

HABITAT SELECTION AND MOVEMENT BEHAVIOR
OF CHIRICAHUA LEOPARD FROGS

by

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ABSTRACT

Degradation of habitat and disruption of dispersal are major drivers of amphibian declines, including that of the Chiricahua leopard frog (*Lithobates chiricahuensis*). Currently, the Chiricahua leopard frog is federally threatened and restricted to anthropogenic sources of water, including ponds maintained for livestock, throughout much of its range. Habitat selection and patterns of dispersal between disjunct water sources are not well understood for this species. We captured frogs leaving ponds using pitfall traps and attached radio transmitters to frogs on the Ladder Ranch in southern New Mexico during summers 2013 and 2014. We checked pitfall traps and located telemetered frogs daily for up to 8 weeks. We assessed cues affecting the number of frogs emigrating from ponds using linear models, distances moved by frogs each day using linear mixed models, and fine-scale habitat selection using conditional logistic regression. Emigration of frogs from ponds was related to rainfall and was greatest at an intermediate level of rain. Daily movement distances were highly variable among individual frogs and not related to sex or size of the frog, which suggests that individual heterogeneity in dispersal behavior may be an adaptation of this species. We observed daily and total movement distances longer than any previously recorded for the species. Habitat selection was very consistent among individuals. Frogs chose habitats with more low-lying cover, a tree overstory, and a mud substrate, features created by summer monsoon rains. We suggest preservation and restoration of habitat features important for frogs and selecting translocation sites and times based on movement behavior observed in this study. Our findings will inform reintroductions of and habitat improvements for Chiricahua leopard frogs, with the eventual goal of delisting this species.

CHAPTER ONE

INTRODUCTION TO THESIS

Of the described species of amphibians worldwide, one-third are threatened with extinction (IUCN, 2009). In North America, 26% of amphibian species are at some risk, which is five times higher than that of terrestrial fauna (Ricciardi and Rasmussen, 1999). Current declines exceed the threshold that would be expected with natural population oscillations, approaching rates seen only in prehistoric mass extinctions (Blaustein and Wake, 1990; Wake and Vredenburg, 2008). Although many possible sources have been proposed as mechanisms for declines (climate change, Wake and Vredenburg, 2008; solar UV-B radiation, Blaustein et al., 1994; introduced predators, Pilliod and Peterson, 2001, Adams, 2000; infection by a pathogenic fungus, *Batrachochytrium dendrobatidis* ["Bd"], Berger et al., 1998), habitat destruction, fragmentation, and degradation are almost certainly major causative agents of the observed trends (Green, 2005).

Wetlands in the Chihuahua region of the southwest United States and Mexico have been designated as one of the "Global 200" ecosystems of highest conservation concern (Olson and Dinerstein, 1998). Minckley et al. (2013) found that 19% of animal and plant species in Arizona listed under the Endangered Species Act or candidates for such listing were associated directly with permanent desert wetlands. Climate models predict warming temperatures and modified precipitation regimes in the southwestern US, which will result in decreased soil

moisture and vegetation cover, as well as altered vegetation composition (Notaro et al., 2012). Amphibians require moisture on their skin for effective respiration (Wake and Vredenburg, 2008), and vegetation cover at breeding sites, important for avoiding predators, is positively correlated with amphibian species richness (Shulse et al., 2012). Because amphibians in the southwest may be particularly susceptible to habitat-related changes, future management actions that actively mitigate the effects of habitat loss or fragmentation will be essential for amphibian conservation.

The Chiricahua leopard frog (*Lithobates* [= *Rana*] *chiricahuensis*) is a medium-sized frog native to central and southeastern Arizona, southwestern New Mexico, and northern Mexico (Platz and Mecham, 1979; Stebbins, 1985). The historical distribution of *L. chiricahuensis* is poorly known (Sredl and Jennings, 2005), and its range in Mexico is not well studied, although there seems to be at least one healthy, robust population in Durango, Mexico at the southern edge of the animal's range (Streicher et al., 2012). Chiricahua leopard frogs are found in natural streams with rocky pools, springs, and ponds, but man-made stock tanks also provide important habitat (Stebbins, 1985). Adults are highly aquatic and are rarely found far from water, although frogs can survive periods of surface water loss via an unstudied mechanism (Clarkson and Rorabaugh, 1989; Sredl and Jennings, 2005). Chiricahua leopard frogs are affected by a variety of threats common in amphibians, including *Bd* infection (Boykin and McDaniel, 2008) and introduced predators such as American bullfrogs (Rosen and Schwalbe, 1995). In 2002, Chiricahua leopard frogs were listed as threatened under the Endangered Species Act due to a

combination of these threats along with fragmentation of existing populations (USFWS, 2002).

Dispersal is any movement of organisms between habitats that results in gene flow among groups of animals (Benton and Bowler, 2012). The evolutionary advantage of dispersal is the potential for colonization of habitat patches where the organism may increase fitness (Bowler and Benton, 2005). Dispersal also reduces interaction between kin, whether through competition or inbreeding, and may allow organisms to escape unfavorable conditions (Mattysen, 2012). The effects of dispersal are important for managers concerned with the conservation of species of concern. Dispersal determines local population sizes through the net effect of organisms emigrating from the patch and immigrating from others (Fahrig and Paloheimo, 1988). The net effect to a local population may be positive or negative, depending on the propensity of organisms to emigrate and the ability of the organisms to locate and immigrate to new patches. The cost of dispersal to the species is the risk to individual organisms (Hanski et al., 2006). Understanding dispersal of animals is an extremely important facet of wildlife ecology. Movement between populations resulting in gene flow may allow for the persistence of populations over time (Turchin, 1998).

Studying movements of amphibians can provide clues about the location and importance of different habitat types used at various life stages. If wildlife managers preserved only breeding habitat (e.g., ponds) for example, this may not be sufficient to support effective foraging, movement, and hibernation (Marsh and Trenham,

2001). Habitat used during non-breeding periods may be of equal importance to breeding sites (Fellers and Kleeman, 2007). In addition to identifying habitat features important to all stages of the amphibian life cycle, movement studies identify landscape attributes such as type and amount of vegetation cover (Fellers and Kleeman, 2007) that affect where or how far an individual may move, the weather conditions conducive to movement (Dole, 1971), or characteristics of the individual animal that influence its propensity for movement, such as sex or size (Pilliod et al., 2002).

We sought to understand factors important for the dispersal of Chiricahua leopard frogs, in order to better inform management decisions for their recovery. Chapter 2 focuses on the cues related to when Chiricahua leopard frogs initiate dispersal and leave perennial ponds, and how far and how quickly the frogs can move. We will examine relationships between these movements and physical characteristics of the animals. Chapter 3 focuses on the habitat selection by frogs during monsoon season on the Ladder Ranch in southern New Mexico. Results from this study will improve our understanding of the habitat features necessary for frogs to persist in desert landscapes. Results from both these studies will be invaluable for recovery and removal of the Chiricahua leopard frog from the Endangered Species List. Understanding the factors that drive dispersal and the habitat features necessary for frogs to survive will allow managers to facilitate dispersal events to establish new populations or promote movement between existing populations.

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CHAPTER TWO

DISPERSAL OF CHIRICAHUA LEOPARD FROGS FROM PERENNIAL PONDS

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CHAPTER TWO

DISPERSAL OF CHIRICAHUA LEOPARD FROGS FROM PERENNIAL PONDS

Abstract

Anthropogenic habitat fragmentation and subsequent disruption of animal dispersal is responsible for extinctions in some species, including amphibians. Amphibians that are able to disperse longer distances may be at less risk of extinction. The Chiricahua leopard frog (*Lithobates chiricahuensis*) is federally threatened and declines are attributed to factors including habitat loss and degradation throughout its range. We sought to add to the limited scientific literature on this species by studying Chiricahua leopard frog dispersal on the Ladder Ranch in southern New Mexico during summers 2013 and 2014. Using pitfall traps, we captured frogs leaving ponds to obtain an index of emigration rate and attached radio transmitters to 47 individuals to characterize dispersal movements. We checked pitfall traps and located 30 telemetered frogs daily for up to 8 weeks. We assessed differences in the number of frogs emigrating from ponds using linear models and distances moved by instrumented frogs each day using linear mixed models. The number of frogs emigrating from ponds was related to rainfall but not water temperature. More frogs emigrated at an intermediate level of rainfall. Daily movement distances were highly variable among individual frogs, and physical characteristics of frogs (sex and snout-urostyle length) did little to explain variation in distances moved after accounting for individual variation. Frogs who

left ponds moved an average of 96 m/day during the study period, although one individual moved 1658 m in a day and another travelled 9888 m over 36 days. These distances are higher than those recorded previously for this species. Our findings about the dispersal cues and movement abilities of Chiricahua leopard frogs will help managers to better choose translocation sites that are within dispersal distances of the frog to improve connectivity of reintroduced populations.

Introduction

Habitat fragmentation, which directly disrupts animal dispersal, is one of the largest drivers of biodiversity loss on the planet (Soulé, 1991). Species that are more mobile can better cope with the effects of fragmentation and are at less risk of extinction (Ficetola and Bernardi, 2004). Pond-breeding amphibians often are portrayed as occupying a series of discrete habitat patches across a landscape (Marsh and Trenham, 2001). Amphibians usually are assumed to have limited dispersal abilities, affecting their ability to colonize habitat patches (Blaustein et al., 1994), but this may not be true for many species (Smith and Green, 2005). Long-distance dispersing amphibians are the most likely to reach distant habitat patches and colonize previously extirpated patches on the landscape (Fellers and Kleeman, 2007), which makes dispersal behavior of great conservation concern. Maintaining connectivity between patches may decrease the risk of species extinction by increasing gene flow (Fagan et al., 2002) to insure persistence over time (Turchin, 1998). Identifying individual or landscape factors important for dispersal may be a

way to facilitate recolonization of habitat patches and increase persistence of imperiled amphibian species.

Conserving “ecological connectivity” is a main focus for any effective amphibian management plan (Semlitsch, 2000), which requires including information about the dispersal capabilities of any species of interest (Seburn et al., 1997). Because amphibians need an array of terrestrial and aquatic habitat features, much of the work on amphibian movement has been centered on quantifying movement between seasonally-used sites (Bull and Hayes, 2002; Matthews and Pope, 1999) and through habitat corridors (Baldwin et al., 2006; Fellers and Kleeman, 2007; Pilliod et al., 2002; Tatarian, 2008). Studying amphibian movement also can help identify weather conditions conducive to movement (Dole, 1971) or characteristics of the individual animal that influence its propensity for movement, such as sex or size (Pilliod et al., 2002), which can guide reintroductions where species have been extirpated.

Amphibian species are declining worldwide at a rate not seen except during prehistoric mass extinction events (Blaustein and Wake, 1990; Wake and Vredenburg, 2008). One-third of the amphibian species known to science now are threatened with extinction (IUCN, 2009). The Chiricahua leopard frog (*Lithobates* [= *Rana*] *chiricahuensis*) is a species native to Arizona, New Mexico, and northern Mexico (Platz and Mecham, 1979, Stebbins, 1985), although the historical distribution is poorly known (Sredl and Jennings, 2005). In 2002, Chiricahua leopard frogs were listed as threatened under the Endangered Species Act due to

fragmentation of extant populations, loss of animals from some ranges, as well as threats from invasive species and disease (USFWS, 2002). Suggested conservation strategies for the Chiricahua leopard frog have included predator removal, restoring breeding habitat and corridors, and translocations of individuals (Sredl and Howland, 1994). Aside from some basic information about natural history and documentation of population declines, there is very little scientific literature about Chiricahua leopard frogs (USFWS, 2002), including about their movement habits and abilities.

Studying dispersal of an animal requires an understanding of the basic components of the process. Dispersal consists of three stages: emigration, transfer, and immigration (Matthysen, 2012). We were interested in better understanding the first two stages of dispersal in Chiricahua leopard frogs - emigration out of and transfer between habitats. Our study aimed to identify the cues for emigration of frogs out of ponds and their ability to transfer between habitat patches to inform management of extant populations and advise reintroduction efforts in their former range.

Materials and Methods

Study Site.- We conducted research on the Ladder Ranch, a private, 63,300-ha working bison ranch in Sierra County, New Mexico, adjacent to the Gila National Forest (Fig. 2.1). The Ladder Ranch holds 33% of the known populations of Chiricahua leopard frogs in New Mexico, and is therefore of great importance to

conservation efforts for the species (Kruse and Christman 2005). The ranch is comprised of Chihuahua Desert grasslands to ponderosa pine forests at higher elevations. Riparian vegetation consists mainly of oak (*Quercus* spp.), cottonwood (*Populus*), juniper (*Juniperus*), and willow (*Salix*). Elevation in our study area ranged from approximately 1700 to 2050 m. Up to 50% of annual precipitation may fall during July-September in monsoon-dominated areas of the southwest (Sheppard et al., 2002). For this reason, we conducted our work during monsoon season, when Chiricahua leopard frogs are thought to travel overland between water bodies (USFWS, 2007).

We specifically focused our work within the Seco Creek drainage on the Ladder Ranch. The Seco Creek drainage holds a persistent population of Chiricahua leopard frogs, especially in livestock tanks along the creek's length (M. McCaffery, pers. comm.). Within this drainage, we captured frogs at North Seco Well and Johnson Well (Fig. 2.1), two livestock tanks along the creek course with apparently large populations of frogs (based on visual encounter surveys over the past decade, M. McCaffery, pers. comm.).

North Seco and Johnson Wells (13S, 0249044E, 3667208N and 0260489E, 3664241N, respectively, datum WGS84) are small (approximately 20 m diameter), excavated livestock watering tanks ("ponds") filled with groundwater by solar pumps. Both are vegetated with aquatic plants (especially *Typha*, *Potamogeton*, and *Scirpus* spp.) and contained breeding Chiricahua leopard frogs during the summers of 2013 and 2014 (R. Hinderer, pers. obs). Johnson Well is approximately 12 km

downstream from North Seco Well. Three other ponds lie between our study sites at 2.5-3.5 km intervals, and there are several more upstream and downstream of our sites (Fig. 2.1). During the dry season, there is little to no standing water in this section of Seco Creek save these ponds. During monsoons with sufficient rainfall, Seco Creek may flow, and pools may remain in the creek between storms (R. Hinderer, pers. obs.). North Seco Well is 22 m from the Seco Creek channel, and Johnson Well is 205 m from the creek channel (Fig. 2.1).

Frog Capture.- To capture frogs, we encircled Johnson and North Seco Wells with drift fences made of landscape fabric and pitfall traps made of 5-gallon, plastic buckets (Dodd and Scott, 1994) beginning in July of 2013 and 2014. We buried the drift fence at least 0.1 m into the soil and secured the fence to existing livestock exclusion fences with zip-ties. The landscape fabric was 1-m wide, so fences were approximately 0.8-m tall. We installed pairs of pitfall traps, one on each side of the fence, approximately every 10 m around the ponds, for a total of 16 traps at each site. We designed the traps with a removable cover to provide shade and prevent desiccation of captured animals. We added drain holes above the bottom of the bucket to allow retention of some standing water, while still draining water above the level of the holes. We checked pitfall traps twice daily as weather permitted during July and August each year. We also opportunistically captured frogs in Seco Creek using dipnets.

We recorded morphometric data including snout-urostyle length (SUL), mass, and sex (indicated by the presence of nuptial pads on the thumbs of adult

males) for every captured frog. Male frogs began to show secondary sex characteristics when they reached approximately 50 mm SUL (R. Hinderer, pers. obs.). As such, we considered frogs ≤ 50 mm SUL without evidence of nuptial pads as subadults. We considered frogs > 50 mm as adults and we also determined sex. We released frogs on the opposite side of the fence from where they were captured (e.g., frogs that were captured in traps inside the drift fence were released on the outside).

Radio Telemetry.- We selected a subset of captured animals for radio telemetry. Selection was not random: we selected animals where transmitter mass did not exceed 10% of the animal's mass (Richards et al., 1994) and attempted to select animals from all size classes and both sexes. Blomquist and Hunter (2007) found little effect on the vagility of *Rana* [*Lithobates*] *pipiens*, a closely related leopard frog species, with transmitters up to 10% of frog body mass. We attached a transmitter (Holohil Systems model BD-2, 0.62, 0.9, or 1.2 g, www.holohil.com) to frogs with a flexible piece of elastic, strung through small glass beads and the transmitter, which was secured around the frog's waist (Muths, 2003). We sized belts so that they were just snug over the thighs when the legs were fully extended rearward, but loose on the waist when the frog was sitting normally. We assigned each frog a transmitter with a unique frequency and located animals every day or as conditions allowed. We also tracked a small subset of frogs (8 total) that were translocated from Seco Creek to an adjacent drainage for a concurrent project.

Weather Data Collection.- We deployed temperature loggers (Hobo Pendant, Onset Computer Corporation, www.onsetcomp.com) at both Johnson and North Seco Wells to monitor water and air temperature. We attached one temperature logger to a piece of rebar driven into the bottom of the pond, so that the temperature logger was approximately 0.2 m below the water's surface, in shade created by emergent vegetation. We placed another temperature logger in the shade of trees <30 m from each pond to monitor air temperature. Loggers were set to record air or water temperatures at 10-minute intervals throughout the trapping period, which we then averaged for each day. We also fixed simple glass rain gauges (AcuRite 6-inch rain gauge, www.acurite.com) to fencing around Johnson and North Seco Wells to monitor precipitation. We checked and emptied rain gauges once daily during trap checks.

Analysis of Capture Data.- We used captures of frogs and weather data to explore which cues trigger Chiricahua leopard frogs to emigrate from ponds and initiate dispersal. We compiled the number of frogs caught every day at pitfall traps during the summers of 2013 and 2014. Because we were interested in the outward migration of frogs from ponds, we only counted frogs caught in traps on the inside of the drift fence to avoid double counting individuals who left the pond and returned later. We lagged average daily temperatures by a day to account for the fact that frogs were overwhelmingly found in traps in the morning, after being caught the night before (R. Hinderer, pers. obs.). We did not lag rainfall data when

attempting to explain captures, as rain fell during the period before trap checks, at the same time frogs were captured.

We used linear regression models to determine whether lagged average daily water temperature, rainfall, and site (Johnson or North Seco) helped to explain the number of frogs leaving ponds (that were captured in pitfall traps). Average daily water and air temperatures were correlated, so we only used water temperature in analysis because water temperature was more directly descriptive of the environment that a frog was experiencing before leaving a pond. We hypothesized and that frogs may emigrate from ponds more at an intermediate level of rainfall (and tested a quadratic term for rainfall), and hypothesized that the relationship of rainfall to numbers of frogs emigrating may depend on site (tested an interaction between rainfall and site). We rejected a more parameterized model if it was unlikely to better explain the number of frogs leaving ponds ($P > 0.1$ from a likelihood-ratio test). We analyzed all data in R (R Core Team, 2014).

Analysis of Tracking Data.- We used relocation data from radio-tracked Chiricahua leopard frogs to study what factors affect frogs' dispersal ability. We calculated the distance moved by frogs each day based on straight-line Euclidean distances. When we did not track a frog for multiple days, we computed the average distance moved per day over that period; there were 260 cases (out of 745) where we used averaged daily movement distances. Because we were interested in understanding transfer of frogs between aquatic habitats, we discounted any

locations when a frog remained in the same pond. This eliminated some animals' locations, leaving 30 individuals for analysis between 2013 and 2014.

We used linear mixed models to test whether sex (male, female, or subadult), SUL, or year were related to the distances moved by frogs. We included individual frog as a random effect to account for differences in movement distances among individuals and different numbers of observations per animal (Freitas et al., 2008). We hypothesized that the relationship between daily distance moved and SUL may depend on sex, so we tested an interaction between sex and SUL. We also hypothesized that intermediate-sized frogs may move more than small and large frogs, so we tested a quadratic term for SUL. We rejected a more parameterized model if it was unlikely to better explain the distances moved by frogs ($P > 0.1$ from a likelihood-ratio test). We analyzed all data in R (R Core Team, 2014) and used package lme4 to formulate mixed models.

Results

Capture Data.- We caught a total of 2609 Chiricahua leopard frogs in pitfall traps as they left ponds (i.e., were caught on the inside of drift fences) in 2013 and 2014. We caught almost four times more frogs in 2014 (2067 frogs) than in 2013 (542 frogs). The overwhelming majority (95%) of frogs caught in interior pitfall traps were subadults (2459 captures), compared to only 5% for adults (125 captures), while 25 frogs were of indeterminate sex.

We caught frogs more on the inside of drift fences (2609 times, 81%) than on the outside of drift fences (594 times, 19%). Frogs also appeared to be preferentially leaving and entering ponds on the side nearest Seco Creek, though this phenomenon may have been more pronounced at North Seco well (Figs. 2.2, 2.3).

There was no evidence that body condition, as a function of grams mass per mm SUL, differed between frogs captured at Johnson Well and North Seco Well ($t_{1625} = 1.15$ $P = 0.251$; Fig. 2.4).

The number of frogs emigrating from ponds depended on daily rainfall and site. Emigration from ponds was greatest at an intermediate level of rainfall, and the relationship between amount of rainfall and emigration differed by site (Table 2.1). At North Seco Well, daily captures in pitfall traps increased with increasing rainfall, up to a maximum of 154 frogs/day (95% CI = 130 - 179) with 2.84 cm of rain. After that point, captures declined with increasing rainfall (Fig. 2.3). At Johnson Well, daily captures in pitfall traps increased with increasing rainfall, up to a maximum of 36 frogs/day (20 - 52 frogs/day) with 1.47 cm of rain, and declined after that point (Fig. 2.3). We found little evidence that frogs emigrated based on lagged daily water temperatures, after accounting for rainfall and site differences ($\chi_1^2 = 1.88$, $P = 0.170$).

Tracking Data.- Frogs that left ponds ($n = 30$ individuals) moved an average of 2427 m over the tracking periods from July through early September 2013 and 2014. One individual moved 9888 m over 36 days. Frogs moved an average of 97

m/day, but some moved much further (up to 1658 m/day; Fig. 2.3). Frogs moved different distances based on their length, but not based on sex or the year (Table 2.2). Larger frogs moved less, specifically, 1.46 m less per day for each 1 mm increase in SUL, but uncertainty around this estimate was high (95% CI = 3.34 m less - 0.41 m more). We found that movement distances varied greatly among individuals (SD of the random effect = 61 m/day, Fig. 3.4), suggesting that other individual differences (unrelated to SUL, sex, or year) affect daily movement distances in this frog species. There was no evidence that the relationship of distance moved to SUL depended on sex after accounting for sex and SUL ($\chi_4^2 = 1.71$, $P = 0.789$), and little evidence that the relationship of distance moved to SUL was maximized at some intermediate level ($\chi_1^2 = 2.01$, $P = 0.157$).

Frogs moved more often upstream than downstream. Out of 613 individual movements portrayed as the east-west displacement between successive locations (not necessarily successive days), 209 movements (34%) were towards the east (e.g., downstream) while 404 movements (66%) were towards the west (upstream; Fig. 2.6).

Discussion

The three stages of dispersal- emigration, transfer, and immigration- are rarely distinguished in empirical studies (Cote et al., 2010). We partitioned dispersal of Chiricahua leopard frogs from natal ponds and focused on the first two stages. First, we trapped frogs as they left ponds in order to determine the

environmental factors related to emigration. Second, we followed frogs that left ponds to determine their capacity for transfer to other aquatic habitats across the landscape and factors that influenced that capacity.

Previous research on northern leopard frogs (*Lithobates pipiens*), a closely related species, also found that emigration movements from ponds were correlated positively with rain events (Dole, 1971; but see Seburn et al., 1997). In another study, Chiricahua leopard frogs also moved out of ponds more often with increasing amounts of rainfall (Kruse and Christman 2005). We expected that our study would also show a simple positive relationship between rain amount and emigration. This is logical, as water loss by desiccation is the largest limiting factor in the utilization of terrestrial habitats by amphibians (Thorson, 1955). Our findings that frogs emigrated more at an intermediate level of rainfall are somewhat surprising, but may be due to the specific environmental conditions created during monsoons. We observed periods of extremely heavy, localized rainfall with high winds throughout the duration of our study. These sorts of violent storms may reduce the chances that frogs emigrate if their movement or ability to locate habitat features is hampered.

Although we did not find any relationship between water temperature and emigration, Kruse and Christman (2005) found that the number of frogs leaving ponds was related to pond water temperature. If water temperature was indeed related to emigration rate during our study, the effect was small enough to be effectively masked by the effect of precipitation.

We found more juvenile Chiricahua leopard frogs than adults leaving ponds, although we do not know the overall age structure of the populations we studied. Similarly, juvenile wood frogs (*Lithobates sylvaticus*) and northern leopard frogs also emigrate more frequently than adults (Berven and Grudzien, 1990; Dole, 1971). If juveniles are more likely to emigrate, and if the goal of reintroduction is to establish a population at the introduction point, adults may be better candidates as translocated animals due to their higher site fidelity. Frog reintroduction efforts can be hampered if individuals “home” to their former location (Chelgren et al., 2008). Although we have no way to predict the homing behavior of Chiricahua leopard frogs, if adult frogs are less likely to emigrate they may also be less likely to attempt homing behavior.

We found that the relationship between rainfall and emigration behavior differed by site, which may be due to specific characteristics of each pond. North Seco Well is only 22 m from the creek, whereas Johnson Well is 205 m from the creek. The difference in distance to Seco Creek may explain why frogs appeared to prefer to leave on the creek side of North Seco Well, but did not exhibit such a strong preference at Johnson well (Figs. 2.2 2.3). Frogs may be able to detect the creek a short distance away from North Seco Well, but leave Johnson Well without any purposeful orientation. Johnson Well is surrounded by fairly open terrain, with little overstory providing shade and little understory to retain moisture. In contrast, the landscape around North Seco Well is forested with mature ponderosa pines and walnut trees and includes significant annual plant growth around the pond during

the rainy season. The chance of a frog reaching the creek channel from Johnson Well, even during a rain event, is probably lower than from North Seco Well due to the intervening terrain. Exposure to predators or the risk of desiccation may limit animals' ability to travel to the creek effectively. We found that body condition, as a function of mass and length, did not differ between the two sites, and therefore find it unlikely that some systematic difference in individual frogs was related to the difference in emigration rates between North Seco and Johnson Wells.

We used the number of frog captures in interior traps as an index of emigration from ponds and made inference to the emigration of different age classes. Identifying animals individually would have allowed us to distinguish animals that only briefly left ponds and returned immediately (e.g., that may have been foraging and were captured on the bank) from frogs that left ponds and never returned (e.g., that likely emigrated). We observed more frogs leaving ponds than returning (Figs. 2.2, 2.3), which seems to indicate that at least some proportion of animals captured on the inside of drift fences never returned to the pond.

The second stage of dispersal, transfer, relies on animals being able to travel intervening distances between habitat patches. Sex, developmental stage, and body size all may influence transfer ability, but relationships differ based on taxon or among studies (reviewed in Bowler and Benton, 2005). The distances frogs moved did not differ by sex in our study. Even if males and females were moving different distances, we may not have been able to determine as much due to limitations of assessing sex of frogs in the field. Immature individuals were recorded as

“unknown” sex. This Although we included body length in our inferential model explaining movement distances, SUL did little to explain distances moved after accounting for variation among individual frogs. Similarly, wood frogs (Freidenfelds et al., 2011) and northern leopard frogs (Dole, 1971) also showed very high variation in movement distances among individuals. Individual heterogeneity in animal behavior is becoming more widely accepted as an important factor in population dynamics (Cam et al., 2002, Cote et al., 2010, Vaupel et al., 1979). Predicting which Chiricahua leopard frogs may move more than others is difficult based on the morphometric data we collected. For a manager interested in the ability of individuals to move long distances and colonize nearby habitat patches, the distances between patches may be a better metric of transfer probability than characteristics of individual frogs. Phenotypic traits such as body condition or reproductive status and environmental cues such as temperature or overcrowding may interact to influence dispersal ability, although this area of research is not well explored (Clobert et al., 2009).

We found that frogs traveled upstream more often than downstream. Other amphibians exhibit a similar bias towards upstream movements (Robertson et al. 2008; Twitty et. al 1967). Factors driving this bias are not well understood, but they may be related to increased chances of an individual finding preferred habitat features in the headwater portion of a stream (Lowe 2003). In the system we studied, upstream reaches of Seco Creek were more heavily vegetated, densely shaded, and usually held water for longer periods (R. Hinderer, pers. obs.).

Upstream movement likely increases the chances that frogs can find suitable reaches for breeding and decreases the chances of desiccation. Assuming that most animals will tend to move upstream if they disperse, managers should focus translocations at locations downstream from other potential habitat patches to give dispersing frogs a better chance of finding new colonization sites.

The daily movement distances we recorded (average = 97 m/day, maximum = 1658 m/day) are higher than many anuran species. The Chiricahua leopard frog recovery plan bases management recommendations on movement distances previously recorded for this species, although the maximum distance reported in the recovery plan is 5 miles, far less than distances we observed (USFWS 2007). Chiricahua leopard frogs in a previous study moved up to a maximum of 540 m a day (Kruse and Christman, 2005). The closely-related northern leopard frog may move 800 m a day as a juvenile, which is the stage at which their dispersal was greatest (Dole, 1971), whereas Sierra Nevada yellow-legged frogs (*Rana sierrae*) only moved an average of 8.6 m per day (Fellers et al., 2013). Although our use of radio telemetry allowed us to monitor frogs' movements daily, maximum dispersal distances over an entire season are more commonly recorded in mark-recapture studies. We observed one Chiricahua leopard frog that traveled a total of 9888 m over 36 days, which is farther than the 5720 m over 18 days documented previously in this species (Kruse and Christman, 2005). California red-legged frogs have been shown to travel up to 3600 m over approximately 35 days (Bulger et al., 2003) and wood frogs may move upwards of 1 km between ponds over 3-6 years (Berven and

Grudzien, 1990). Most other examples in the literature of long-distance movements by anurans are by toads, which are usually more terrestrial and therefore less restricted to travel through aquatic habitats. Western toads (*Anaxyrus boreas*) traveled an average of 717 m during the fall season as they moved to hibernation sites in Alberta (Browne and Paszkowski, 2010). Finally, possibly the longest-recorded distance moved by any anuran species is 34 km over 15 months, by a Fowler's toad (*Bufo fowleri*) in Ontario (Smith and Green, 2006). Although these studies differ in methods, scope, and species, our results demonstrate that Chiricahua leopard frogs are capable of movements that are exceptionally far for anuran species, especially for frogs

Because we were limited to radio-tracking larger frogs that could safely carry the transmitter mass, we were not able to follow juveniles as they moved. Mark-recapture studies showing that juveniles move greater distances than adults (Dole, 1971) suggest that this may be an important avenue for future research, especially as transmitter technology improves and radio transmitters become smaller. Indeed, studies focused only on movements of adults may seriously underestimate the potential dispersal ability of amphibians (Berven and Grudzien, 1990). Conclusions of most movement studies also are limited by size of the study area. The scale at which the researchers are able to examine movement (e.g., how far apart sampling sites were located) explains much of the variation in movement distances recorded across many amphibian studies (Smith and Green, 2005). Dispersal distances recorded during mark-recapture or telemetry studies should be regarded as case

histories of individuals, and extrapolation to a species level should be undertaken with care. We do not imply, therefore, that the results of our study accurately describe the maximum distance that Chiricahua leopard frogs travel, but offer examples of dispersal events that are more extreme than those documented for this species in the past.

The degree of dispersal between habitat patches has the potential to affect local extinction and colonization and population density (Bowler and Benton, 2005). Amphibians are no exception- empirical studies confirm that isolation by distance increases extinction risk for some amphibian species (Sjogren, 1991). For this reason, dispersal must be understood to effectively manage a species of concern. Our findings during this study and a concurrent study of habitat selection (Chapter 3) will inform translocations of Chiricahua leopard frogs by allowing managers to target efforts on life stages more or less likely to emigrate (depending on the objectives), within dispersal distances to other populations that are reasonable, and in a habitat matrix conducive to dispersal.

Tables

Table 2.1. Likelihood-ratio tests comparing our final model of Chiricahua leopard frog emigration (accounting for all terms) to the same model without the specified term. In the case of Rain and Site, the results are for a test comparing models without interactions.

Variable	χ^2	<i>P</i>
Rain	23.65	<0.001
Site	23.78	<0.001
Rain*Site	35.93	<0.001
Rain*Rain	45.24	<0.001

Table 2.2. Likelihood-ratio tests comparing a model simply accounting for variation in movement distance among individual frogs and a model containing the specified term, while also accounting for individual variation (random effect).

Variable	<i>df</i>	χ^2	<i>P</i>
Sex	2	1.49	0.475
SUL	1	105.77	<0.001
Year	1	1.48	0.224

Figures

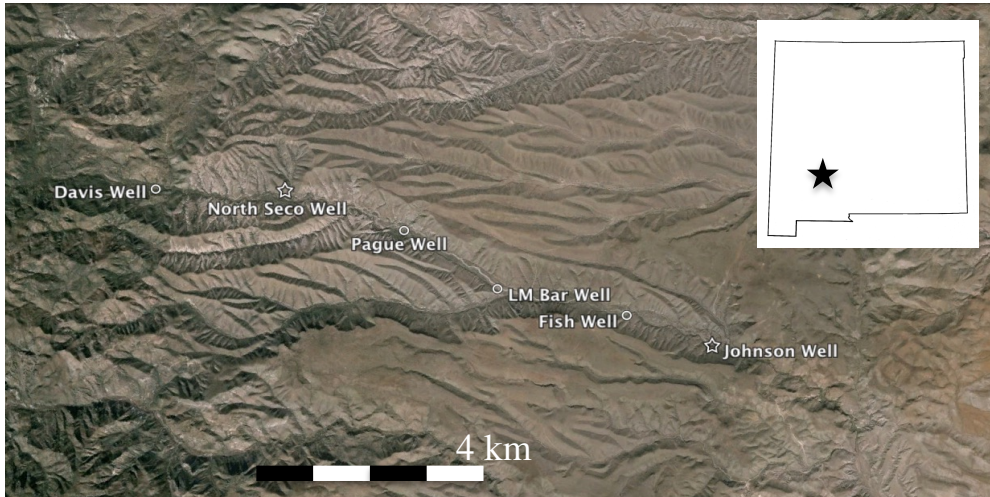


Fig. 2.1. Location of Ladder Ranch in New Mexico (star on inset) and layout of livestock watering tanks along the Seco Creek drainage. Wells indicated by white stars were focal sites for pitfall trapping and radio telemetry, summer 2014. (Imagery copyright Google, Inc.)

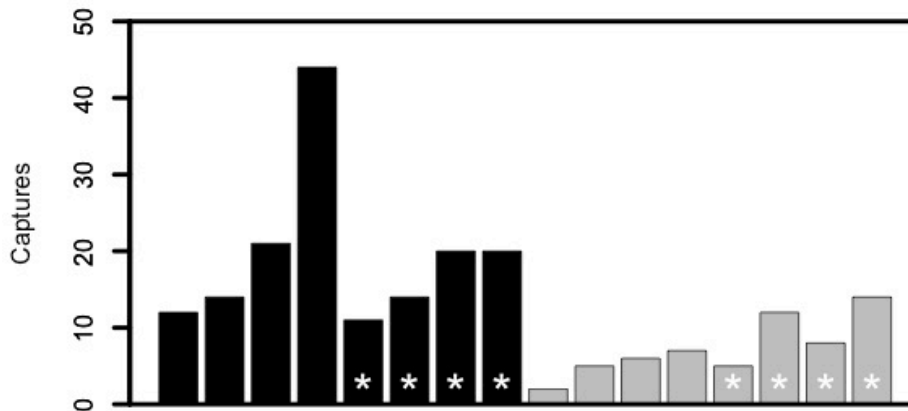


Fig. 2.2. Chiricahua leopard frog captures by trap at Johnson Well, totaled for summers 2013 and 2014. Black bars represent traps inside the drift fence, gray bars represent traps outside the drift fence. Asterisks designate traps that were on the side of the pond nearest Seco Creek.

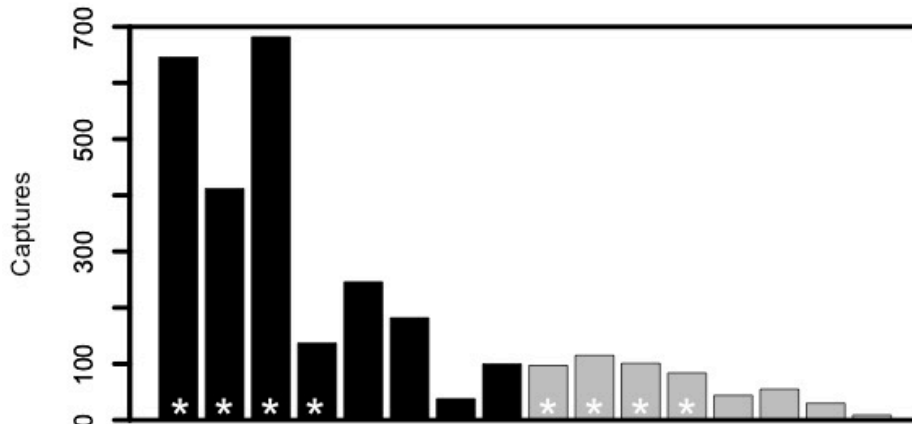


Fig. 2.3. Chiricahua leopard frog captures by trap at North Seco Well, totaled for summers 2013 and 2014. Black bars represent traps inside the drift fence, gray bars represent traps outside the drift fence. Asterisks designate traps that were on the side of the pond nearest Seco Creek.

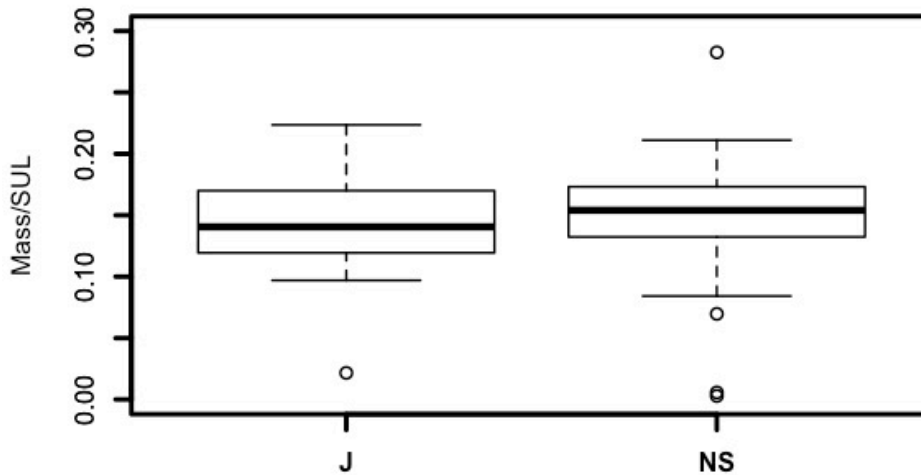


Fig. 2.4. Differences in body condition (as a function of grams mass per mm SUL) between Chiricahua leopard frogs captured leaving Johnson Well and North Seco Well ("J" and "NS", respectively) during summers of 2013 and 2014. Heavy lines represent medians, light lines the first and third quartile values, whiskers the most extreme value within 1.5 times the interquartile range, and dots are values outside that range. Three large observations between 0.7 and 1.2 g/mm were removed to increase figure clarity.

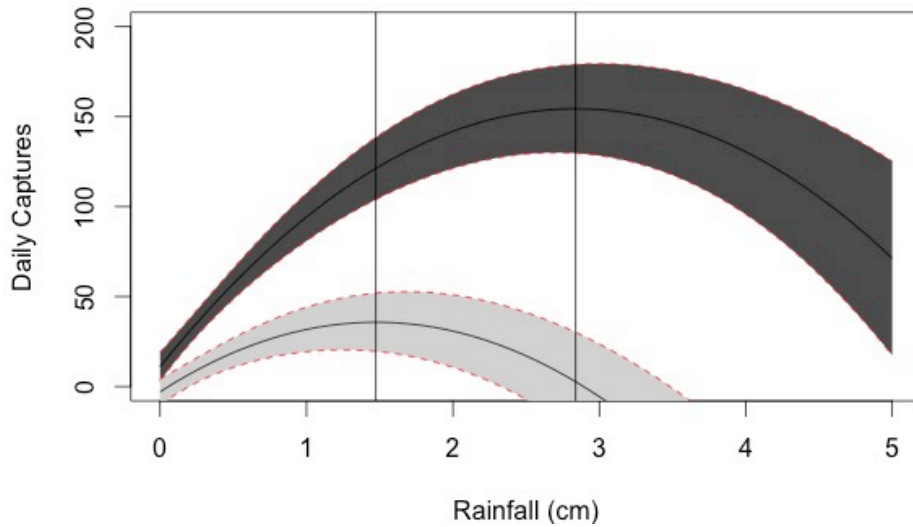


Fig. 2.5. Changes in daily captures (shaded area is 95% CI) of Chiricahua leopard frogs predicted at North Seco Well (dark gray) and Johnson Well (light gray), based on daily rainfall, summers 2013 and 2014, Ladder Ranch, NM. The maximum capture rate is predicted at 2.84 cm of rain at North Seco and 1.47 cm of rain at Johnson (noted by vertical lines).

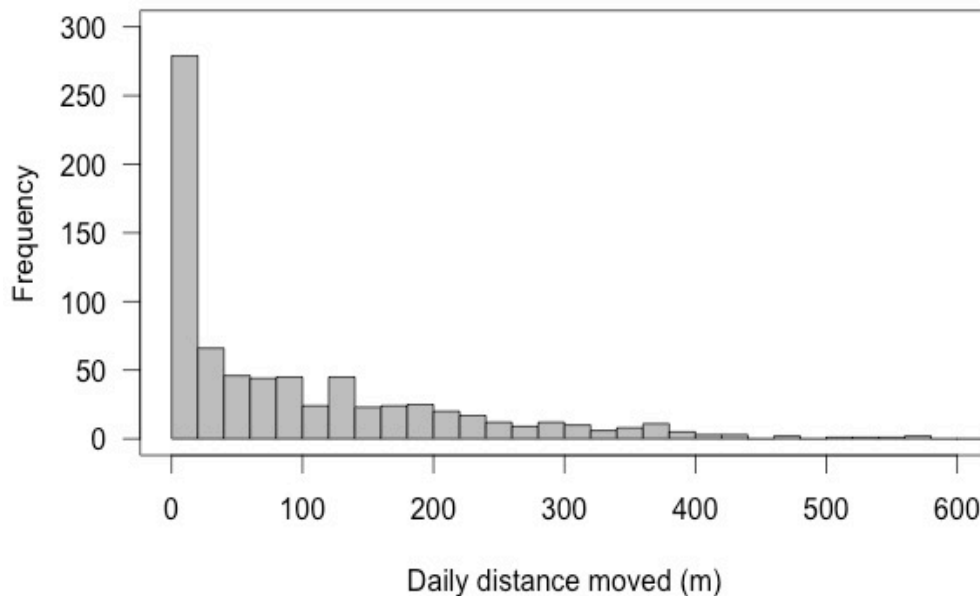


Fig. 2.6. Frequency of daily movement distances of 30 Chiricahua leopard frogs during summers 2013 and 2014, Ladder Ranch, NM. We removed one long movement (1658 m) to increase resolution of remaining observations.

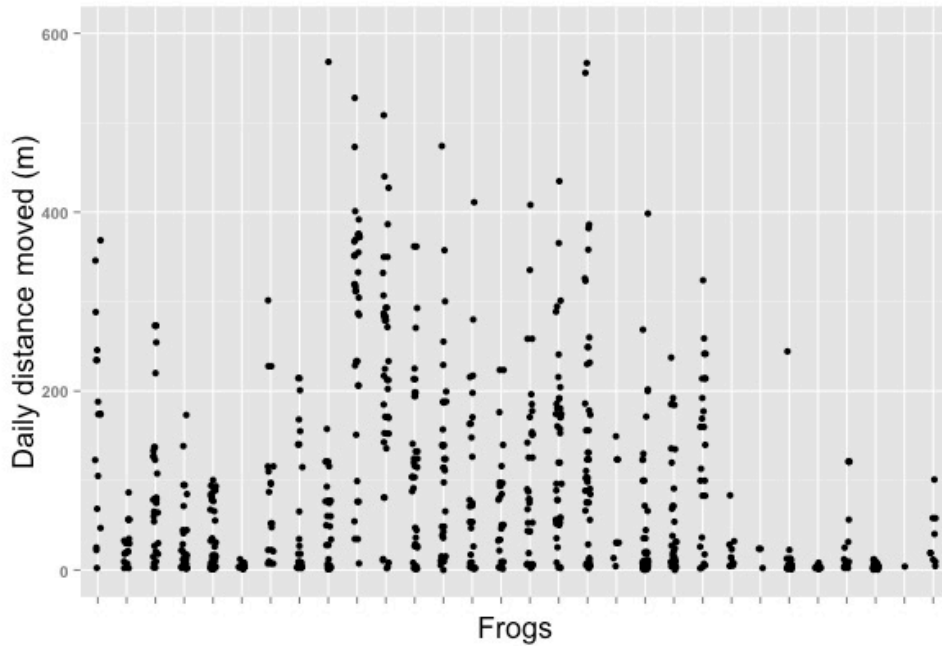


Fig. 2.7. Variation in daily distances moved by individual Chiricahua leopard frogs ($n = 30$), summers 2013 and 2014, Ladder Ranch, NM. Columns of points represent individual frogs and each point is a distance that frog moved in a day. We removed one observation (1658 m moved in a day) to increase resolution of the remaining points.

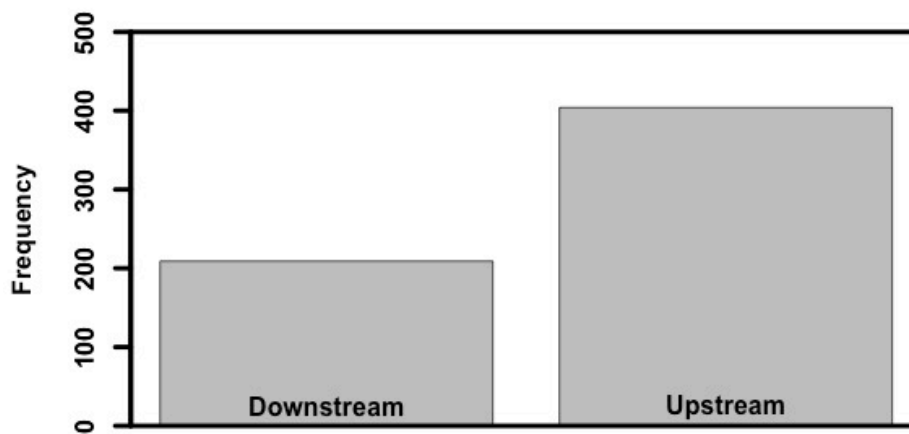


Fig. 2.8. Frequency of Chiricahua leopard frog movements downstream or upstream during tracking periods in the summers of 2013 and 2014.

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CHAPTER THREE

HABITAT SELECTION BY CHIRICAHUA LEOPARD FROGS

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CHAPTER THREE

HABITAT SELECTION BY CHIRICAHUA LEOPARD FROGS DURING SUMMER MONSOONS

Abstract

Land use changes and habitat degradation are major drivers of amphibian declines. The southwest United States is projected to become drier over the coming years, and wetland habitat important for amphibians may become scarce. Scarcity and fragmentation of habitat may disrupt the dispersal ability of organisms reliant on this resource. Currently, the Chiricahua leopard frog is restricted to anthropogenic sources of water, including tanks maintained for livestock, throughout much of its range. Movement habits of this frog and patterns of dispersal between disjunct water sources are not well understood. In order to study their movement patterns and habitat preferences we attached radio transmitters to 44 total frogs on the Ladder Ranch in southern New Mexico during summer 2014. We located each frog daily for up to 8 weeks (median = 30 days). We assessed fine-scale habitat selection by quantifying habitat characteristics at each frog location and a random location 5 meters away. We compared characteristics of used and random locations using conditional logistic regression and also explored the degree of variation in selection among individual frogs. Frogs chose areas in water with more low-lying cover, especially aquatic vegetation and woody debris, a tree overstory, and a mud substrate. Variation among individuals was low, suggesting

that all frogs were selecting similar habitat characteristics. Managers can use our findings to focus specifically on enhancing important habitat for Chiricahua leopard frogs between occupied sites to improve population connectivity. We specifically recommend enhancing habitat features similar to those produced during monsoon flows by creating or enhancing muddy creek bottoms, woody debris, riparian overstory cover, low-lying ground cover, and water-retaining pools.

Introduction

Amphibian species worldwide are becoming extinct at an alarming rate (Blaustein and Wake, 1990; Wake and Vredenburg, 2008). Changes in land use and anthropogenic disturbances to habitat are responsible for population- and species-level declines and extinctions in many taxa, including amphibians (Green, 2005). These declines differ in severity based on the particular habitat associations of species, but amphibians in North America and Europe are overwhelmingly affected by degradation of habitat (Stuart et al., 2004).

Understanding how amphibians utilize habitat features can give insight into the specific requirements of species of concern. For example, landscape attributes such as type and amount of vegetation cover can affect where or how far an individual amphibian may move with lower risk of desiccation (Fellers and Kleeman, 2007). Based on this ecological understanding, active management practices may decrease the risks of movement and enhance the permeability of landscapes around amphibian habitats. In another study, Graeter and others (2008)

studied the permeability of forest clearcuts for several amphibian species and made recommendations for forestry practices that could enhance the ability of amphibians to reach habitat within a matrix of clearcuts and reduce negative effects. Even with these guidelines, however, changes in climate patterns and land use may complicate managing wetland habitat.

The southwestern United States has experienced drought conditions for much of the early 21st century that are likely to persist, given predictions from climate models of an overall trend towards a drying landscape (Seager et al., 2007). In addition to the overall trend, droughts are likely to be longer and more severe (MacDonald et al., 2008) and decadal variations in precipitation are becoming more extreme (Sheppard et al., 2002). Such shifts in climate patterns lead to uncertainty about the future of water supplies for a growing human population in the southwest (Diaz and Anderson, 1995). Groundwater pumping for use in agriculture and ranching is responsible for depletion of groundwater resources throughout the world, especially in semi-arid ecosystems (Aeschbach-Hertig and Gleeson, 2012). In the US, natural desert springs are disappearing due to many causes, including diversion or pumping for agriculture (Unmack and Minckley, 2008). More than 20% of desert wetlands in the southwest US and northern Mexico no longer provide functioning wildlife habitat (Minckley et al., 2013). Without natural sources of surface water, amphibians must take advantage of human-subsidized aquatic resources. Earthen cattle tanks can provide essential habitat for amphibians in southwestern ranchlands when the quantity or quality of natural water bodies

declines (Rosenstock et al., 1999). Conservation strategies for amphibians might require anthropogenic manipulation of water levels to mimic seasonal patterns that occurred prior to climate changes (Shoo et al., 2011).

The Chiricahua leopard frog (*Lithobates* [= *Rana*] *chiricahuensis*) is a medium-sized frog native to central and southeastern Arizona, southwestern New Mexico, and northern Mexico (Platz and Mecham, 1979; Stebbins, 1985), although the historical distribution is poorly known (Sredl and Jennings, 2005). Individuals are herbivores as larvae and carnivores as adults, and are consumed throughout their life by various species of birds, reptiles, amphibians, predaceous insects, and mammals (Sredl and Jennings, 2005). Chiricahua leopard frogs are found in natural streams with rocky pools, springs, and ponds, but man-made stock tanks also provide important habitat (Stebbins, 1985). Adults are assumed to be highly aquatic and rarely are found far from water, although frogs can survive periods of surface water loss (Clarkson and Rorabaugh, 1989; Sredl and Jennings, 2005). Frogs are thought to move through drainages, especially those containing perennial water, although movement outside of perennial water probably occurs during summer monsoon rains (USFWS, 2002). Chiricahua leopard frogs are affected by a variety of threats common in amphibians, including *Batrachochytrium dendrobatidis* infection (Boykin and McDaniel, 2008) and introduced predators such as American bullfrogs (Rosen and Schwalbe, 1995). In 2002, Chiricahua leopard frogs were listed as threatened under the Endangered Species Act due in part to anthropogenic loss of habitat (USFWS, 2002). Researchers have identified restoration of breeding habitat

and movement corridors as a priority for Chiricahua leopard conservation (Sredl and Howland, 1994), although there is little published information about how frogs use landscape features.

Identifying habitat characteristics important to the Chiricahua leopard frog is a crucial conservation goal due to the Chiricahua leopard frog's limited range in the desert southwest, uncertainty about the future of water resources, its listing under the Endangered Species Act, and the limited amount of information available about the species' habits. The movement of Chiricahua leopard frogs and the habitat features they require is a focus of the species recovery plan (USFWS, 2007). Restoration of the species to its former range will be more likely when individuals can disperse long distances to reach breeding sites (Fellers and Kleeman, 2007), especially in a human-dominated landscape where connectivity of populations may be an important factor in their persistence (Ficetola and Bernardi, 2004). We set out to identify the habitat features selected by Chiricahua leopard frogs during the 2014 monsoon season, with the goal of informing management to facilitate increased population connectivity and gene flow, colonization of extinct habitat patches, and persistence of the species.

Materials and Methods

Study Site.- We conducted research on the Ladder Ranch, a private 63,300 ha working bison ranch in Sierra County, New Mexico adjacent to the Gila National Forest (Fig. 3.1). The Ladder Ranch holds 33% of the known populations of

Chiricahua leopard frogs in New Mexico, and is therefore of great importance to conservation efforts for the species (Kruse and Christman 2005). The ranch consists of Chihuahua Desert grasslands to ponderosa pine forests at higher elevations. Riparian vegetation consists mainly of oak (*Quercus* spp.), cottonwood (*Populus*), juniper (*Juniperus*), and willow (*Salix*). Elevation in our study area ranged from approximately 1700 to 2050 m. Up to 50% of annual precipitation may fall during July-September in monsoon-dominated areas of the southwest (Sheppard et al., 2002). For this reason, we focused our work during this peak in precipitation, when Chiricahua leopard frogs are thought to travel overland between water bodies (USFWS, 2007).

We specifically focused our work within the Seco Creek drainage on the Ladder Ranch. The Seco Creek drainage holds a robust population of Chiricahua leopard frogs, especially in livestock tanks along the creek's length (M. McCaffery, pers. comm.). Within this drainage, we captured frogs at North Seco Well and Johnson Well (Fig. 3.1), two livestock tanks along the creek course with apparently large populations of frogs based on visual encounter surveys over the past decade (M. McCaffery, pers. comm.).

North Seco and Johnson Wells (13S, 0249044E, 3667208N and 0260489E, 3664241N, respectively, datum WGS84) are small (approximately 20-m diameter), excavated livestock watering tanks filled with groundwater by solar pumps. Both are vegetated with aquatic plants (especially *Typha*, *Potamogeton*, and *Scirpus* spp.) and contained breeding Chiricahua leopard frogs during the summers of 2013 and

2014 (R. Hinderer, pers. obs). Johnson Well is approximately 12 km downstream from North Seco Well, and 3 other livestock tanks lie between our study sites at 2.5-3.5 km intervals (Fig. 3.1). During the dry season, there is little to no standing water in this section of Seco Creek save livestock tanks. During monsoons with sufficient rainfall, Seco Creek may flow and pools may remain in the creek channel between storms (R. Hinderer, pers. obs.). North Seco Well is 22 m from the Seco Creek channel, and Johnson Well is 205 m from the creek channel.

Frog Capture.- To capture frogs, we encircled Johnson and North Seco Wells with drift fences made of landscape fabric and pitfall traps made of 5-gallon, plastic buckets (Dodd and Scott, 1994) beginning in July 2014. We buried the drift fence at least 0.1 m into the soil and secured the fence to existing livestock exclusion fences with zip-ties. The landscape fabric was 1-m wide, so fences were approximately 0.8-m tall. We installed pairs of pitfall traps, one on each side of the fence, approximately every 10 m around the ponds, for a total of 16 traps at each site. We designed the traps with a removable cover to provide shade and prevent desiccation of captured animals. We added drain holes above the bottom of the bucket to allow retention of some standing water, while still draining water above the level of the holes. We checked pitfall traps twice daily as weather permitted during July and August 2014. We also opportunistically captured frogs in Seco Creek using dipnets.

Radio Telemetry.- We selected a subset of captured animals for radio telemetry. Selection was not random: we selected animals where transmitter mass did not exceed 10% of the animal's mass (Richards et al., 1994) and attempted to

select animals from both sexes and all size classes that met the mass criteria. Blomquist and Hunter (2007) found little effect on the vagility of *Rana* [*Lithobates*] *pipiens*, a closely related leopard frog species, with transmitters up to 10% of frog body mass. We attached a transmitter (HoloHil Systems model BD-2, 0.62, 0.9, or 1.2 g, www.holohil.com) to frogs with a flexible piece of elastic, strung through small glass beads and the transmitter, which was secured around the frog's waist (Muths, 2003). We sized belts so that they were just snug over the thighs when the legs were fully extended rearward, but loose on the waist when the frog was sitting normally. We assigned each frog a transmitter with a unique frequency and located animals every day or as conditions allowed. We also tracked a small subset of frogs (8 total) that were translocated from Seco Creek to an adjacent drainage for a concurrent project.

Habitat Data.- Each time we located a frog, we recorded the time, UTM location, the presence of water at the frog location (WATER), and the distance to any source of standing water if there was none at the frog (DISTANCE). We also quantified several habitat characteristics within a 1-m diameter circle centered on the frog's location, including the dominant substrate type (SUBSTRATE), the dominant type and percentage of low-lying cover ("frog cover") that would be useful for a frog to hide from a predator (FCOVERTYPE, FCOVERPCT), and the dominant type and percentage of overstory cover above the circle that provided shade but was not low enough to hide the frog from a predator (OCOVERTYPE, OCOVERPCT; Table 3.1).

We also quantified the same characteristics at a random location, 5 m away from the frog in a random direction. Collecting the data in this way results in pairs of locations, one location where the frog was found and another location that was “available” to the frog, but not occupied. We assumed that a location within 5 m was accessible and available to a frog, but was far enough away to be selected differently. Scale of resource selection functions is important (Boyce, 2006) and broad-scale habitat characteristics may not be important in habitat selection by amphibians (Gorman and Haas, 2011). Comparing the paired used and random locations allowed us to quantify characteristics important to provide habitat for frogs on a fine scale.

Analysis.- We made exploratory plots of each explanatory variable to examine the distribution of observations among levels of categorical variables and across the range of continuous variables. Distance to water was distributed very similarly for used and available points, owing to the nature of the variable; the largest pairwise difference in distance to water possible between a used location and an available location was 5 m, the distance between paired locations. For this reason, we elected to not use the distance to water variable in our inferential model. Where there were very few observations of a certain category, we condensed categories in a logical manner. We used single categories for all types of soil, sand, or rock substrates, and condensed substrate types that we documented infrequently (e.g., moss, pine duff, and leaf litter) to an “other” category. We also condensed rarely-used types of frog cover (e.g., cholla, shrub, cedar, bank, etc.) and overstory

cover (e.g., shrubs, bank, cattail, grapevines, etc.) into “other” categories for those variables. We maintained separate categories of overstory type for juniper and willow, which are commonly-utilized riparian vegetation types, but condensed all other tree species encountered (e.g., beech, oak, birch, walnut, etc.) into a “tree spp.” category. More than half of all locations were in areas with no overstory cover (65%, 1348 out of 2072 total observations). As such, we converted the percentage of overstory cover into a categorical variable with 2 levels, little to no overstory cover ($\leq 10\%$) or greater overstory cover ($> 10\%$) at the location.

We analyzed important features for habitat selection with a conditional logistic regression model using Cox proportional hazards regression in the *coxme* package in R (R Core Team, 2014) (*sensu* Poole et al., 2009; Popescu et al., 2013; Zeller et al., 2014). This model formulation allows the explicit pairing of observations, to match our data collection, where selection is *conditional* on the habitat available. If we had aggregated used and available locations across all locations, we would not be able to focus on habitat selection at a fine scale (Hosmer and Lemeshow, 2000). We accounted for variability in habitat selection among frogs by incorporating a random effect for individual frogs. This relaxes the assumption that all frogs are selecting habitat in the same way and accounts for differing numbers of observations per animal (Duchesne et al., 2010).

We selected an inferential model based on the methods of Hosmer and Lemeshow (2000). The initial global model included all single terms. We reached a tentative additive model by eliminating single variables that did not help explain

variation in selection. We then tested interactions between remaining terms to assess whether the relationship between selection and an explanatory variable was dependent on another variable. We hypothesized that frogs' selection of substrate may depend on the amount of frog cover (SUBSTRATE*FCOVERPCT), selection of overstory type may depend on the amount of frog cover (OCOVERTYPE*FCOVERPCT), selection of substrate may depend on the type of frog cover (SUBSTRATE*FCOVERTYPE), selection of substrate may depend on type of overstory (SUBSTRATE*OCOVERTYPE), selection of frog cover type may depend on overstory type (FCOVERTYPE*OCOVERTYPE), and selection for the amount of frog cover may depend on the type of frog cover (FCOVERPCT*FCOVERTYPE). We tested all interactions one at a time by adding them to the tentative model, with one exception. When frog cover type was categorized as "none", the percentage of frog cover was limited to 0, producing an inestimable interaction between cover type and amount. We also examined evidence for a quadratic relationship between selection and percentage of frog cover, as we hypothesized that frogs may prefer an intermediate level of cover that provides refuge from predators, but is not so dense as to preclude effective foraging. We used likelihood-ratio tests to compare nested models, examining χ^2 statistics to compare models that differed by a discrete variable and *t*-tests to compare models that differed by a continuous variable. We removed terms that did not explain sufficient variation ($P > 0.1$) or where the model failed to converge. We present results as effect sizes and confidence intervals in the text, and test stats and *p*-values in tables.

Results

We tracked 44 Chiricahua leopard frogs using radio telemetry in July and August, 2014. We located frogs a total of 1036 times and tracking times varied among individuals (range 1-66 days, median = 30 days). Frogs preferentially selected locations based on presence of water, percent cover available to a frog (quadratic relationship), type of cover available to a frog, type of overstory cover, and substrate (Table 3.2), but did not select locations based on the amount of overstory cover (categorized as $>$ or \leq 10% cover). Frogs did not select areas differently based on the interactions of habitat characteristics we postulated.

Presence of Water.- Frogs were 2.92 (95% CI = 2.78 – 3.07) times more likely to select a location with water compared to one without.

Frog Cover.- Frogs were more likely to select an area with greater frog cover available up to a maximum level of 70%, where selection was 19.49 (4.08 – 93.22) times more likely than an area with no cover, though uncertainty around this estimate is high (Fig. 3.2). Frogs were more likely to select locations with any type of cover compared to no cover at all (Fig. 3.3). Individuals were 6.03 (2.83 – 12.85) times more likely to select woody cover, 4.14 (2.01 – 8.53) times more likely to select rock, and 3.98 (1.83 – 8.65) times more likely to select aquatic vegetation, compared to no cover. We also found some evidence that open water (2.03 times, 0.95-4.37) and annual plants (1.69 times, 0.80-3.58) were preferred over no cover (Fig. 3.3).

Overstory Cover.- Frogs were more likely to select areas with any type of overstory cover than areas without (Fig. 3.4). Frogs were 2.22 (2.09 – 2.36) times more likely to select a location with a willow overstory, 1.99 (1.90 – 2.09) times more likely to select a tree other than juniper or willow, and 1.54 (1.38 – 1.71) times more likely to select a juniper overstory than no overstory at all.

Substrate.- Frogs were more likely to select mud compared to any other substrate (Fig. 3.5). They were 0.43 (0.38 – 0.49) times as likely to select sand, 0.26 (0.23 – 0.30) times as likely to select soil, and 0.16 (0.14 – 0.18) times as likely to select rock, compared to a mud substrate.

Discussion

Water loss by desiccation is the largest limiting factor in the utilization of terrestrial habitats by amphibians (Thorson, 1955). We found that the presence of water was important to habitat selection by Chiricahua leopard frogs at the 5-m scale, which we felt represented a distance sufficiently far to be selected differently, but not so far as to not be available to a Chiricahua leopard frog. This finding is line with work by Blomquist and Hunter (2009), who found that northern leopard frogs (*Lithobates pipiens*) selected habitat based on proximity to standing water in a managed forest in Maine. They also found that northern leopard frogs selected for greater amounts of low-lying cover (“frog cover” in our study), similar to what we discovered for Chiricahua leopard frogs. Due to the scarcity of standing water in arid landscapes, desert amphibians probably also select other habitat features that

decrease their propensity for drying. Lowland leopard frogs (*Lithobates yavapaiensis*), a closely-related species found in similarly arid landscapes, selected pool habitats with more vegetation on edges, more overstory cover, and greater habitat heterogeneity around the edges of pools during the dry months of the year (Wallace et al., 2010). The results from our study mirror this selection for low-lying cover, but our work focused on the habitat features that leopard frogs utilize during the rainy season, rather than their selection for pool characteristics during the dry season. Chiricahua leopard frogs' selection for a mud substrate and a tree overstory cover, even after accounting for the presence or absence of standing water at the animal's location, also indicate a preference for habitats that decrease the chance of desiccation.

Frogs' preference for low-lying and overstory cover may reflect selection of sites that providing nearby refugia and reduce susceptibility to predation. However, extremely dense cover may not allow frogs to detect and capture small invertebrates and vertebrates, which are important in the Chiricahua leopard frog's diet (Stebbins 1985). The threshold of 70% frog cover that we observed may suggest selection of sites that balance the need for refuge from predators and effective foraging for small prey, though uncertainty in our estimate of selection is large.

Based on the results of this study, we recommend that managers enhance or maintain habitat with a moderately-high percentage of low-lying cover comprised of woody debris, aquatic vegetation, and rock, an overstory cover of juniper, willow, or

other trees, and a mud substrate. Perhaps unsurprisingly, these are the exact features created by floods resulting from summer monsoons (R. Hinderer, pers. obs.). High flows create piles of woody debris and deposit mud in stream bottoms that otherwise may be dry for nearly the entire year. We suggest that regardless of whether standing water is present consistently, the features created by monsoon flows reduce the potential for desiccation and provide a preferential travel corridor for Chiricahua leopard frogs. Because the southwestern US is likely to experience a more arid climate in the near future (Seager et al., 2007), maintaining habitat for Chiricahua leopard frogs may require that managers pay special attention to micro-environments created by monsoon flows and avoid activities such as cutting riparian overstory cover, removing deadfalls and woody debris from streams, dredging creek or canal channels, thereby reducing water retention in natural pools, and mowing potential habitat corridors. Our recommendations further reinforce the importance of terrestrial habitats to desert amphibians (Wallace et al., 2010), but focus specifically on enhancing habitat for Chiricahua leopard frogs during monsoon season, when movement is likely to occur (Chapter 2). Jennings and Scott (1991) and Sredl and Jennings (2005) noted that terrestrial habitat may be of great importance to Chiricahua leopard frogs during seasonal migrations, but ours is the first study to examine fine-scale habitat use by this species in detail.

The US Fish and Wildlife Service, in its recovery plan for the Chiricahua leopard frog, cite a lack of understanding about their movement abilities (USFWS, 2007). In addition, habitat requirements of Chiricahua leopard frogs during

monsoon season, when movement is more likely, had not been studied previously. Northern leopard frogs are sufficiently mobile that the distance between patches, even when > 1 km, may not be important to colonization or persistence as long as connectivity among patches is maintained (Pope et al., 2000). In disturbed areas of peat forests, northern leopard frogs lose more water and are less likely to reach distant habitats; undisturbed areas are more conducive to longer movements by frogs (Mazerolle and Desrochers, 2005). Maintaining habitat connectivity is an essential component of an effective amphibian management plan (Semlitsch, 2000) and our findings about important habitat characteristics can enhance dispersal of Chiricahua leopard frogs between patches. Long-distance dispersing amphibians are those most likely to colonize extinct patches (Fellers and Kleeman, 2007) and disturbance may limit dispersal, with concomitant effects on population dynamics. Given the high potential for disturbance of natural water sources for human consumption, enhancing habitat conducive to Chiricahua leopard frog dispersal is essential to conservation of this species. Where we cannot alter the distances between sources of surface water (i.e., viable year-round habitat) due to limits imposed by human use or regulations, habitat between existing water sources may be enhanced to ensure connectivity.

The composition of the matrix between habitat patches can change movement rates of amphibians (Eycott et al., 2012). Variation in permeability of different matrix types differs from the classic dichotomous classification of core amphibian habitats embedded within a matrix of non-habitat, which may not reveal

features of fine-scale heterogeneity important to amphibians (Pope et al., 2000). Rather than just selecting ponds as viable habitat patches (Marsh and Trenham, 2001), amphibians select habitat at such a small scale that more general landscape features may not be useful to describe their preferences (Gorman and Haas, 2011). We focused on identifying habitat features used by Chiricahua leopard frogs on a fine scale; we think this approach can identify potential habitats for conservation or restoration efforts.

In a typical model for conservation of amphibian habitat, arbitrary buffers are delineated around known locations for breeding and overwintering, with the recommendation to limit anthropogenic disturbance within that buffer area (e.g., Semlitsch and Bodie, 2003). Although there is a logical appeal to this sort of model, balancing the needs of amphibians with human needs may be challenging, especially in working landscapes where access to water may be a limiting factor. For example, in the southwest, many water-obligate species rely on tanks provided for livestock because surface water may only be present for part of the year (Rosenstock et al., 1999). By enhancing connectivity between these water sources, managers may be able to augment wildlife habitat without totally curtailing appropriation of surface water for agriculture or other uses. Targeting high-priority habitats for preservation will make it possible to avoid the kind of conflicts between land managers and conservation authorities that arise when habitat preservation is based on simple buffer models (Baldwin et al., 2006). Focusing on preserving or improving habitat for amphibians, especially habitat important for dispersal, also

can act as an effective “umbrella,” where other species benefit from conservation action due to overlapping requirements (Breckheimer et al., 2014).

Anthropogenic activities have altered the structure and function of nearly all ecosystems, to the point of modifying geologic processes (Steffen et al., 2007). Conservation in this new age will require human effort to mitigate or reverse environmental changes to preserve at-risk species. Especially under climate change scenarios, human intervention will be required to “engineer a future” for amphibians in anthropogenic landscapes (Shoo et al., 2011). In the case of the Chiricahua leopard frog, an improved understanding about habitat requirements based on the results of this study can be used to develop more effective guidelines for active management practices that can contribute to the recovery of this threatened species.

Tables

Table 3.1. Habitat variables collected at Chiricahua leopard frog locations and random locations, Sierra County, NM, summer 2014. Excluding WATER and DISTANCE, all variables were collected within a 1-m circle centered on the location.

Variable	Definition
WATER	Presence of standing water at the location, yes or no
DISTANCE	Distance (in m) to the nearest source of standing water (not used in analysis)
SUBSTRATE	Most common substrate type - mud, sand, rock, soil, or other
FCOVERPCT	Percentage (0-100%) of low-lying cover useable to a frog to hide from predators ("frog cover")
FCOVERTYP	Most common type of frog cover - none, annuals, open water, rock, aquatic vegetation, woody cover, or other
OCOVERPCT	The percentage (0-100%) of overstory cover above (converted to OCOVERPRES, below)
OCOVERTYP	Most common type of overstory cover - none, juniper, willow, tree spp., or other
OCOVERPRES	A categorical indicator for whether there was >10% overstory cover, yes or no

Table 3.2. Likelihood-ratio tests comparing the inferential model (where we accounted for WATER, FCOVERPCT, FCOVERTYPE, OCOVERTYPE, SUBSTRATE, and FCOVERPCT²) to the same model without the specified term.

Variable	df	χ^2	P
WATER	1	24.76	< 0.001
FCOVERPCT	1	67.78	< 0.001
FCOVERTYPE	6	61.11	< 0.001
OCOVERTYPE	4	17.78	0.001
SUBSTRATE	4	43.58	< 0.001
FCOVERPCT ²	1	48.42	< 0.001

Figures

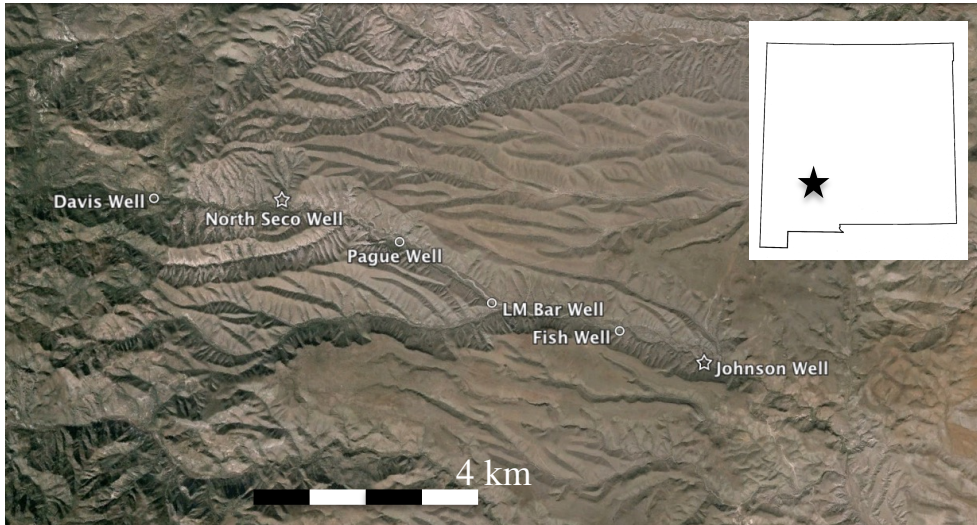


Fig. 3.1. Location of Ladder Ranch in New Mexico (star on inset) and layout of livestock watering tanks along the Seco Creek drainage. Wells indicated by white stars were focal sites for pitfall trapping and radio telemetry, summer 2014. (Imagery copyright Google, Inc.)

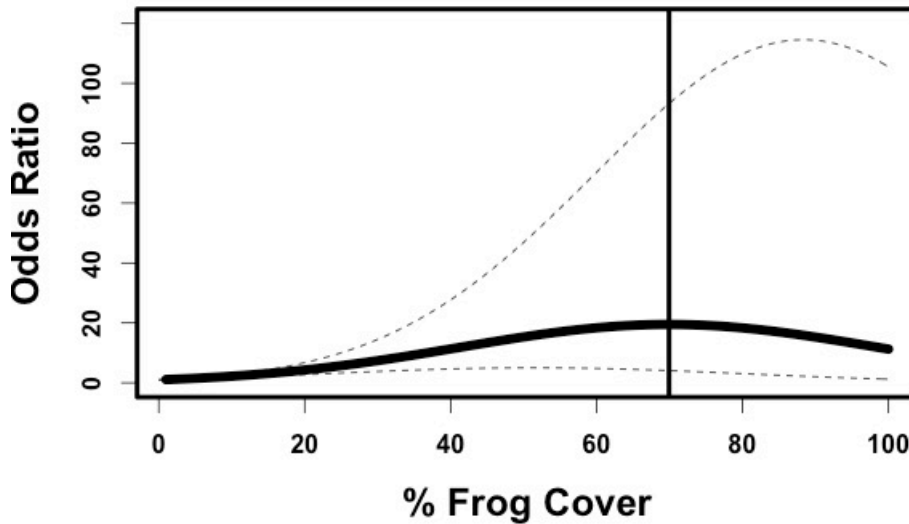


Fig. 3.2. Odds of a frog selecting a location with increasing amounts of frog cover, compared to a location with 0% cover (where odds ratio = 1). Selection was maximized at 70% cover (indicated by vertical line). Dashed lines indicate 95% confidence interval.

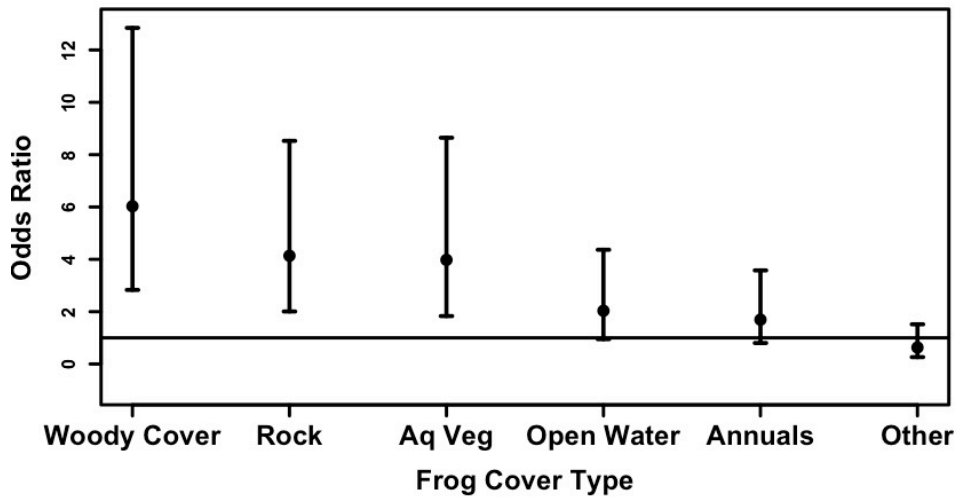


Fig. 3.3. Odds (\pm 95% confidence intervals) of a frog selecting a location with different types of frog cover, compared to a location with no frog cover (reference line where odds ratio = 1).

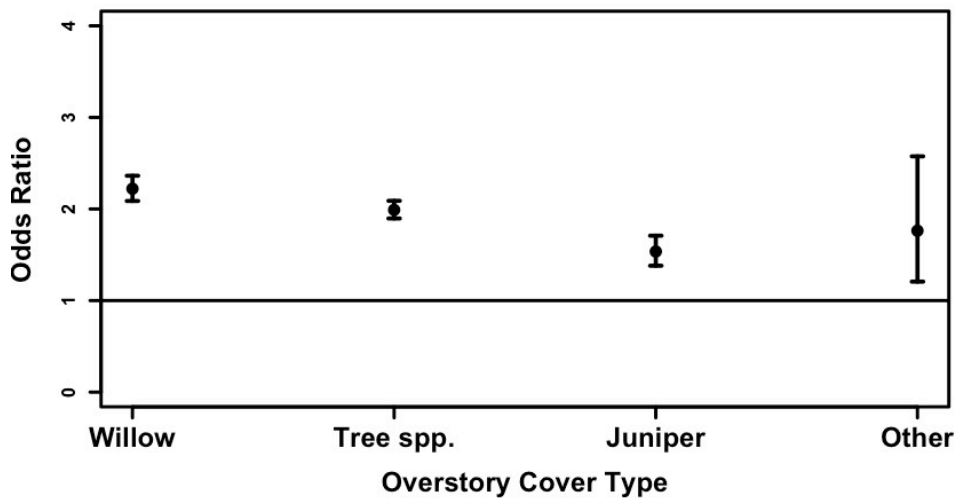


Fig. 3.4. Odds (\pm 95% confidence intervals) of a frog selecting a location with different types of overstory cover, compared to a location with no overstory cover (reference line where odds ratio = 1).

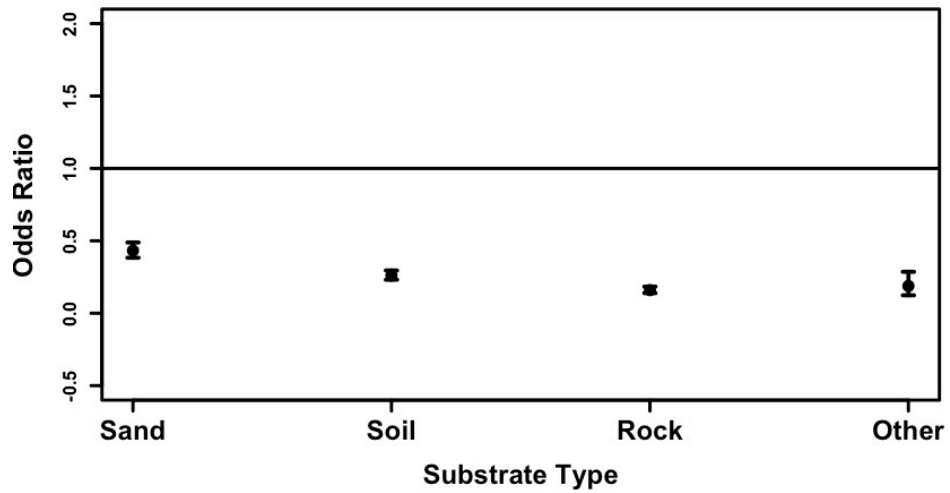


Fig. 3.5. Odds (\pm 95% confidence intervals) of a frog selecting a location with different substrate types, compared to a location with a mud substrate (reference line where odds ratio = 1).

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CHAPTER FOUR

CONCLUSIONS

Habitat destruction, degradation, and fragmentation are responsible for biodiversity loss worldwide (Soulé, 1991), including amphibian declines observed over the past decades (Green, 2005). In the face of anthropogenic changes to environment, management of endangered species will require an understanding of how fragmented populations are connected and how their connectivity can be enhanced.

Dispersal may allow fragmented populations to persist (Turchin, 1998) through exchange of genetic material (Bowler and Benton, 2005). We sought to understand factors important to the dispersal of Chiricahua leopard frogs, as they occupy an inherently fragmented landscape of stock ponds and perennial pools (Stebbins, 1985). We examined environmental variables that cued frogs to leave perennial pools and quantified physical characteristics of individuals related to movement ability. We also studied habitat selection during summer monsoon season, when frogs are more likely to move out of perennial ponds (USFWS, 2007).

Our results paint a picture of an animal that is highly-adapted to its surroundings in the semi-arid southwest United States and northern Mexico. Dispersing frogs chose to use habitat characteristics created by monsoon flows, such as piles of woody debris and muddy creek bottoms, which decreased their chances of desiccation. Frogs left ponds during rain events, which likely increased the

probability of their encountering water as they traveled and also decreased desiccation risk. The extraordinary dispersal ability of Chiricahua leopard frogs allowed them to quickly travel long distances between perennial habitats during monsoons. Variation in movement distances among individual frogs may be an example of diversified bet-hedging, where evolution favors individual variation in fitness to buffer against stochastic variability (Starrfelt and Kokko, 2012). In dry years, most of the frogs dispersing long distances may die before they reach another patch of perennial habitat, whereas in wet years, long-distance dispersers could be responsible for colonizing new habitats and expanding the population's range.

Management of current Chiricahua leopard frog populations and efforts to restore extirpated populations will include habitat improvement, along with translocations of individuals to improve viability of populations (Sredl and Howland, 1994). Our work will inform both of these strategies. Management strategies should include preservation, improvement, or creation of important habitat characteristics, by mimicking monsoon action, to allow frogs to disperse and maintain extant populations, while also founding new ones. With the information we provide on the dispersal abilities of Chiricahua leopard frogs, managers can better plan translocation sites within a reasonable dispersal distance to other populations or potential colonization sites that frogs might reach on their own. Our work adds to the limited number of observations of movement distances currently used to inform Chiricahua leopard frog management, as recommended by the US Fish and Wildlife Service's recovery plan (USFWS 2007). Planning translocation

activities during dry periods of the year will discourage translocated animals from dispersing from perennial habitats, possibly increasing the chance of establishing a viable frog population at the translocation site.

Our work will broaden the scope of amphibian conservation, and especially that of Chiricahua leopard frogs, by providing background on the dispersal of these animals. Rather than assuming that amphibians have very limited dispersal abilities (Blaustein et al., 1994), we advocate the use of evidence-based techniques for informing management decisions. Studies such as ours will allow managers to fully understand the effects of management actions and better target limited conservation funds in a way that maximizes benefits to wildlife.

Useful future topics for research include large-scale mark-recapture work in current populations of Chiricahua leopard frogs and telemetry of translocated individuals in new drainages. Mark-recapture studies across multiple perennial habitats would be the best way to monitor large-scale movements of individuals from one habitat patch to another, and is not limited by size of the animals. In our study, we were only able to track larger frogs due to the mass of the transmitter package. Studying only larger frogs may underestimate the species' movement abilities if juveniles move more. Researchers could also detect whether movement between habitat patches is more common for juveniles, subadults, or adults, and determine what proportion of the population is involved in dispersal events. These data would be useful for understanding the population dynamics of Chiricahua leopard frogs and explaining declines in areas where a proximal mechanism for

observed trends has not been established. The life history of the Chiricahua leopard frog may be adapted to rely on a fraction of animals dispersing and finding viable new perennial habitats, and they may not be able to do so in recently fragmented landscapes. Telemetry of translocated individuals would be a useful way to detect differences in the behavior of animals that were hatched in a particular environment versus those brought in from elsewhere. If translocated frogs act differently, predicting their behavior when managers attempt to establish new populations may prove challenging. Research avenues such as these will continue to add to the sparse information available about Chiricahua leopard frogs in the scientific literature. Conclusions from our and future work will contribute to the understanding of global amphibian declines and the challenges faced by other desert-dwelling, water-obligate species worldwide.

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