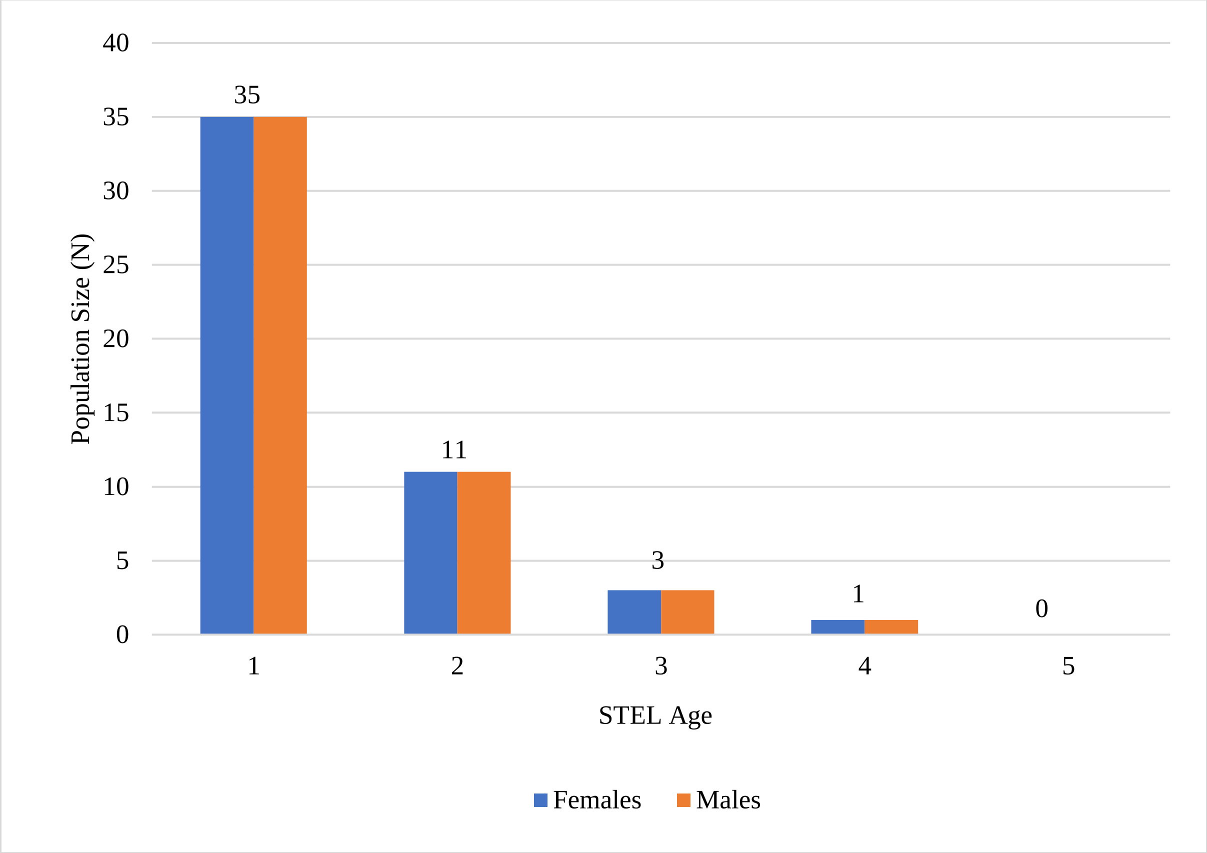

Figure 4.2. Stable age distribution representative of a *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard) population consisting of 100 individuals.

When the effects of demographic and environmental stochasticity (e.g., such as weather, catastrophic events) were accounted for in the model, the population demonstrated the potential to grow 40.8% per year and obtained a mean final population size (N-all = 178) that reached 89% of the carrying capacity (K = 200; Table 4.6). The model predicted that the population was sufficiently resilient, with a 99% chance of survival (PE = 0.01) over the next 100 years. This conclusion may be overly optimistic as real data refutes this due to the observed decline of STEL populations throughout their historic range (Duran and Axtell 2010); however, it is important to note that the baseline model is representative of a best-case scenario. Similarly, a population viability analysis for the Dune Sagebrush Lizard in New Mexico, which is another species currently under review due to drastic population declines, also indicated that metapopulations of the species are secure and have a relatively low risk of extinction (P_E = 0.0 – 0.001%; Leavitt and Acre 2021).

Table 4.6. Stochastic results of the baseline model for *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard).

Parameter	**Estimate**
Mean Growth Rate (Stoch-r)	0.41
Probability of extinction within 100 years (P_E)	0.01
Probability of survival within 100 years (P_S)	0.99
Mean N across all populations (N-extant)	178
Mean time to first extinction (T_E)	15

Demographic Sensitivity Analyses

Correlation between survival and reproduction due to environmental variation (EV)

Varying the EV correlation value between survival and reproduction did not cause a detectable effect to the annual rate of change but all values exhibited positive growth ($\lambda = 1.49$ – 1.51; Figure 4.3). The stochastic population growth rates increased slightly ($r_s = 0.40 - 0.41$) when the EV correlation value was set from 0 to 1 (Table 4.7); therefore, whether environmental factors affect both reproductive output and survival of STEL simultaneously or independently, does not have a strong influence on altering STEL population growth. However, it is important to note that the minimal effect on the population trajectories generated by the model is most likely accounted for by how small the estimated EV inputs for the baseline demographic rates were (Lacy et al. 2021).

Table 4.7. Results of scenarios with varied EV correlation between reproduction and survival. (0 = EV in reproduction is independent of EV in mortality; 0.50 = EV in reproduction is partly correlated to EV in mortality; 1 = EV in reproduction and EV in survival are synchronized).

EV Correlation Value	**Stoch-r**	**P(extinct)**	**N-all**
0	0.40	0.00	181
0.5	0.41	0.00	178
1	0.41	0.00	177

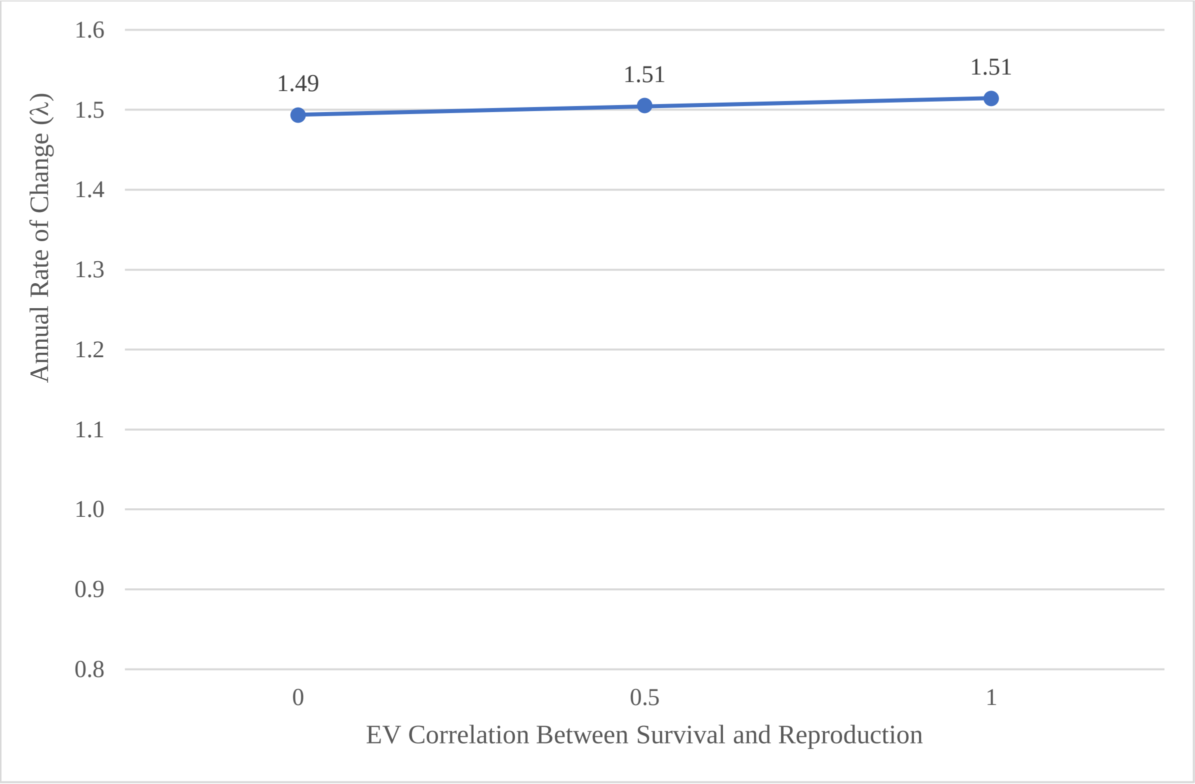

Figure 4.3. Predicted annual rate of change, λ, in relation to environmental variation between reproduction and survival (0, 0.5, and 1.0) for *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard).

Age of first reproduction

The model simulations demonstrated that increasing the age of first reproduction had a great effect on STEL population growth and probability of extinction. When the age of first reproduction is set at 1, the population experienced a positive annual rate of growth ($\lambda = 1.49$) that declined when the age of first offspring was increased to 2 ($\lambda = 0.95$) and 3 ($\lambda = 0.74$; Figure 4.4). At age 3, the population experienced a negative growth rate of 0.30 (Table 4.8). The probability of extinction increased from 3% to 95% when STEL produced their first offspring at the age of 2. The population only experienced positive growth when the age of first reproduction occurred at 1; therefore, this parameter has a significant effect on population persistence, which could be negatively impacted if a significant portion of adult female STEL delay their first offspring after their first year.

Table 4.8. Results of different age of first reproduction on *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard). Population growth rate (Stoch-r), probability of extinction (P_E), and final population size (N-all) are reported for each of the simulations.

Age of First Reproduction	**Stoch-r**	**P_E**	**N-all**
1	0.40	0.03	172
2	-0.06	0.95	3
3	-0.30	1	0

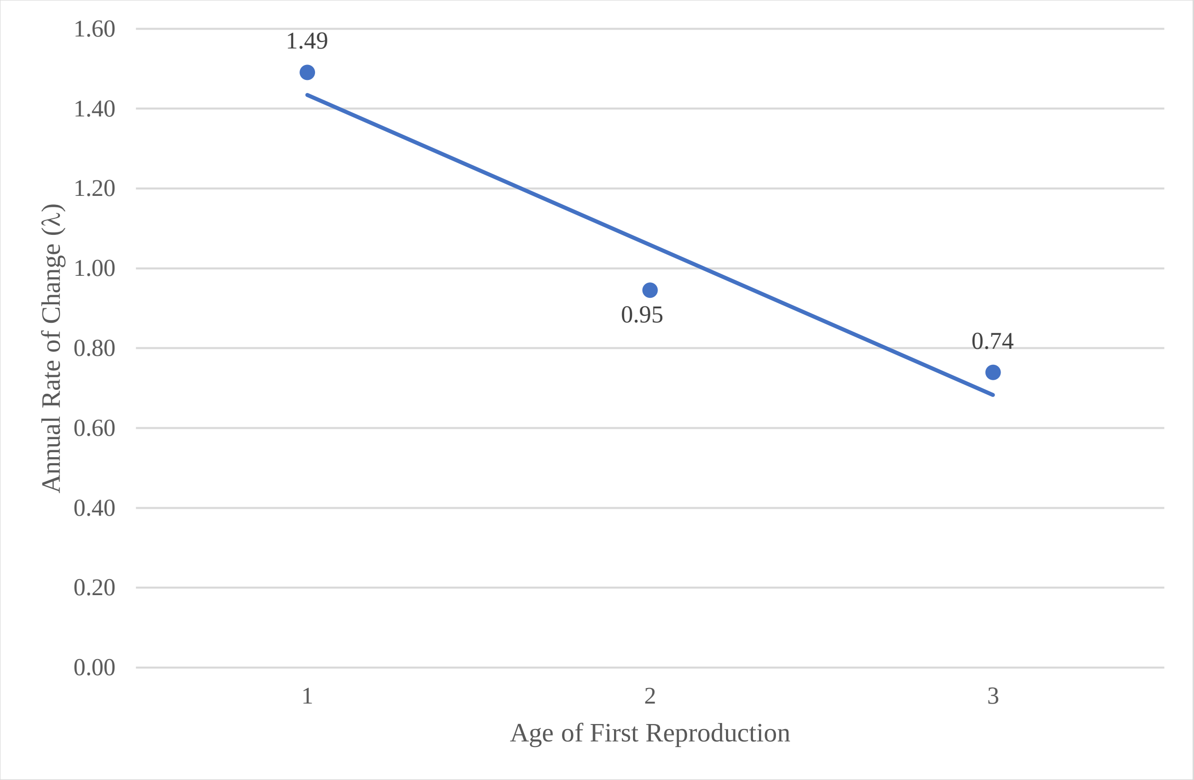

Figure 4.4. The annual rate of change of different ages of first reproduction (1, 2, and 3) on *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard).

The age of sexual maturity is an important life-history trait because it is correlated with fitness and it is usually more sensitive to natural selection than any other life-history trait (Stearns 2000). Both STEL species display similar reproductive traits to *Holbrookia maculata,* which are characterized as an early-maturing, multiple-brooded species with a short life expectancy (Tinkle et al. 1970). Therefore, it is imperative to reproduce within their first year to increase their genetic contribution to the population and to compensate for their short life spans. Delayed reproduction can have significant implications for individual fitness and population dynamics, but the specific consequences depend on the combination of environmental conditions, predation pressure, and competition for resources within the STEL's habitat.

Maximum age of reproduction

Varying the maximum age of reproduction did not cause a detectable change on the annual rate of change and all growth was positive (λ=1.49 – 1.50; Figure 4.5). The probability of extinction for each of the values tested in this analysis were all below 1%, which indicated that increasing STEL reproductive longevity does positively impact the population, but not substantially (Table 4.9). This is likely because the predicted majority of STEL in a population are 0-2 years old (Figure 4.1). Moreover, species that exhibit early maturity normally have shorter life expectancies (Tinkle 1969), thus it is not necessary to aim conservation efforts at lengthening the lifespan of STEL to increase the number of individuals in the breeding pool.

Table 4.9. Results from varied maximum age of reproduction (4, 5, and 6) on *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard). Population growth rate (Stoch-r), probability of extinction (P_E), and final population size (N-all) are reported for each of the simulations.

Maximum Age of Reproduction	**Stoch-r**	**P_E**	**N-all**
4	0.40	0.04	170
5	0.40	0.02	173
6	0.41	0.02	173

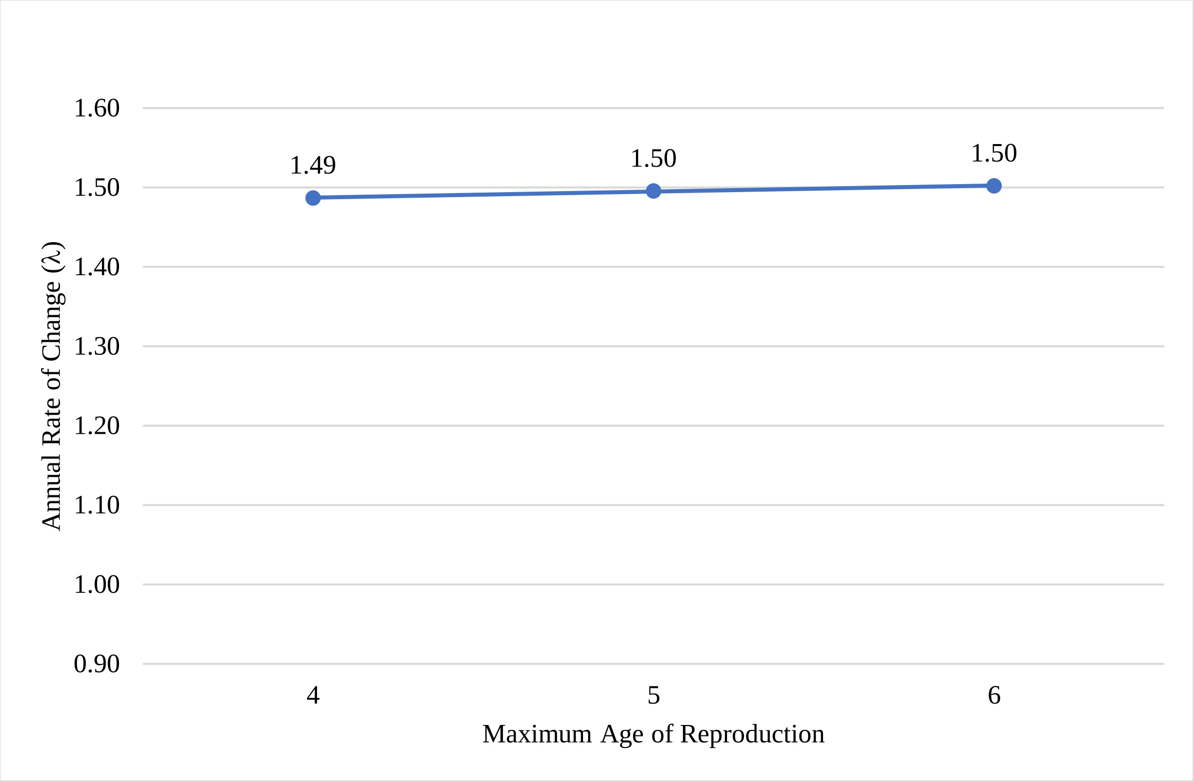

Figure 4.5. The annual rate of change of different maximum age of reproduction values (4, 5, and 6) on *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard).

Sex Ratio (M:F)

The results of the sensitivity analysis suggested that changes in the male-to-female ratio alter STEL population dynamics. The annual rate of change and stochastic population growth decreased yet remained positive with an increased male proportion in the population ($\lambda = 1.70$ to 1.30; stoch-r = 0.53 to 0.26). An increase in the annual rate of change and stochastic growth rate were observed with increased female proportions. The simulations also highlighted a threshold at which an imbalanced male-to-female ratio could substantially increase the risk of population extinction for STEL. The probability of extinction for each of the values tested in this analysis remained below 5% until the male:female ratio reached 60:40, at which the extinction risk rose to 12% (Table 10).

Table 4.10. Results of varied male:female sex ratios at birth for *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard). Population growth rate (Stoch-r), probability of extinction (P_E), and final population size (N-all) are reported for each of the simulations.

Percentage of Males	**Stoch-r**	**P_E**	**N-all**
40	0.53	0.01	183
45	0.47	0.01	179
50	0.40	0.02	180
55	0.33	0.05	163
60	0.26	0.12	143

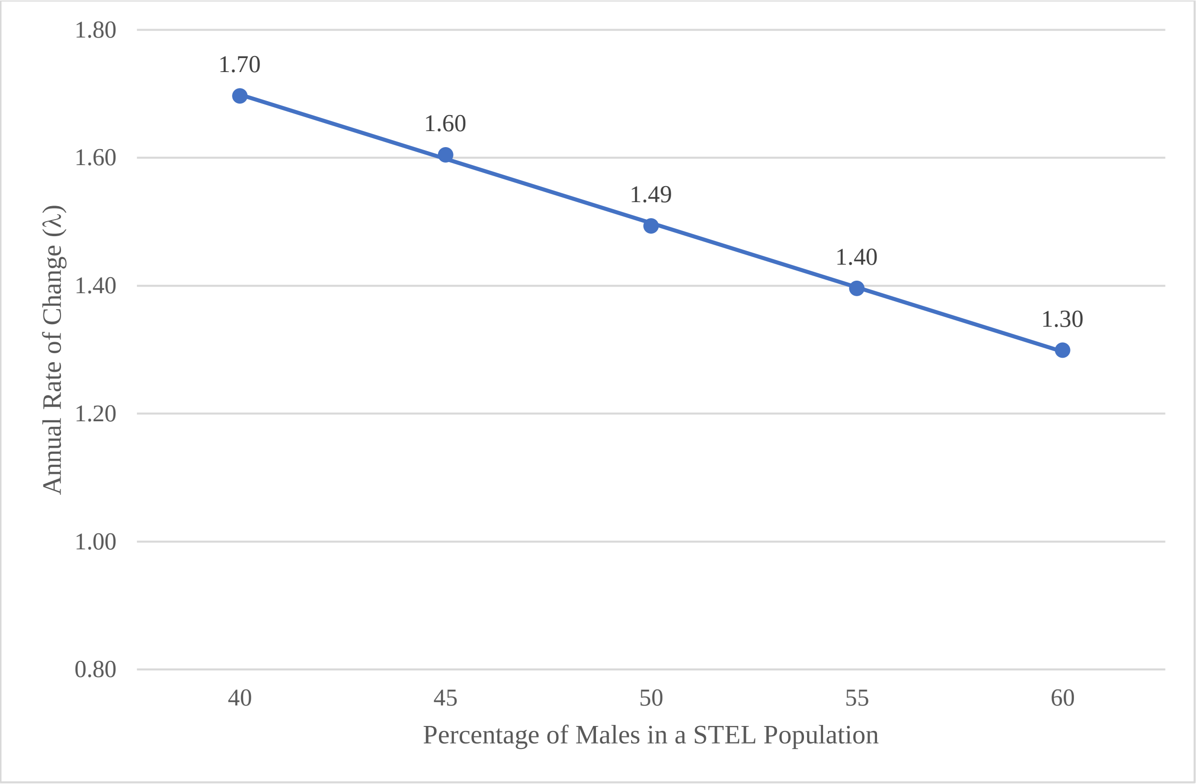

Figure 4.6. The annual rate of change for different percentages of males (40 to 60%; increments of 5) in a *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard) population.

The sensitivity results demonstrated that sex ratio dynamics can result in fluctuations of STEL population dynamics. Specifically, years of consistent male-biased STEL populations lead to a decrease in the population growth and increase in extinction risk. This is likely because fewer females born into the population is reflective of the number of females that are subsequently able to reach adulthood (i.e., reproductive maturity); thus, leading to a decreased reproductive output.

Although little information exists on environmental sex determination in this species, these results have important implications relative to changing weather patterns and climate. For example, if changes in weather patterns and their associated effects on climate alter sex ratios of clutches on long-term time scales as a result of environmental sex determination, STEL populations may decline. Skewed sex ratios of reptile populations as a result of climatic changes also have been a concern in other species that exhibit environmental sex determination. For instance, in the American alligator (*Alligator mississippiensis*), eggs incubated below 31.5°C and above 34.5°C produced mostly female offspring, while temperatures between 32.5°C and 33.5°C produce mostly male offspring (Bock et al. 2020). On the other hand, sea turtles, such as Kemp's Ridley (*Lepidochelys kempii*), produce females at temperatures above 30°C and males at temperatures below 27°C. A 50:50 sex ratio is exhibited at a temperature close to 29°C (Shaver et al. 1998).

Additionally, it has been discovered that the thermal environment can influence or override the sex of the offspring of certain lizard species that exhibit genetic sex determination (Shine et al. 2002, Pen et al. 2010, Quinn et al. 2007, Holleley et al. 2015). For example, the central bearded dragon (*Pogona vitticeps*) is a terrestrial, oviparous lizard that exhibits genetic sex determination and has equal offspring sex ratios over most temperatures (Quinn et al. 2009; Holleley et al. 2015). However, at incubation temperatures above 32°C, the signal from the ZZ (nominally male) sex chromosomes is overridden, resulting in female biased sex ratios (Quinn et al. 2007, Holleley et al. 2015).

With the onset of warmer climate patterns, further research is warranted to determine if environmental conditions affect sex determination of STEL clutches and if skewed sex ratios are already present within STEL populations. However, because STEL are polygynous species, meaning a single male can mate with multiple females, having a 50:50 sex ratio may not be necessary. My results demonstrated that rather than compromising population viability, female biased offspring sex ratios can help population growth by increasing the number of breeding females and egg production. The finding that having a limited number of males may not have a harmful effect on STEL populations aligns with the documented instances of skewed sex ratios favoring female hatchlings in other reptile species such as loggerhead sea turtles (*Caretta caretta*) in Florida and green turtles (C*helonia mydas*) on Ascension Island (citation). Despite this imbalance, these populations are flourishing, as demonstrated by their robust size, sustained presence over time, and upward trends in population growth (Broderick et al. 2006; Hays et al. 2014; Brost et al. 2015).

Percent of adult females breeding

The changes in the percentage of successfully breeding females in a STEL population had a large effect on the population growth and extinction risk. The model simulations demonstrated that the populations experienced a negative growth rate with a high risk of extinction (P_E values: 40% = 0.98; 30% = 1; 20% = 1.00; 10% = 1.00) when the percentage of adult females breeding dipped below 50 (Table 4.11). When only 50% of sexually mature females in a STEL population breed, the stochastic growth rate is 0.04, which indicates relatively low population growth. The extinction risk was high for this input value as well (P_E = 72), and only an average of 31 individuals of the initial population size of 100 remained at the end of the 100 years. Annual rate of change and population growth expanded with an increased number of sexually mature STEL females breeding in a population (Figure 4.7). At ≥ 90% of sexually matured females breeding, the STEL population exhibited a relatively low probability of extinction (P_E = 2%).

Table 4.11. Results of varied percentages of adult female *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard) breeding annually (10 to 100%; increments of 10). Population growth rate (Stoch-r), probability of extinction (P_E), and final population size (N-all) are reported for each of the simulations.

Females Breeding (%)	**Stoch-r**	**P_E**	**N-all**
10	-0.64	1	0
20	-0.34	1	0
30	-0.22	1	0
40	-0.07	0.98	1
50	0.04	0.72	31
60	0.15	0.28	102
70	0.23	0.11	143
80	0.33	0.10	154
90	0.40	0.02	171
100	0.46	0.02	173

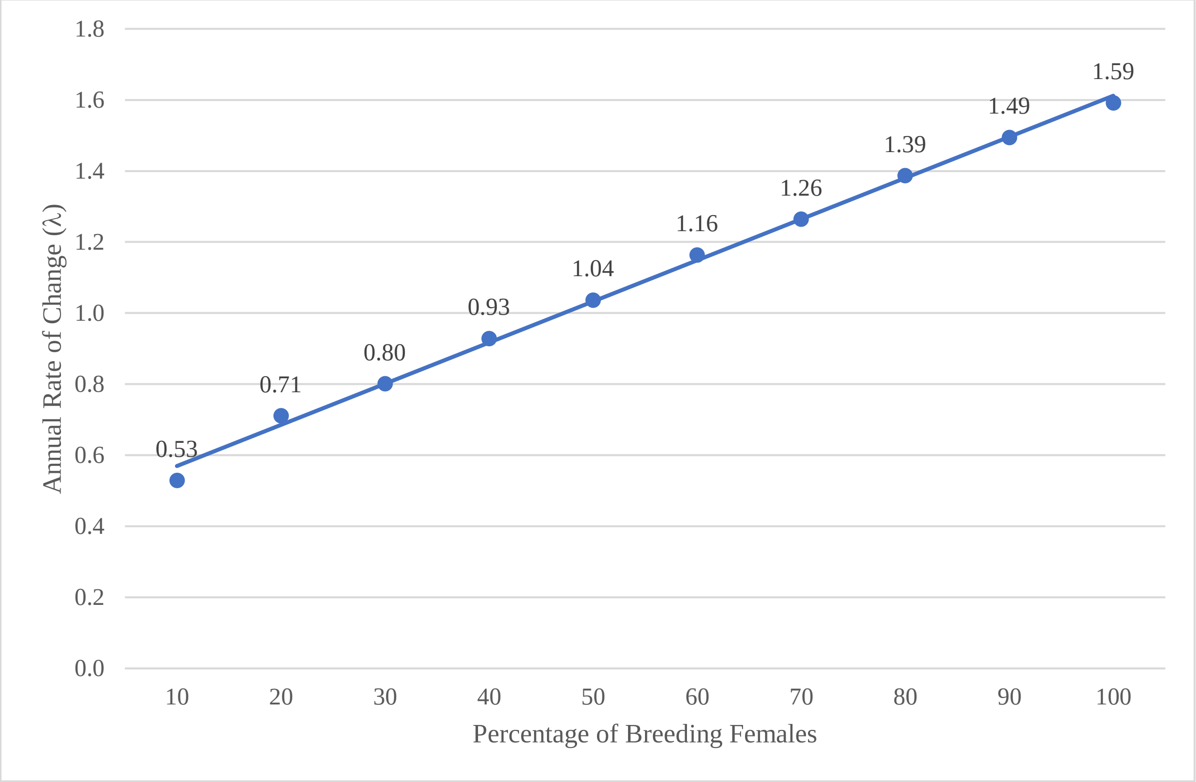

Figure 4.7. The annual rate of change for different percentages (10 to 100%; increments of 10) of adult female *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard) breeding in the population.

Field investigations have demonstrated precipitation is a highly influential factor of reproduction success for many terrestrial lizards due to its positive correlation with food availability (Ballinger and Congdon, 1980; Dunham, 1978). In periods of rainfall shortages coupled with high temperatures, long-lived reptile species are expected to forgo reproduction if it enhances chances of surviving to reproduce in future years when conditions are better. In contrast, because short-lived species are theorized to already exhibit low adult survival, they may benefit from maintaining their levels of reproduction despite poor environmental conditions (Drent and Daan 1980). These predictions suggest that adult female STEL will continue to allocate energy to reproduction during dry periods but may produce fewer offspring. Periods of below-average rainfall have been associated with less or delayed reproduction in other lizard species such as Fringe-toed Lizards (*Uma*; Mayhew 1965, 1966a, 1966b), Tree Lizards (*Urosaurus ornatus*; Martin 1973, 1976; Ballinger 1977), Southwestern Earless Lizards (*Cophosaurus texanus scitulus;* Punzo 2007), Flat-tailed Horned Lizards (*Phrynosoma mcallii;* Young 2010), and Striped Plateau Lizards (*Sceloporus virgatus*; Vinegar 1975).

If less than half of the adult females in the STEL population breed annually, there could be profound effects on population dynamics. Low fecundity rates lead to a decline in population size over time, consequently making the population more vulnerable to environmental fluctuations and elevating the risk of extinction. Reduced reproductive participation also can result in a decrease in genetic diversity, which can negatively impact the long-term viability and adaptability of the population. A high percentage of adult female STEL that successfully reproduce is crucial for sustaining healthy population numbers because it leads to a greater number of offspring recruited into the breeding pool, especially if potential losses due to predation, disease, or other environmental factors occur.

Percent of females that double clutch

The model indicated that a STEL population will experience growth ($\lambda > 1$) if 100% of the breeding adult females produce at least a single clutch annually (Figure 4.8). No detectable negative effect (i.e., one that caused negative growth) on annual population growth rates was observed (λ range 1.12 - 1.63) as a result of varying the percentage of females that double clutch. The annual rate of change increased as the number of adult females producing two clutches increased annually. The probability of extinction was below 10% for all modeled scenarios

(Table 4.12). Adult females producing more than one clutch emerged as a variable that positively contributed to STEL population growth.

In many lizard species, producing a second clutch is possible only if sufficient energy reserves can be stored in the fat bodies prior to reproduction (Ballinger 1977). Without adequate energy reserves, the added fecundity is either not physiologically possible or it might greatly lower adult survivorship because of the reduced energy reserves for maintenance and growth (Ballinger 1977). An abundance of resources, such as prey and water, increases the energy reserves allocated for reproduction. Therefore, a multiple-brooded, highly fecund lizard may be expected to produce smaller clutches and even to be single brooded if resource availability is greatly reduced (Ballinger 1977). The percentage of adult female STEL producing two clutches within a wild population is unknown, but it is well-documented that sexually matured female STEL can double-clutch within a given year (Axtell 1956; Rangel et al. 2022) and the percentage that do may be correlated to the number of female STEL past the age of 1.

Table 4.12. Results for varied percentages (0 to 90%; increments of 10) of females that have two clutches, annually, in a *H. lacerata* (Plateau Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard) population. Population growth rate (Stoch-r), probability of extinction (P_E), and final population size (N-all) are reported for each of the simulations.

Females that have two clutches (%)	**Stoch-r**	**P_E**	**N-all**
0	0.25	0.07	143
10	0.29	0.08	155
20	0.36	0.01	174
30	0.40	0.01	176
40	0.46	0.03	173
50	0.50	0.01	187
60	0.55	0.01	183
70	0.59	0.02	183
80	0.63	0.01	186
90	0.66	0.01	190

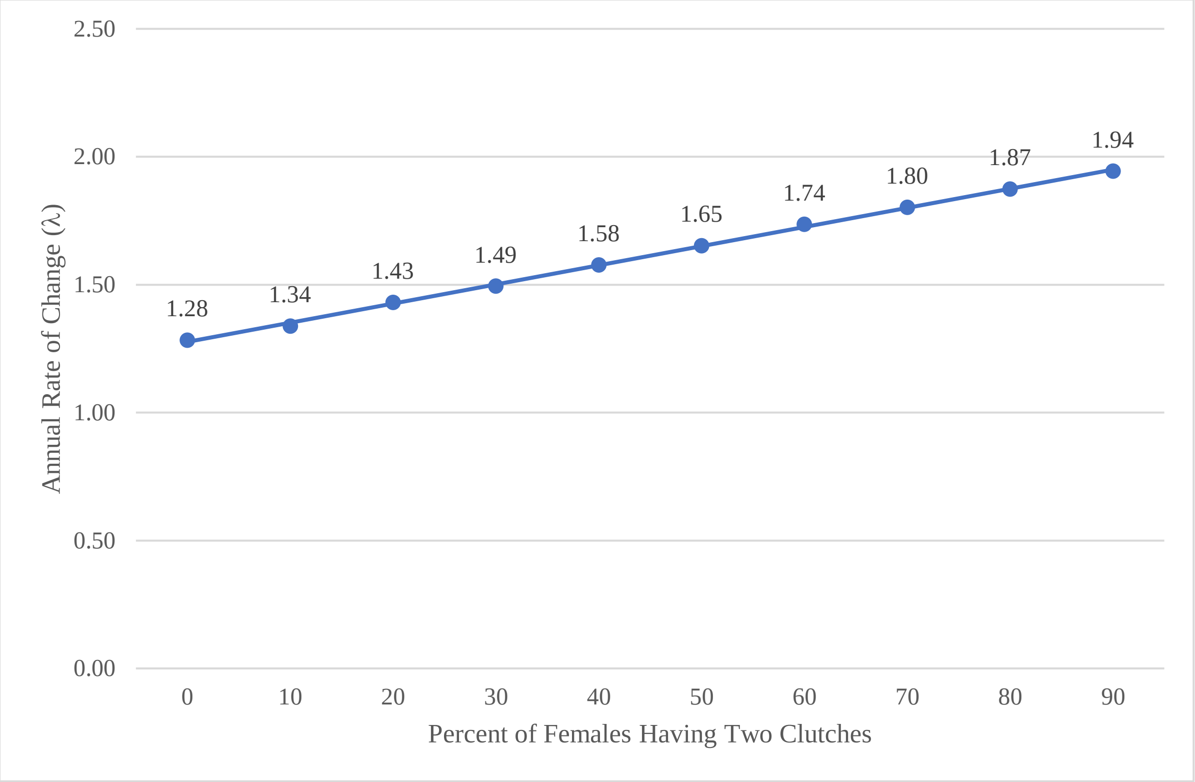

Figure 4.8. The annual rate of change for different percentages (0 to 90%; increments of 10) of adult *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard) females having two clutches annually.

Mean clutch size

The sensitivity analysis demonstrated that changes in the clutch size had a great influence on population growth estimates and extinction risk. If females lay fewer than 5 eggs, the population is not able to sustain itself, thus resulting in a population decline ($\lambda < 1$; Figure 4.9) with a 100% estimated probability of extinction. An average clutch size of 6 eggs revealed positive growth rate estimates (0.08) but exhibited a high probability of extinction (PE = 50%;) and a final population size lower than the initial size (Table 4.13). In comparison, when the clutch size was increased to 8 eggs, the extinction risk decreased to 5%, which suggests there is a threshold at a clutch size of 7 eggs. Moreover, a clutch size ≥10 eggs exhibited a zero percent probability of extinction across the 100-year simulation (Table 4.13).

Table 4.13. Results for varied mean clutch sizes in a *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. Subcaudalis* (Tamaulipan Spot-tailed Earless Lizard) population. Population growth rate (Stoch-r), probability of extinction (P_E), and final population size (N-all) are reported for each of the simulations.

Clutch size	**Stoch-r**	**P_E**	**N-all**
2	-0.36	1.00	0
4	-0.10	1.00	0
6	0.08	0.50	62
8	0.26	0.05	160
10	0.41	0.00	188
12	0.52	0.00	184
14	0.64	0.00	190

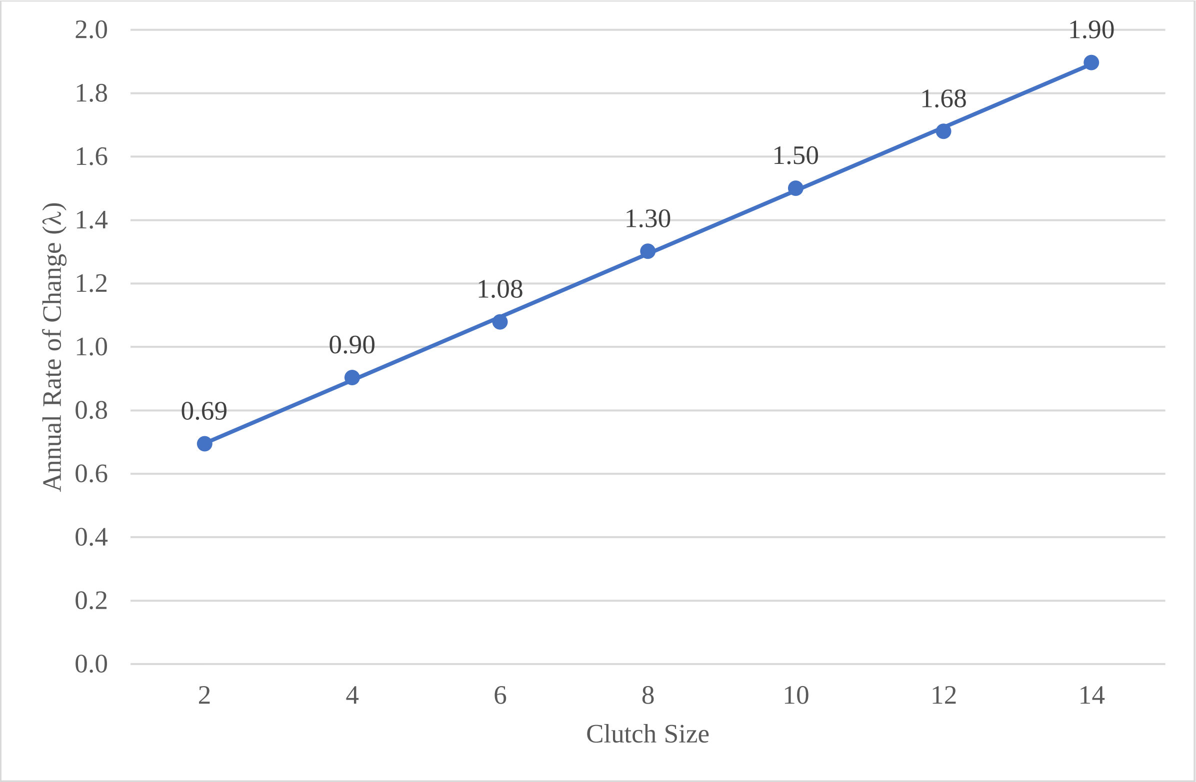

Figure 4.9. The annual rate of change for different mean clutch sizes (2 to 14 eggs; increments of 2) on a *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard) population.

Clutch size has been repeatedly found to increase with increasing body size, thus an individual at the minimum age (reflecting the minimum body length) for sexual maturation will lay fewer eggs, and the maximum clutch size will be laid at the maximum age, reflecting the maximum obtained body size (Fitch 1970; Tinkle et al. 1970, Seigel and Ford 1987). This was observed in STEL, wherein females in captivity laid an average of 6–8 eggs on their first clutch after reaching sexual maturity, but older females laid an average of 7–9 eggs, and up to 12 eggs per clutch (Duran 2017).

Additionally, in captive settings, female Tamaulipan STEL (*H. subcaudalis*) with an SVL of >60 mm had clutch sizes of 10 to 13 eggs, whereas a female with a SVL of < 60 mm (51 mm) laid a clutch size of 8 eggs (Rangel et al. 2022). In the same study, a single Plateau STEL (*H. lacerata*) female with a SVL of 70 mm laid a clutch of 12 eggs, which was two additional eggs compared to the clutch size of a female with a SVL of 60 mm. The correlation of female lizard body size and clutch size is due to larger females having more internal space for egg production (Du et al. 2005); therefore, larger adult female STEL can help increase the overall growth within a population because they produce more offspring.

Several factors might explain variation in growth rates and clutch size among female STEL in wild populations including environmental conditions such as temperature (Adolph and Porter, 1993, 1996) and precipitation (Wang et al. 2016; Zani and Stein 2018), as well as activity patterns and prey availability (Dunham, 1978). A large body size can be acquired in good environmental conditions (i.e. warm temperatures with periodic rainfall) that support an abundance of arthropod populations. Although STEL are adapted to arid environments, wet years can increase the abundance and distribution of vegetation, thus affecting arthropod numbers (i.e. food resources; Cesne et al. 2015), which, in turn, determine body size (Ballinger and Congdon 1980). In contrast, drought events can hinder STEL development causing juvenile females to acquire sexual maturity at a smaller body size, consequently lowering their reproductive potential and decreasing the number of offspring that are recruited into the population. One of Texas's worst droughts occurred from 1950 to 1957, during which Axtell (1956) reported female STEL laid an estimated average of 4–6 eggs on the first oviposition after reaching sexual maturity and 5–7 eggs on the second oviposition. The small clutch sizes reported by Axtell contrast with the recently documented larger clutch sizes by Rangel et al. (2022), which provides some evidence that drought events can influence clutch size variation.

Percent mortality per age class

When we decreased the mortality rates, the sensitivity analysis demonstrated that mortality of hatchlings had a greater effect on STEL population growth compared to the mortality of adults. The annual rate of change (λ) rates increased to an estimated value of 5.66 when hatchling mortality was decreased to 10% (Figure 10). In comparison, the annual rate of change (λ) reached an estimated value of 1.93 when the adult mortality rate was decreased to 10% and hatchling mortality rate remained at the baseline value (80%). When we increased the hatchling mortality rate to 90%, the simulation model exhibited a 100% extinction risk, which is a 97% increase from the baseline's estimated probability of extinction (PE = 3%; Table 14). At an adult mortality <50%, the probability of extinction (P_E) was 0.00 (Table 4.15). Although the simulation reflected a positive annual rate of growth ($\lambda > 1$) when the adult mortality percentage rate was increased to 80%, the probability of extinction was 95% (Table 4.15). This is likely because fecundity is high within the population (percentage of females breeding = 90%, avg clutch size = 10, and sexual maturity is at 1), however the high mortality rates for both age classes override the growth and elevate the risk of extinction (Table 4.15).

Table 4.14. Results for varied mortality rates (10 to 90%; increments of 10) of *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard) hatchlings. Population growth rate (Stoch-r), probability of extinction (PE), and final population size (N-all) are reported for each of the simulations.

Hatchling Mortality Rate (%)	**Stoch-r**	**P_E**	**N-all**
10	1.73	0.00	200
20	1.63	0.00	200
30	1.50	0.00	200
40	1.36	0.00	200
50	1.20	0.00	200
60	1.00	0.00	200
70	0.76	0.00	197
80	0.40	0.03	172
90	-0.13	1.00	0

Table 4.15. Results for varied mortality rates (10 to 90%; increments of 10) of *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard) adults. Population growth rate (Stoch-r), probability of extinction (P_E), and final population size (N-all) are reported for each of the simulations.

Adult Mortality (%)	**Stoch-r**	**P_E**	**N-all**
10	0.65	0.00	197
20	0.60	0.00	195
30	0.54	0.00	192
40	0.48	0.00	186
50	0.40	0.03	172
60	0.32	0.17	135
70	0.23	0.55	66
80	0.22	0.95	8
90	0.11	0.99	1

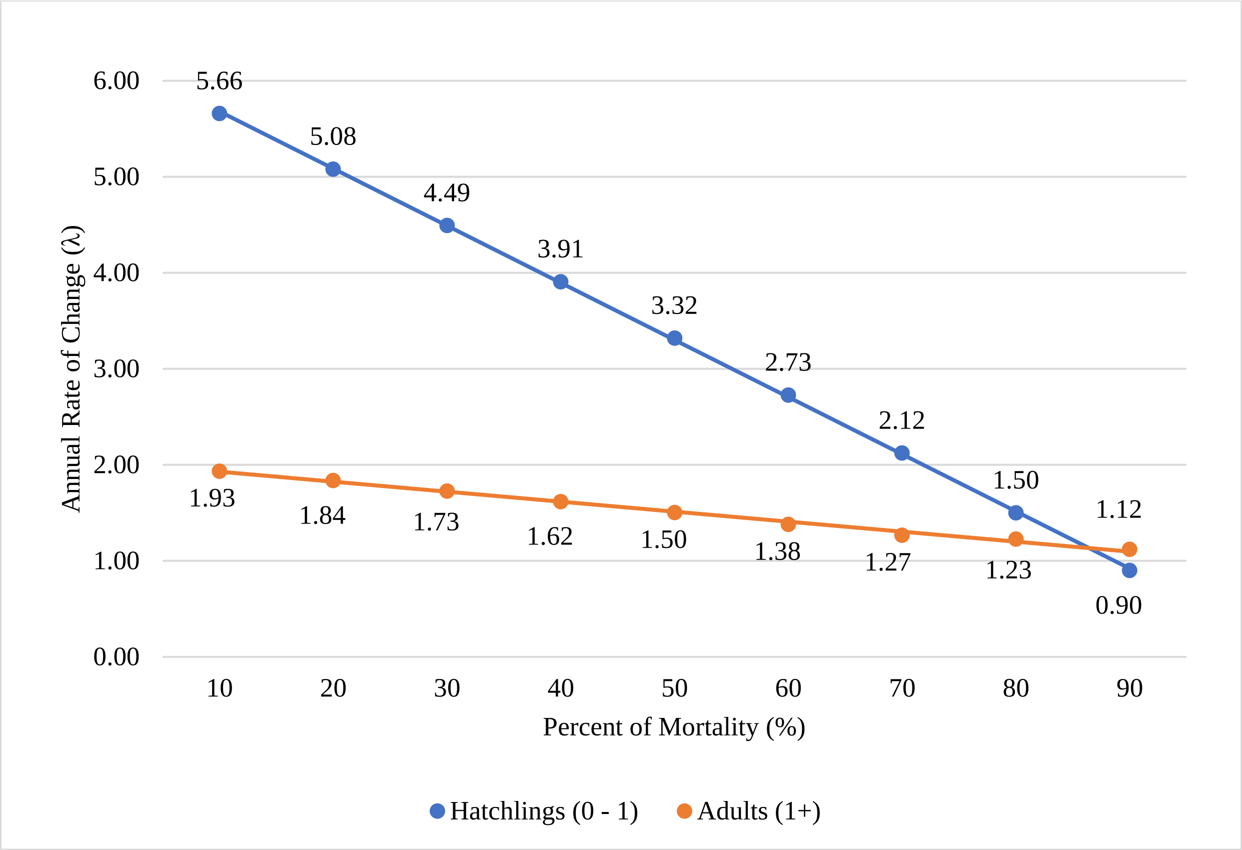

Figure 4.10. The annual rate of change for different mortality rate percentages on two age classes, hatchlings (age 0–1) and adults (age 1 and up), of *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard).

The analysis highlighted the importance of high hatchling survival in a STEL population. Hatchling mortality rates have a large influence on population persistence because this age group comprises a major part of the population. Adult mortality indeed extends its impact on other demographic parameters, but when hatchling survival is ≥20% and a large percentage of sexually matured females breed annually, the population can safely lose adults without having a significant effect on the population's persistence. On the other hand, when hatchling mortality is >80%, losing more than half of the adults in the population can further exacerbate the decline of the population because there are not enough individuals in the breeding pool to produce offspring. In small populations of 100 individuals or less, even a positive growth rate may not be sufficient to overcome the initial small numbers, especially if the population is vulnerable to changes in the environment, such as habitat destruction or climate change.

Initial population size

Variations in the initial population size showed no change in the annual population growth. For all scenarios, the annual rate of change, λ, was 1.5, indicating that the population does not experience a decline as a result of changes in the initial population size ($\lambda > 1$; Figure 4.11). With all other baseline parameters held constant, the P_E decreased from 2% to 0% when the initial population size is increased from 25 to 100 individuals (Table 4.16).

Smaller populations are predicted to be at a higher risk of extinction because they are disproportionately susceptible to stochastic variation and inbreeding, whereas population sizes that are larger tend to be more resilient. However, the outcomes of the modeled scenarios contradicted this expectation. This was because the inputs for demographic factors, such as age of first offspring, mortality, and fecundity, had a greater influence in the model trajectory, and facilitated the population's expansion far beyond its initial size.

Table 4.16. Results for varied initial population sizes (N_0 = 25, 50, 75, and 100) of *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard). Population growth rate (Stoch-r), probability of extinction (P_E), and final population size (N-all) for each of the simulations.

Initial Population Size	**Stoch-r**	**P_E**	**N-all**
25	0.41	0.02	174
50	0.41	0.01	176
75	0.41	0.02	178
100	0.41	0.00	178

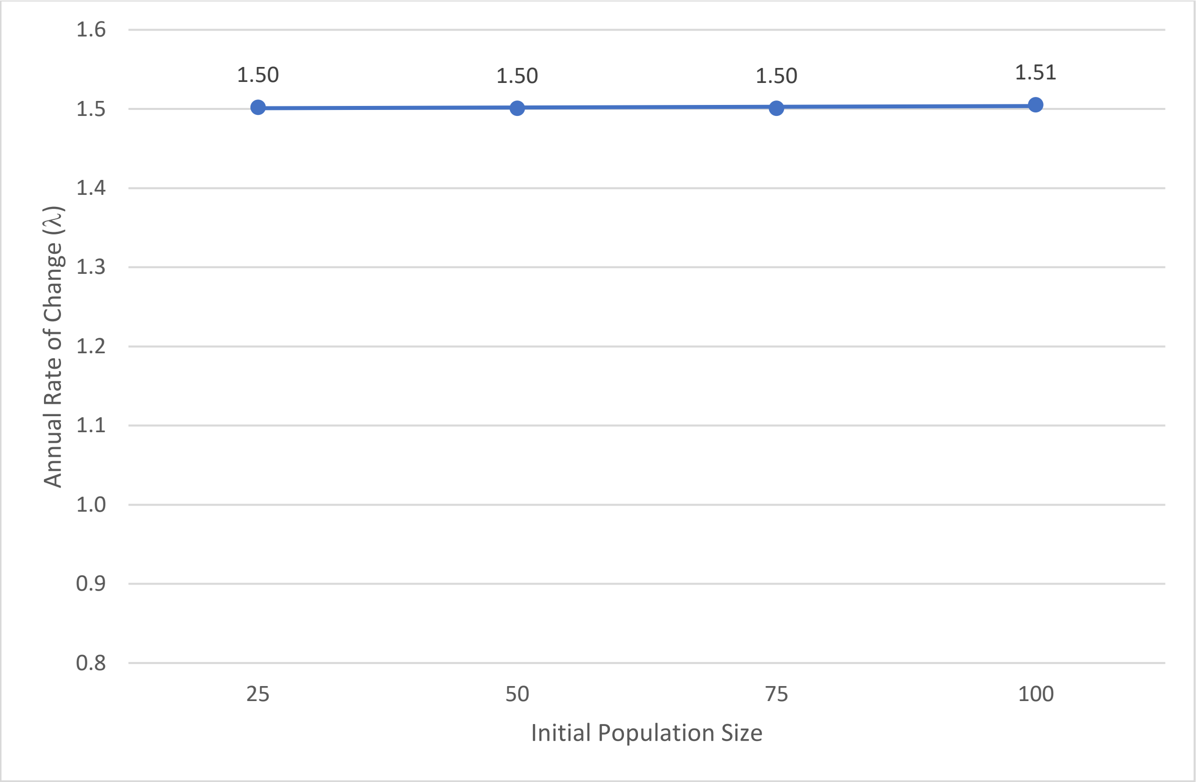

Figure 4.11. The annual rate of change for different initial population sizes (N_0 = 25, 50, 75, and 100) of *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard).

Relative Analysis

A conventional elasticity analysis demonstrated that four of the ten parameters varied by ±10% had a disproportionate effect on population growth rate (i.e., the relative sensitivity values were >1 or <-1; Table 4.17). The mortality rate percentage for hatchlings had the largest slope and greatest sensitivity of all parameters tested (S = -6.82), which indicated this parameter exhibits the strongest influence on the persistence of a STEL population (Figure 4.12). The mean clutch size (S = 1.44), the sex ratio at birth (S = -1.39), and the percentage of breeding females (S = 1.31) followed, in decreasing order of importance as key factors in STEL population dynamics. Female adult mortality was more sensitive to change compared to combined adult mortality of both sexes, but neither displayed a great effect on population growth rate in the elasticity analyses (i.e. the relative sensitivity values were not > 1 or < -1). Simulated changes in environmental variation did not demonstrate a strong sensitivity to change; however, the elasticity analyses revealed that environmental variation, especially in hatchling mortality, had a greater impact on the population growth rate than changes in environmental variation associated with fecundity.

Table 4.17. Relative sensitivity values derived from conventional sensitivity analyses for *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard) by changing baseline values by ± 10%. Demographic parameters followed by an asterisk (*) show the highest sensitivity, *S*, as listed in the far right-hand column of the table (*S* values >1 or <-1 are considered to show the greatest sensitivity).

Model Parameter	**Minimum (-10%)**	**Baseline**	**Maximum (+10%)**	***S***
Mean Clutch Size*	9	10	11	1.44
Sex Ratio at Birth*	45	50	55	-1.39
% Females Breeding*	81	90	99	1.31
SD due to EV on % Females Breeding	9	10	11	-0.03
% Hatchling Mortality (0 – 1)*	72	80	88	-6.82
% Combined Adult Mortality (1+)	72	80	88	-0.75
% Female Adult Mortality (1+)	45	50	55	-0.78
% Male Adult Mortality (1+)	45	50	55	-0.04
SD due to EV on hatchling mortality	9	10	11	-0.44
SD due to EV on adult mortality	9	10	11	-0.09

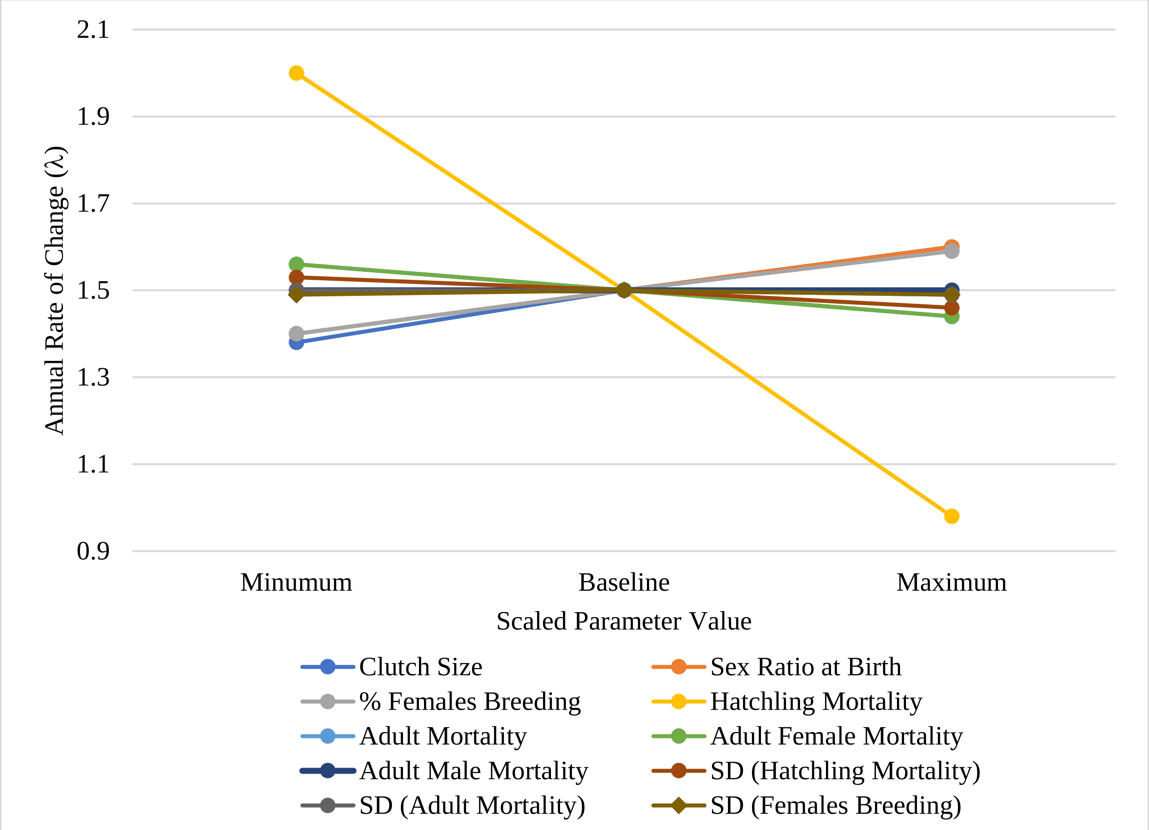

Figure 4.12. Sensitivity of ten demographic parameters on the annual rate of change (λ) for *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard). See Table 4.3 for the minimum, baseline, and maximum lambda values of each demographic parameter. Curves with the steepest slope indicate the model parameters with the greatest overall sensitivity.

A comparison of the results of different sensitivity tests allowed me to determine the relative importance of different parameters for the persistence of the population. For both the manual perturbation and elasticity analyses, hatchling survival exhibited the greatest effect on STEL population growth rates and persistence. Despite the prediction that adult mortality would also have a great effect on the persistence of the population, the sensitivity tests indicated that variables that support recruitment (e.g., % females breeding, clutch size, and hatchling survival (age 0 -1)) of the population were critical for population growth and outranked adult survival in importance.

Population projection matrices used to model the population dynamics of the knob-scaled lizard, *Xenosaurus grandis* (Zuniga-Vega et al. 2007), also documented the important influence of recruitment on annual population growth. For *X. grandis*, hatchling and juvenile survival had the largest effects on population persistence (Zuniga-Vega et al. 2007). Similar results were also obtained in a long-term study of two different populations of Texas horned lizards, *Phrynosoma cornutum*, which indicated that *P. cornutum* hatchling survival had the strongest influence, while adult survival had the weakest effect on annual population growth over time (Wolf et al. 2014).

Currently, there is a dearth of information available about the mortality or survivability rates for all age stages of STEL from the wild and the type and degree of threats that impact these stages. Although small-bodied animals and juveniles are more susceptible to predation by other animals, the mortality rate for hatchling STEL in the wild has not been explored or estimated. Future work on STEL should consider conducting intensive mark-recapture studies to obtain more precise and accurate estimates of STEL survival across all age classes. Moreover, it is important to explore potential methods for tracking younger age groups in small herpetofauna (weighing less than 100 grams). Ongoing endeavors to advance these and alternative approaches are essential in gaining insights into the dynamics of reptile populations, which would aid in improved model accuracy and conservation management decisions.

Catastrophe Analyses

Under the mild severity level, the simulation demonstrated that the impact on a small STEL population ($N_0 = 50$) decreased the population growth rate from 0.40 in the baseline simulation to 0.34, while still maintaining an extinction risk of less than 10% (PE = 0.07). A drought event with a moderate severity level decreased the population growth by 30% from the baseline simulation, and the likelihood of extinction increased to 16%. Both simulations indicated these severity levels are not detrimental to the viability of a STEL population. However, under the severe drought scenario, the risk of extinction rose to 86% and the mean final population size was less than 50 individuals.

Table 4.18. Growth rates and extinction risk of varied severity effects due to a drought event with an annual frequency of 9% on an initial *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard) population of 50 individuals. Population growth rate (Stoch-r), probability of extinction (P_E), and final population size (N-all) are reported for each of the simulations.

	Stoch-r	**P_E**	**N-all**
Baseline	0.40	0.03	171
Mild Scenario	0.34	0.07	156
Moderate Scenario	0.28	0.16	124
Severe Scenario	0.21	0.86	17

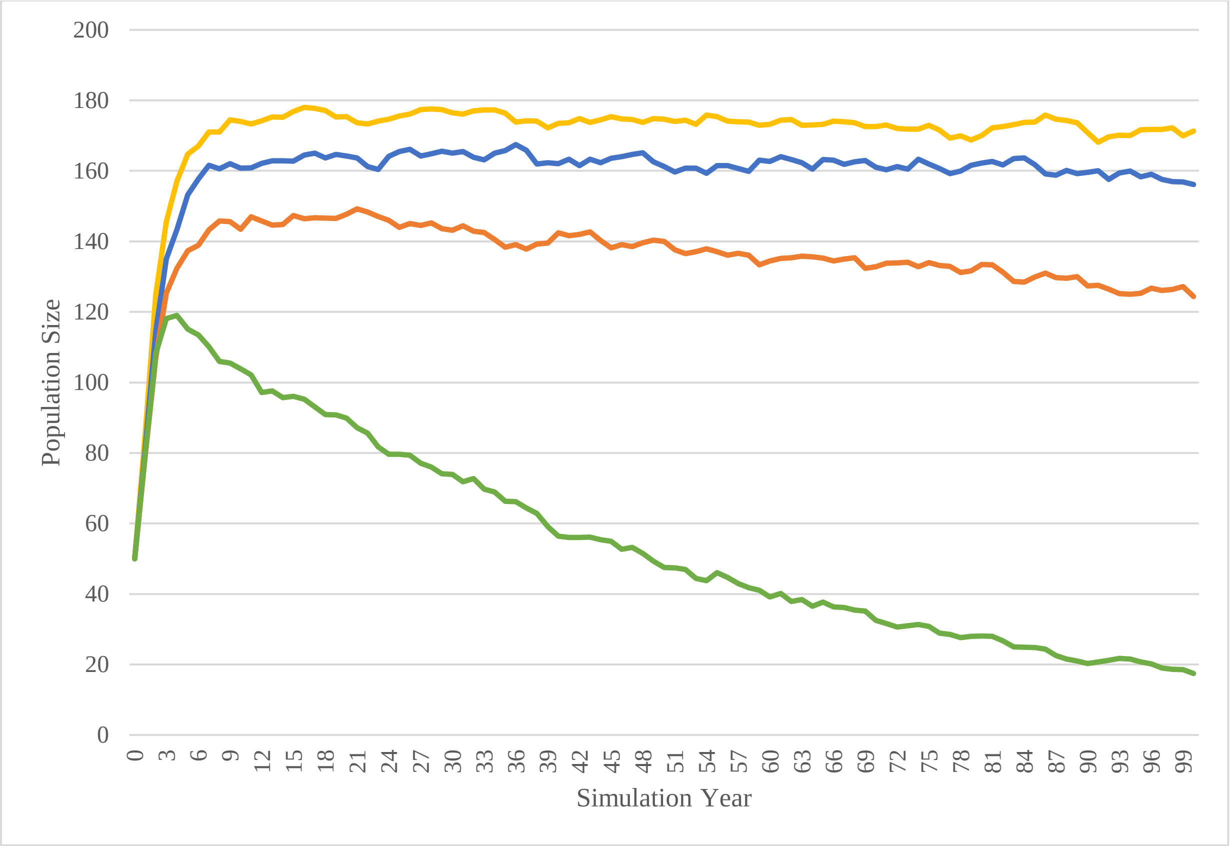

Figure 4.13. Predicted population size of *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard) under varied severity effects to reproduction and survival. These factors range from 0.0 (maximum or absolute effect) to 1.0 (no effect). The baseline (yellow) is incorporated as a reference. Under mild effects (blue), severity to reproduction and survival are 0.50 and 0.75, respectively. Under moderate effects (orange), severity to reproduction and survival are 0.25 and 0.50, respectively. Under severe effects (green), severity to reproduction and survival are 0 and 0.25, respectively. ($N_0 = 50$; K = 200 for all scenarios).

Because droughts are expected to increase in frequency with climate change (Diffenbaugh et al. 2015), we tested an additional drought event occurring at a higher frequency (18%) in the catastrophe analysis. Increasing the annual frequency of a drought event lowered the mean population growth rate and increased extinction risk for all three severity levels. Under the moderate effects, the likelihood of extinction rose from 16% to 59% when the frequency of occurrence was doubled. Under the severe effects, the model demonstrated that an initial population of 50 STEL declined to extinction by the end of the 85th year of the simulation (Table 4.19). Under the mild effects, the population growth rate decreased from 0.40 to 0.27, but the final population size reached 85.5% of the carrying capacity (N-all = 132).

Table 4.19. Growth rates and extinction risk of varied severity effects due to a drought event with an annual frequency of 18% on an initial Spot-tailed Earless Lizard population of 50 individuals. Population growth rate (stoch-r), probability of extinction (P_E), and final population size (N-all) are reported for each of the simulations.

	Stoch-r	**P_E**	**N-all**
Mild Scenario	0.27	0.15	132
Moderate Scenario	0.16	0.59	46
Severe Scenario	0.03	1.00	0

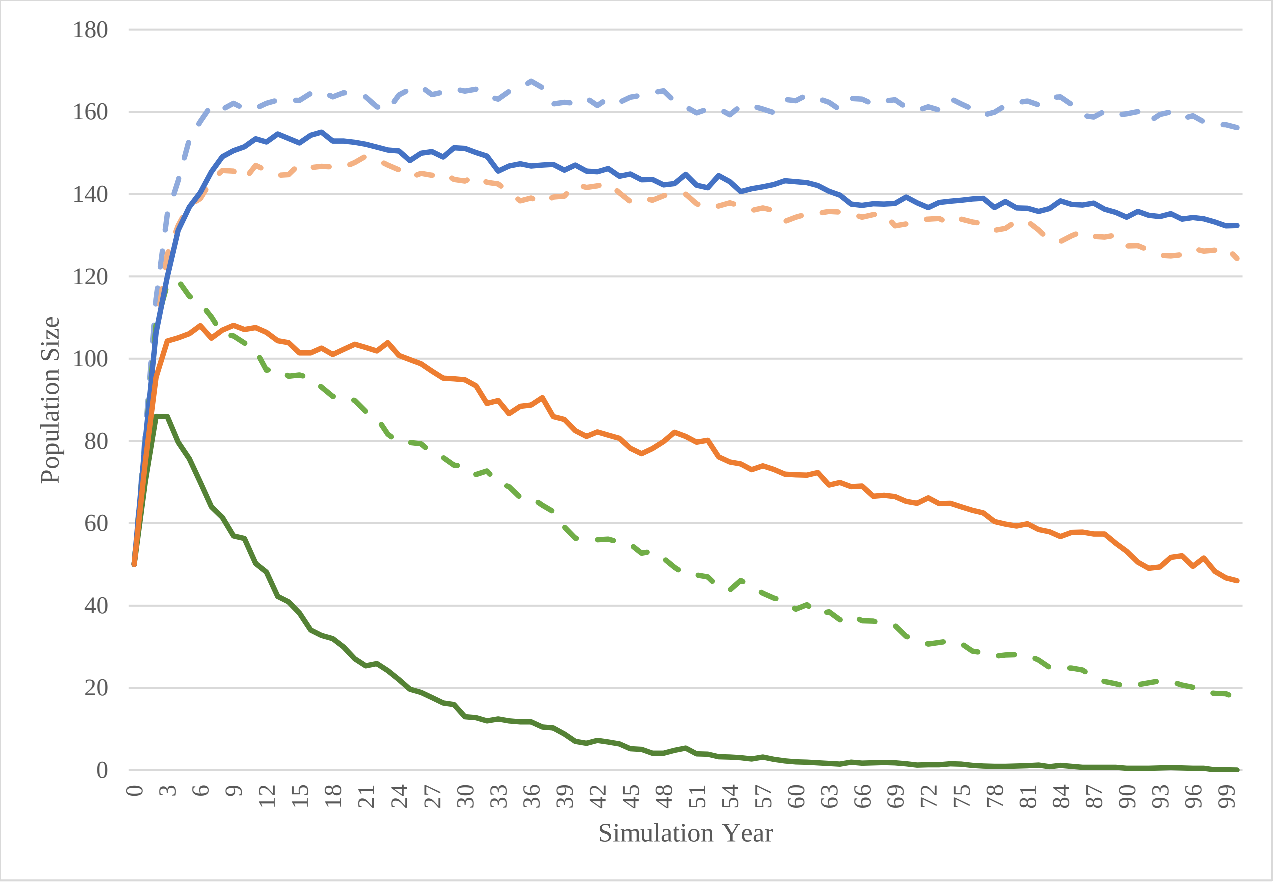

Figure 4.14. The effects of increasing the annual frequency of a drought event from 9% (dashed) to 18% (solid) on a *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard) population of 50 individuals. Under mild effects (blue), severity to reproduction and survival are 0.50 and 0.75, respectively. Under moderate effects (orange), severity to reproduction and survival are 0.25 and 0.50, respectively. Under severe effects (green), severity to reproduction and survival are 0 and 0.25, respectively. ($N_0 = 50$; K = 200 for all scenarios).

The impact of drought on STEL remains largely unexplored, which can create uncertainties in predicting their response to changing climate conditions. This knowledge gap is further compounded by the unpredictable nature of future climate scenarios, which may compromise the accuracy of predictive models. However, it is reasonable to assume that the actual influence of a drought event for STEL lies somewhere between the moderate and worst-case scenario.

This assumption is supported by previous research that has documented the effects of long-term drought on desert lizards, which include reduced food availability (Germano et al. 1994; Mayhew 1965, 1966), reduced survival (Whitford and Creusere 1977), fewer offspring per reproductive attempt (Hoddenbach and Turner 1968; Zweifel and Lowe 1966), reduced juvenile recruitment (Whitford and Creusere 1977), slowed body growth, and delayed sexual maturity (Grimm-Seyfarth et al. 2018). In the modeled moderate scenario, the portion of adult females breeding in the STEL population is dramatically reduced to 22.5%. Although anecdotal, this does correspond to field surveys, as juvenile Plateau STEL were observed in June of 2022, which was drought year for most of Texas (Donald and Grubbs 2022). Survival, for this scenario, was reduced to 10% and 25% for hatchlings and adults, respectively; however, the percentage could be higher in certain cases given that allocating energy for survival may take precedence over reproduction.

In a study involving the common side blotched lizard, *Uta stansburiana*, researchers subjected the species to drought conditions while ensuring an ample food supply (Zani and Stein 2018). The findings revealed that the simulated drought environment led to a notable decline in recruitment, resulting in a shift in the body-size distribution of lizards over subsequent years. The study also highlighted how water scarcity alone can disrupt breeding seasons and lead to reproductive failure in females. Further research supports that, for lizards in arid habitats, it is water availability rather than high temperatures or food availability that predominantly limits population growth as reproduction is a physiologically demanding and often requires proper hydration in oviparous species for successful egg production (Zweifel and Lowe, 1966; Jones et al. 1987; Grimm-Seyfarth et al. 2018).

Applying this knowledge to STEL, it is plausible in that the species do not face a shortage of food during drought events as one of their preferred prey, grasshoppers (Hibbits 2018; Rangel et al. unpubl.), is adapted to and commonly thrives during dry, rainless periods. Although free water dependence (i.e., dietary and metabolic processes help produce water) is common in many reptiles, the amount of water produced through such means is relatively small compared to the water needs of most organisms; therefore, it's important to note that the water obtained from prey is typically a supplementary source (Wright et al. 2013). It is likely that low water availability due to the lack of rainfall combined with high rates of water loss due to high temperatures may result in water loss stress that can hinder STEL reproduction and life history, leading to a decline in population viability.

Additionally, the occurrence and severity of natural catastrophes are key factors in STEL population projection. For my models, we doubled the rate of drought events occurring in regions of STEL habitats, but the true annual frequency of drought can be smaller or greater; nonetheless, the models demonstrated that an increase in the frequency of drought events can have big implications for STEL persistence. Additionally, the increased frequency of drought events also could contribute to STEL habitat loss by creating shifts in the composition of plant communities (Karl et al. 2009) and reduce native grass species to other more drought-adapted vegetation (Fullbright et al. 2013) that may be contributing to the decline of STEL populations.

Severe drought events can have detrimental effects on the reproduction of STEL, leading to a decline in population growth and ultimately threatening their sustainability. Moreover, an increasingly arid environment can pose even greater challenges to the survival of STEL. Considering the role lizards play in local food chains (Pianka 1986), the reduction or loss of STEL populations due to climate warming could impact the regional biodiversity. It is imperative for future research to delve into the impact of increased temperatures on reproductive physiology and survival of both STEL species to better understand its implications for conservation.

Habitat Loss Analyses

As expected, the extinction risk increased concurrently with an increasing annual rate of loss for all population sizes (Table 4.20). The probability of extinction was high when the annual rate of loss was set to 1%, which totaled a 100% habitat reduction by the end of the 100-year simulation, resulting in the total extinction of populations composed of <200 individuals (Figure 15). Populations ≥200 individuals were more resilient to extinction at an annual rate of loss of 1% but were drastically reduced to a final population size of <5 individuals if they didn't go extinct by the 100th year. At the lowest rate of loss tested (0.25%), the initial population size of 20 individuals was reduced to less than half by the end of the 100th year (Figure 4.15); whereas the larger population sizes of 50, 100, and 300 were reduced by approximately 20, 6, and 1% (N-all = 40, 94, and 297), respectively. At an annual rate of loss of 0.75%, the same population exhibited an extremely high probability of extinction (PE = 93%).

Simulations with 2% habitat loss had a more drastic effect causing all populations, regardless of size, to go extinct before the start of the 55th year. The stochastic growth rates were similar to their counterparts in the baseline scenario even though the carrying capacity was reduced, signifying this element is more sensitive to the changes in the values of demographic parameters related to the survival and fecundity of STEL.

Table 4.20. Demographic results for different initial population sizes (N_0 = 20, 50, 100, 200, 300) of *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard) in scenarios with different habitat loss rates (0, 0.25, 0.50, 0.75, 1%). Stochastic growth rate (Stoch-r), extinction risk (P_E), and mean final population size (N-all).

N	**Loss**	**Stoch-r**	**P_E**	**N-all**
20	0	0.38	0.56	12
	0.25	0.39	0.63	7
	0.5	0.38	0.77	3
	0.75	0.38	0.93	1
	1	0.38	1.00	0
	2	0.38	1.00	0
50	0	0.40	0.15	57
	0.25	0.40	0.18	40
	0.5	0.39	0.24	25
	0.75	0.39	0.41	10
	1	0.39	1.00	0
	2	0.39	1.00	0
100	0	0.41	0.03	130
	0.25	0.40	0.05	94
	0.5	0.40	0.08	62
	0.75	0.40	0.12	30
	1	0.39	0.94	1
	2	0.39	1.00	0
200	0	0.40	0.01	265
	0.25	0.41	0.01	198
	0.5	0.40	0.02	133
	0.75	0.41	0.04	66
	1	0.40	0.55	2
	2	0.40	1.00	0

Table 20. Continued

N	Loss	Stoch-r	Pe	N-all
	0	0.41	0.01	399
300	0.25	0.41	0.01	297
	0.5	0.40	0.01	198
	0.75	0.41	0.01	104
	1	0.40	0.26	4
	2	0.40	1.00	0

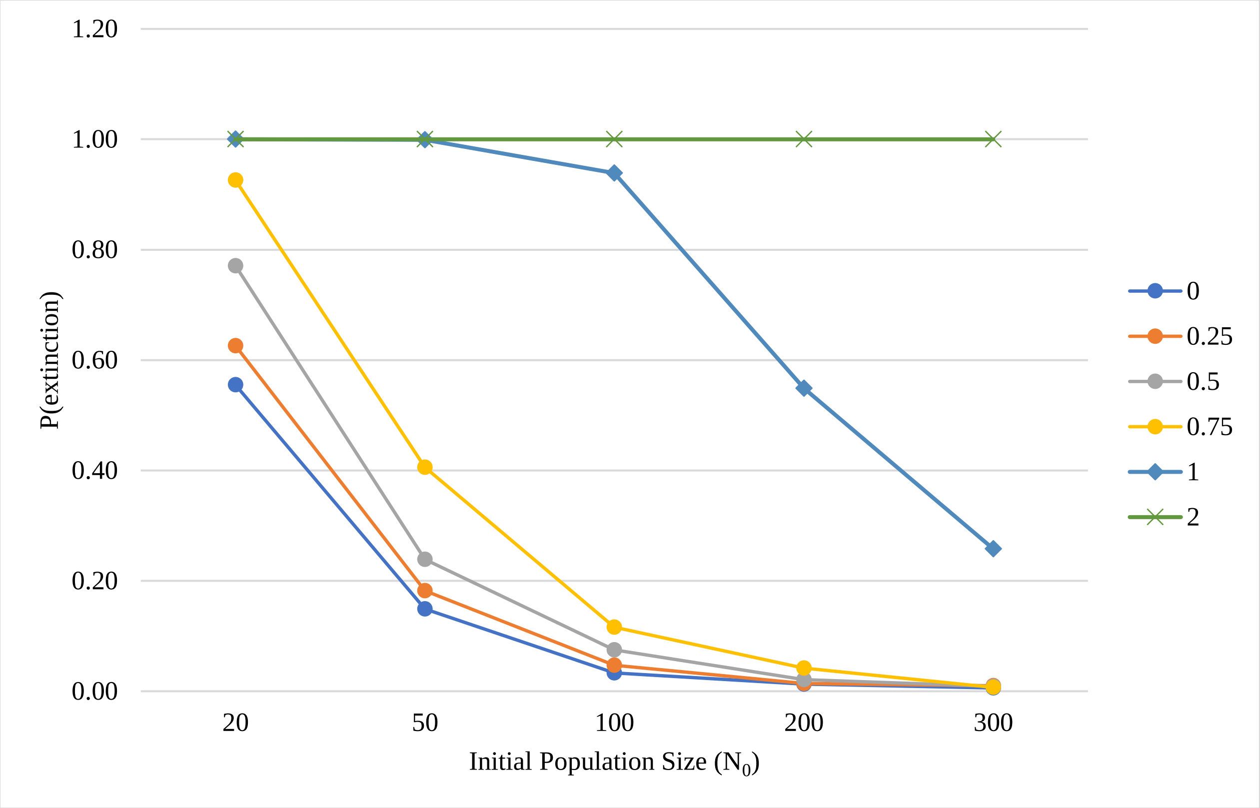

Figure 4.15. Evaluation of the probability of extinction for *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard) under varied annual habitat loss rates (0 to 1%; increments of 0.25) for different initial population sizes (N_0 = 20, 50, 100, 200, 300). The carrying capacity was set at 50% increase of the initial population size (K = 30, 75, 150, 300, 450, respectively), and all other parameters followed the baseline model values.

Population declines in STEL have been attributed to landscape changes that reduce the availability of suitable habitat (Kahl et al. 2022). These include the conversion of native land to cropland, anthropogenic infrastructure development, and the encroachment of invasive species (Torres et al. 2016). Due to the transformation of the landscape, which has resulted in direct loss of habitat and fragmentation, STEL are largely confined to habitat remnants that are not in their original state. The common lesser earless lizard (hereafter, CLEL), *Holbrookia maculata*, is a generalist species that responds negatively to landscape alterations and the effects of habitat fragmentation (Walkup et al. 2017; Leavitt and Fitzgerald 2013). When the effects of changes in habitat composition on lizard communities were examined, it was documented that CLEL were sensitive to land alteration and displayed significantly fewer captures, as well as a disrupted demographic structure (Walkup et al. 2017). CLEL exhibits some similarities in habitat preference as STEL, which include flat slopes with sparse, native vegetation and low woody encroachment (Walkup et al. 2017), as well as some similarity in life history characteristics; therefore, it could be inferred that STEL would reflect similar population declines. However, some reptiles favor an altered landscape, and it is thought that STEL are an early successional species that may favor certain types of anthropogenic changes, such as mowing regimes, in land-use (Axtell 1968, Duran 2017, Kahl et al. 2022).

STEL are thought to be negatively affected by brush and exotic grass encroachment (Duran 2017, Kahl et al. 2022). Studies show that habitat disturbance by woody vegetation encroachment and other invasive species could decrease the presence of important STEL habitat types and reduce native vegetation diversity. The expansion of Buffelgrass (*Pennisetum ciliare*) and Old-world Bluestems (*Dicanthium sp.* & *Bothriochloa sp.*) have dominated native grasslands over much of southern Texas and created dense monocultures that result in the loss of suitable habitat for STEL (Hibbits et al. 2018; Kahl et al. 2022). Disturbance seems to benefit STEL because it reduces brush and maintains an open savannah-like habitat (Eversole et al. unpubl.). For example, one documented population of STEL exists at the Laughlin Air Force Base (LAFB) in southern Val Verde County, Texas. The fragmented habitat at LAFB is continuously disturbed via frequent mowing and trimming activities, which have replenished the topsoil and converted thornscrub into grassland, and has, inadvertently created and maintained a suitable habitat for STEL (Duran 2014).

The conversion of native land to agriculture is considered a form of habitat loss that is believed to have greatly reduced and fragmented historical STEL populations (Gibbons et al. 2000; Todd et al. 2010; Duran 2017). However, presence records from studies indicate a prevalence of STEL observations on or adjacent to agricultural land (Duran and Axtell 2010, 2011; Duran 2017; Laduc et al. 2018), thus cropland conversion does not necessarily appear to extirpate STEL from an occupied area. A further habitat selection analysis demonstrated a significant selection of bare ground, native grasses, and agricultural land by STEL (Kahl et al. 2022). Agricultural land may provide a more open and unobstructed habitat that allows STEL to detect predators and prey more effectively. Agricultural fields, particularly those with areas of short grass (e.g., turn rows), can provide more direct access to sunlight and warmer temperatures, which is beneficial for physiological functions. Additionally, the maintenance of agricultural lands can create new interstices that serve as novel refuge sites from predators and mating grounds for STEL. On the other hand, inhabiting agricultural lands also exposes STEL to the risks related to certain agricultural management practices, such as chemical applications (Amaral et al. 2012a; Amaral et al. 2012b) and discing, which could potentially harm the population. However, the probability that STEL are exposed to these risks is primarily a function of the overlap (in time and space) between their presence and the implementation of these practices in agricultural areas (Ockleford et al. 2018).

Management Analyses

Based on the “no management scenario," the STEL population with imposed high mortality rates on all age classes did not survive by the end of the 100-year simulation (Figure 4.16). This scenario had a 99% extinction risk, and the stochastic growth was negative (-0.05). Supplementing captive-bred STEL past the age of 1 every other year for the first 50 years of the simulation decreased the extinction risk from 99% to 90% (i.e., a 9% decrease). The simulation demonstrated a population increase during the years of supplementation, but the carrying capacity limited growth beyond 200 individuals (Figure 4.16). The population also decreased when supplementation ceased (Figure 4.16). At the end of the 100-year simulation, the final population size consisted of 8 individuals (Table 4.21). Compared to supplementation, an increased difference of 0.32 was exhibited in population growth when management was focused solely on habitat restoration efforts (Stoch-r = 0.41). For this scenario, the annual 1% increase in the carrying capacity (K_0 =200) coupled with a decreased mortality rate for hatchlings and adults greatly decreased the extinction risk by approximately 98% (PE = 0.02 or 2%). In comparison to supplementation, habitat restoration efforts exhibited an increase in the average final population size (N-all = 261; Table 4.21).

When supplementation was combined with habitat restoration efforts, the risk of extinction in the population was 0%. Under this scenario, the population was able to reach a size equal to the carrying capacity at year 50 (Figure 4.16), and it did not experience a decrease in the final population size after both management practices ceased. The stochastic growth rate exhibited a minimal difference from management focused solely on habitat improvement (0.41 to

0.44; Table 20). The genetic diversity was 0.86, which was the highest of all management scenarios simulated (Table 4.21).

Table 4.21. Demographic results of four management model simulations on a *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard) population. Population growth rate (Stoch-r), probability of extinction (P_E), final population size (N-all), and gene diversity are reported for each of the simulations.

Management Type	**Stoch-r**	**P_E**	**N-all**	**Gene Div.**
A) No Management	-0.05	0.99	0	0.37
B) Head-starting/Supplementation	0.09	0.90	8	0.56
C) Habitat Restoration	0.41	0.02	261	0.72
D) Supplementation & Habitat Restoration	0.44	0.00	264	0.86

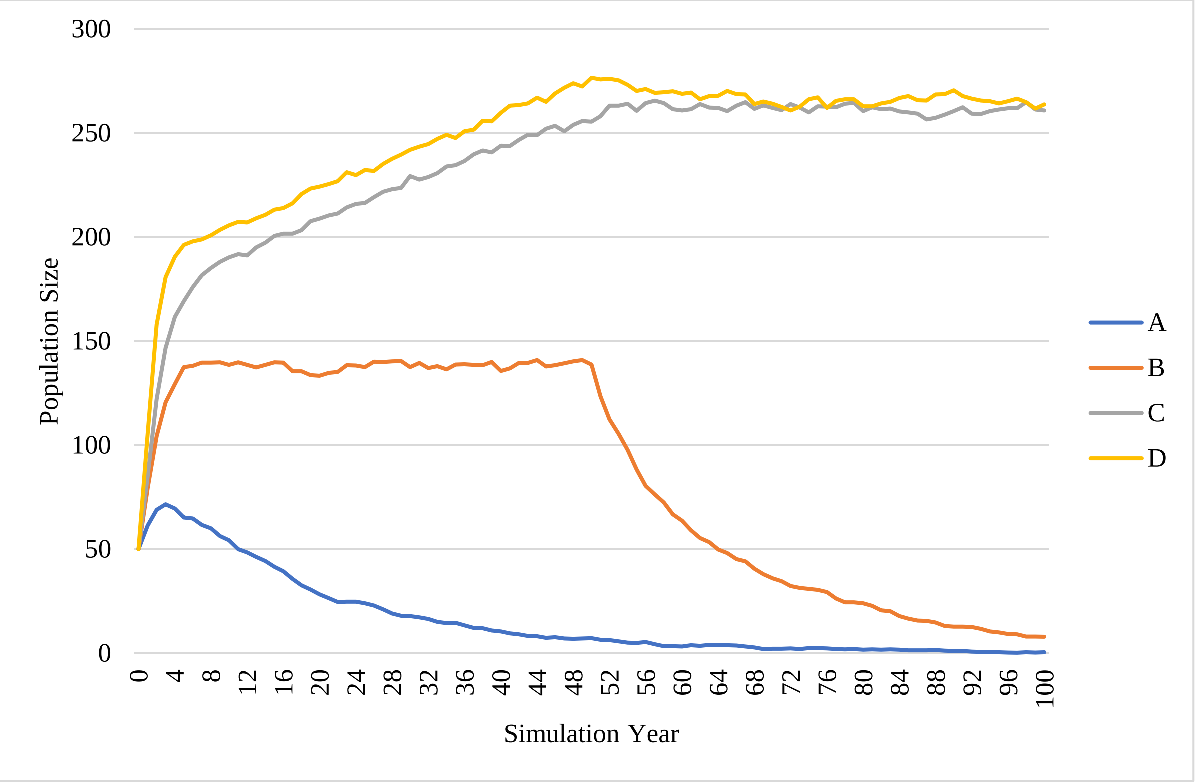

Figure 4.16. Evaluation of four management options on a *H. lacerata* (Plataeu Spot-tailed Earless Lizard) and *H. subcaudalis* (Tamaulipan Spot-tailed Earless Lizard) population with an initial population, N_0, of 50 individuals and a carrying capacity, K, of 200. **A**) no management practices were implemented in this scenario. We used the baseline values for all parameters except "mortality rates," which we increased by 10% of the baseline value ($Mort_H = 88\%$ and $Mort_A = 55\%$). **B**) Supplementation of ten pairs of female and male adult STEL (1+), raised in captivity, were released into a wild STEL population every other year starting from year 1 and ending on year 50 of the simulation. Hatchling and adult mortality was set at 10% above the baseline value ($Mort_H = 88\%$ and $Mort_A = 55\%$). **C**) Habitat restoration and/or extension practices were implemented for a duration of 50 years in this scenario. K (200) increased by 1% annually, and mortality rates for hatchlings and adults decreased by 10% (MortH = 80% and

MortA = 50%). **D**) For this simulation, we combined the management practices described in scenario B and scenario C.

In the management option scenarios, supplementation of STEL into a population with high mortality rates was only effective during the years the program was in place. The supplementation scenario highlights the importance of identifying and mitigating underlying threats as supplementation of adults is not sufficient to counteract the loss of individuals and population declines resulting from stochastic fluctuations in demographic rates which is characteristic of small populations. This is one of the challenges supplementation programs face, where unless the underlying cause of population decline has been identified and addressed, the captive population will act as a source population while the wild population will act as a population sink (Anderson et al. 2015). Additionally, the population size during years of supplementation will reflect the carrying capacity regardless of the number of individuals supplemented, which indicates that these programs must first address issues with the carrying capacity of the receiving population.

Results from the manual perturbation and elasticity analyses highlighted the importance of considering management practices that aid in hatchling survival and fecundity. Head-start programs, in which young animals are born and partially raised in captivity prior to being released, can be effective at increasing recruitment and survival of juvenile cohorts in wild populations of species with low adult survival and high fecundity, such as STEL (Escobar et al. 2010). Even though STEL populations are in decline over a broad range of its distribution, stable populations still exist, such as in Val Verde County and in Agua Dulce, TX, USA, that can allow for individuals to be collected in the case that a captive breeding and release program is implemented. It is important to note that the simulated models did not account for the survival rate of the supplemented individuals after being transferred from captivity settings to the wild. However, the implementation of soft releases, which allow translocated and supplemented individuals to acclimate to the environment of the recipient site in protected enclosures prior to official release, are shown to increase the survival rate of supplemented captive-bred animals (Tuberville et al. 2005; Mitchell et al. 2011; Knox and Monks 2014; DeGregorio et al. 2020).

Moreover, the model results demonstrated that when habitat restoration efforts (i.e., increased carrying capacity) were combined with supplementation, the population size was boosted, both in numbers and genetically, and was able to stabilize itself after the discontinuation of both programs. If captive breeding and release are initiated without habitat improvement, the STEL population will likely become a population sink and struggle to become self-sustaining on its own. On the other hand, even if supplementation is omitted, habitat restoration alone demonstrated the ability to be able to reverse a population decline. However, the model reflected positive results because of the assumption that restoration would create high quality habitat that supports the survival of STEL increase by at least 10%. For example, the removal of invasive grass monocultures can leave behind areas of bare ground that can aid STEL in detecting threats (like predators) or detecting prey. Therefore, habitat recovery can only be successful if it is utilized as a management technique with the aim of addressing underlying threats to STEL rather than with the sole goal of expanding carrying capacity.

Although the model simulations demonstrate habitat restoration can aid in STEL conservation efforts, there are foreseen difficulties in recovering declining populations solely through means of habitat restoration (Schrott et al. 2005). This is because, in certain circumstances, populations can exhibit habitat sensitivity (decline in response to habitat loss and fragmentation), but nevertheless, cannot be rescued through habitat restoration because of demographic limitations. Due to the complexity of natural environments, habitat restoration efforts intended to recover rare or endangered species work best when combined with additional management strategies such as supplementation, predator control, and artificial nest sites, among others (Franzreb 1997, Schrott et al. 2005).

CONCLUSION

The primary aim of this study was to evaluate the risk of extinction of STEL under varied demographic and environmental conditions as well as under a series of alternative scenarios (i.e., catastrophic drought, habitat loss, and management strategies) that the species either does or could face in the near future. It is important to emphasize that, PVAs do not give absolute answers regarding population growth and extinction probabilities (Beissenger and Whestpal 1998; Reed et al. 2002), but the estimates we obtained provide insights into the relative role of demographic and anthropogenic factors on STEL population persistence. Our simulations demonstrate that hatchling survival, age of first reproduction, sex ratios at birth, and reproductive success (i.e., percentage of females breeding and clutch size) have a strong influence on population projection and should be considered in understanding the life history and population dynamics of the species as well as in conservation and management practices.

Results from our baseline, best case scenario, simulations demonstrated that STEL have a relatively low probability of extinction over the next 100 years. However, this result is not expected in natural settings, given that STEL appear to have specific habitat preferences and current populations have declined sharply, which strongly justifies exploratory simulation studies such as this (Axtell 1968; Axtell 1998; Duran and Axtell 2010, 2011). Although the life history characteristics (e.g., early-maturing, multiple-brooded) of STEL favor its persistence, our simulations indicate that anthropogenic factors coupled with a changing climate threaten the species' survival. The simulations demonstrate that habitat loss can be an important limiting factor leading to the species' decline and possible extinction. STEL habitat consists of short-grass prairies with native grass composition, sandy-clay loams, bare ground, and the absence of woody vegetation (Duran 2014; Hibbitts et al. 2021; Kahl et al. 2021); therefore, it is essential to target grasslands identified as STEL habitat for conservation and management action as a way to potentially improve STEL populations and increase the likelihood of the species' continued persistence. Evaluation of the efficacy of habitat restoration efforts indicates that this management strategy has strong potential to reverse the effects of contemporary population declines. Although supplementation of STEL alone did not prove to be sufficient to create a self-sustained population, we recommend implementation of a captive breeding and release program alongside habitat improvement efforts to initiate population recovery. In summary, this study provides an initial step in assessing and quantifying potential threats affecting STEL populations in the wild, particularly in terms of the potential effects of demographic, environmental, and anthropogenic factors on the long-term persistence of this species.

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