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Movement of Imperiled Chiricahua Leopard Frogs during Summer Monsoons

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Abstract.—**Habitat fragmentation and subsequent disruption of animal movement are responsible for extinctions in some species, including amphibians. Amphibians that can travel across fragmented landscapes may be at lower risk of extinction. Chiricahua Leopard Frogs are threatened because of fragmentation associated with habitat loss and degradation. We sought to identify cues leading frogs to leave perennial ponds and factors related to movement ability of Chiricahua Leopard Frogs in New Mexico during the summers of 2013 and 2014. Using pitfall traps, we captured frogs leaving ponds and radio-tracked 30 individuals to characterize overland movements. We checked traps and located frogs daily for up to eight weeks. We assessed factors related to the number of frogs leaving ponds using linear models and to distances moved by frogs using linear mixed models. The number of frogs caught was related to rainfall, but not water temperature, and more frogs were found outside ponds at an intermediate level of rainfall. Frogs who left ponds moved an average of 97 m/day, but distances were highly variable among individuals. Sex and size did not explain differences in distances moved, after accounting for individual variation. One individual moved 1,658 m in a day and another 9,888 m over 36 days. These distances are farther than recorded previously for this species. Movement data are essential for developing recovery plans for threatened species, and our findings will inform planning by predicting the ability of populations to cope with the effects of habitat fragmentation and the ability of animals to colonize new habitats.**

Habitat fragmentation 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). Amphibians usually are assumed to have relatively limited movement capabilities, affecting their ability to colonize discrete habitat patches (Blaustein et al., 1994). Many species, however, may be able to disperse over long distances (Smith and Green, 2005), allowing them to reach distant habitat patches and colonize previously extirpated patches on the landscape (Fellers and Kleeman, 2007). Maintaining connectivity among patches also may decrease the risk of species extinction by increasing gene flow (Fagan et al., 2002) to ensure persistence over time (Turchin, 1998). Identifying characteristics of individuals or landscapes important for animal movement may be a way to predict and facilitate recolonization of habitat patches and increase persistence of imperiled species.

Conserving "ecological connectivity," or the ability of populations to exchange genetic material and colonize nearby areas, is a main focus for any effective amphibian management plan (Semlitsch, 2000) and requires understanding the movement capabilities of the species of interest (Seburn et al., 1997). Because amphibians need an array of terrestrial and aquatic habitat features, much of the research on spatial ecology of amphibians has centered on quantifying movement between seasonally-used sites (Bull and Hayes, 2002; Matthews and Pope, 1999) and through habitat corridors (Pilliod et al., 2002; Baldwin et al., 2006; Fellers and Kleeman, 2007; Tatarian, 2008). In addition to identifying important habitat features, studies also may identify weather conditions conducive to movement (Dole, 1971) or characteristics of the individual animal that influence its propensity for moving, such as sex or size (Pilliod et al., 2002).

Chiricahua Leopard Frogs (*Lithobates chiricahuensis*) are native to Arizona, New Mexico, and northern Mexico (Platz and Mecham, 1979; Stebbins, 1985), although their historical distribution is poorly known (Sredl and Jennings, 2005). In 2002, Chiricahua Leopard Frogs were listed as threatened under the Endangered Species Act because of fragmentation of extant populations, loss of animals from some ranges, and threats from invasive species and disease (U.S. Fish and Wildlife Service, 2002). Suggested conservation strategies for the species have included removing predators, restoring breeding habitat and corridors, and translocating individuals (Sredl and Howland, 1994). Aside from some basic information about natural history and documentation of population declines, little is known about Chiricahua Leopard Frogs, particularly their movement habits and abilities (U.S. Fish and Wildlife Service, 2002). Some recent studies have focused on spatial dynamics (Chandler et al., 2015; Jarchow et al., 2016) and vital rates (Howell et al., 2016) of populations, but we were interested in how environmental and individual-level factors relate to frog movements.

We studied two facets of movement in Chiricahua Leopard Frogs. We aimed to 1) identify the cues associated with frogs leaving water bodies, and 2) assess the ability of frogs to move outside of water bodies to inform management of extant populations and guide translocation efforts in their former range. We hypothesized that rainfall and temperature may influence when frogs leave ponds (Dole, 1971; Kruse and Christman, 2005; Todd and Winne, 2006) and that the relationship between movement and rainfall may depend on the specific characteristics of the landscapes surrounding each pond. We also hypothesized that individual-level characteristics such as sex and size may be related to differences in the distance frogs moved outside of ponds (Fellers and Kleeman, 2007).

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. 1). The Ladder Ranch holds 33% of known populations of Chiricahua Leopard Frogs in New Mexico, and, therefore, is of great importance to conservation efforts for the species (Kruse and Christman, 2005). Elevation in our study area ranged from ~1,700–2,050 m. The

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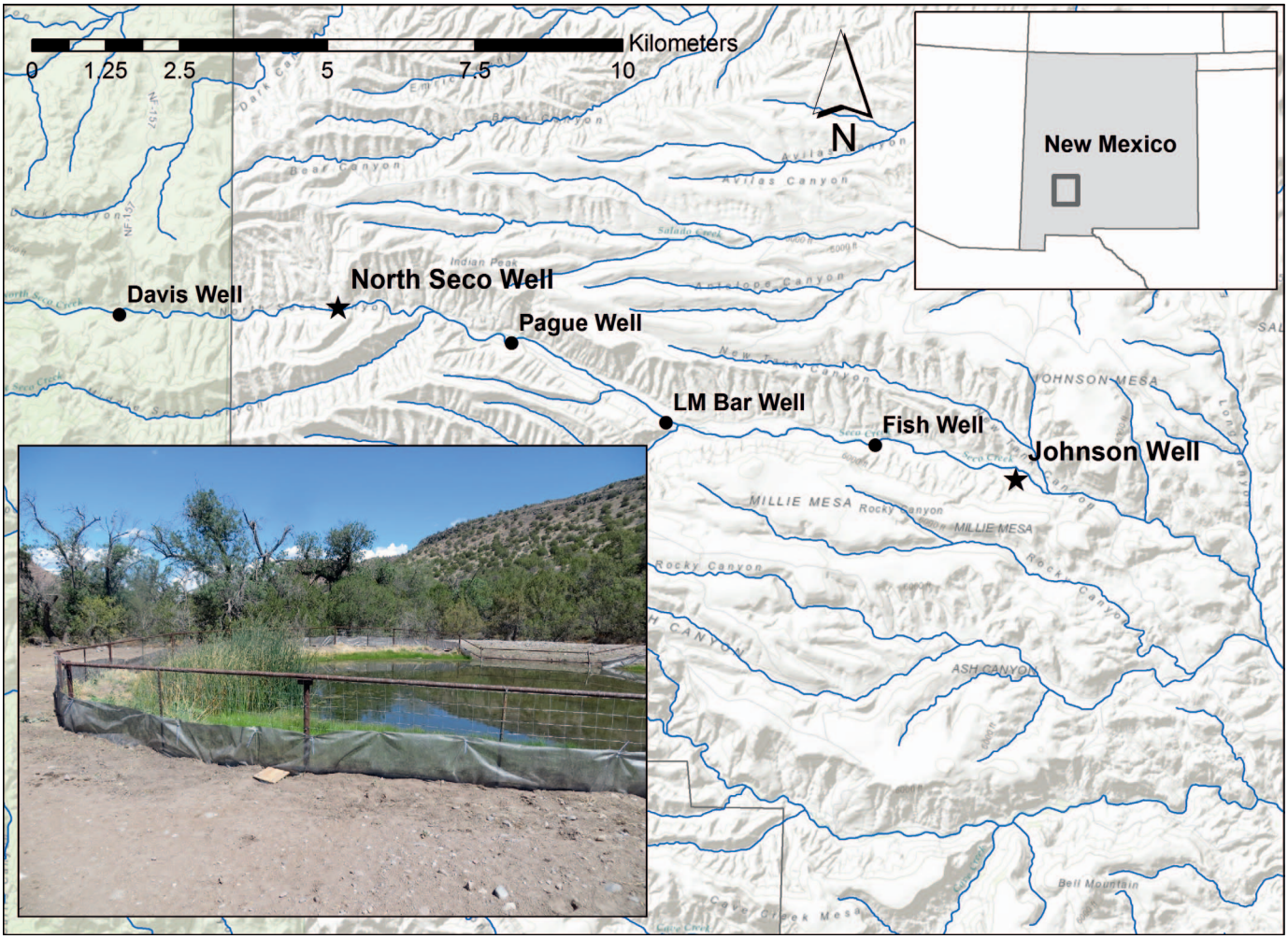

FIG. 1. Location of Ladder Ranch and layout of livestock watering tanks along the Seco Creek drainage. Wells indicated by stars were focal sites for pitfall trapping during summers 2013 and 2014. Inset is a photograph of the drift fence setup at Johnson Well. Map sources: Esri, HERE, DeLorme, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community.

ranch is in the Arizona–New Mexico mountains ecoregion and consists of grasslands at lower elevations and Ponderosa pine forests at higher elevations. Riparian vegetation consists mainly of oak (*Quercus* spp.), cottonwood (*Populus* spp.), juniper (*Juniperus* spp.), and willow (*Salix* spp.). 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 (U.S. Fish and Wildlife Service, 2007).

We focused our work within the Seco Creek watershed on the Ladder Ranch. This drainage basin holds a persistent population of Chiricahua Leopard Frogs, especially in earthen livestock tanks along the creek's length. Within this drainage, we captured frogs at two livestock tanks (North Seco and Johnson Wells) along the creek course with persistent populations of frogs, based on visual encounter surveys conducted over the past decade (MMcC, unpubl. data).

North Seco and Johnson Wells (0249044E, 3667208N and 0260489E, 3664241N, respectively, Zone 13S, datum WGS84) are small (~20 m diameter), excavated livestock watering tanks ("ponds") filled with groundwater by solar pumps (Fig. 1). Both are vegetated with aquatic plants (especially *Typha*, *Potamageton*, and *Scirpus* spp.) and contained breeding Chiricahua Leopard Frogs during the summers of 2013 and 2014. Johnson Well is ~12 km downstream from North Seco Well. Three other ponds lie between our study ponds at 2.5–3.5 km intervals, and there are several others upstream and downstream (Fig. 1). During the dry season, little to no standing water remains 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. North Seco Well is 22 m from the Seco Creek channel, and Johnson Well is 205 m from the creek channel.

Frog Capture.—We encircled Johnson and North Seco Wells with drift fences made of landscape fabric and pitfall traps constructed using 18.9-L plastic buckets (modified from Dodd and Scott, 1994). 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 livestock exclusion fencing was designed to allow herbivores access to water at points along the fence; therefore we installed drift fence 0–5 m from the water's edge (Fig. 1). The landscape fabric was 1 m wide; thus, fences were ~0.8 m tall. We installed pairs of pitfall traps, one on each side of the fence, about every 10 m around the ponds, for a total of 16 traps at each site. We checked pitfall traps at least once daily from

2 July–18 August 2013 and 22 June–5 August 2014. We captured additional frogs for radiotelemetry opportunistically in Seco Creek using dipnets.

We recorded morphometric data for captured frogs as time allowed, including snout–urostyle length (SUL), mass, and sex/age class (male, female, or subadult). When there were large numbers of trap captures we simply recorded the number of animals and their life stages. We considered frogs > 50 mm SUL as adults and determined their sex based on the presence of nuptial pads in males. We released frogs on the opposite side of the fence from where they were captured, based on the assumption that was their direction of travel prior to capture.

Weather Data Collection.—We deployed Hobo Pendant temperature loggers (Onset Computer Corp., Bourne, MA) 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; thus, the temperature logger was ~0.2 m below the water's surface in shade created by emergent vegetation. We placed another 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-min intervals throughout the trapping period, which we then averaged for each day. We also fixed Acurite 15.24 cm rain gauges (Chaney Instrument Co., Lake Geneva, WI) to fencing around each site. 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 move out of North Seco and Johnson Wells. We computed the number of frogs caught every day at pitfall traps during the summers of 2013 and 2014 as an index of the rate of frogs leaving ponds. Because we were interested in frogs moving out of ponds, we counted frogs caught only in traps on the inside of the drift fence (that were coming from the pond when stopped by the fence). We lagged average daily temperatures by 1 day because frogs were overwhelmingly found in traps in the morning, after being caught the night before. We did not lag rainfall data, because rain recorded in gauges 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 temperature, rainfall, or site (Johnson or North Seco) helped to explain the number of frogs caught in interior pitfall traps each day. Average daily water and air temperatures were correlated. We used only water temperature in our analysis, because Chiricahua Leopard Frogs are highly aquatic (Stebbins, 1985); therefore, we assumed that water temperature should be more indicative of the environment an individual frog was experiencing before moving out of a pond. We hypothesized that movement out of ponds would vary linearly with rainfall (Kruse and Christman, 2005), not peaking at an intermediate level of rain or differing by site. As such, we tested linear and quadratic terms for rainfall and 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).

Radiotelemetry.—We selected a subset of captured animals for radiotelemetry. Selection was not random: we attempted to select representatives of all size classes and both sexes, but only animals where transmitter mass did not exceed 10% of the animal's mass (Richards et al., 1994). Blomquist and Hunter (2007) found little effect on the vagility of *Lithobates pipiens*, a closely related leopard frog species, with transmitters up to 10% of frog body mass. We attached BD-2 transmitters (0.62, 0.9, or 1.2 g; Holohil Systems, Ltd., Carp, ON, Canada) 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 when creek conditions permitted access to the frogs' locations. We tracked frogs from 20 July–19 August 2013 and 5 July–6 September 2014. The 2013 tracking season was shortened by availability of captured frogs of sufficient size.

Analysis of Radiotelemetry Data.—We used relocation data from radio-tracked Chiricahua Leopard Frogs to study which individual factors were related to variation in movement distance. We calculated the distance moved by frogs each day based on straight-line Euclidean distances and summed these individual distances to quantify the total movement we observed frogs undertaking during the tracking period. When we did not track a frog for multiple days, we computed the average distance moved per day over those days. We used averaged daily movement distances for 260 of 745 cases (35%). We also calculated the total displacement between first and last location for each animal. Because we were interested in understanding frogs moving outside of ponds, we discounted locations when a frog remained in the same pond. This eliminated some animals from the analysis, leaving 3 study animals (of 3 belted) in 2013 and 27 study animals (of 44 belted) in 2014.

We used linear mixed models to test whether sex (male, female, or subadult), SUL, or year explained variation in 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 tested an interaction between sex and SUL and tested a quadratic term for SUL to determine whether the relationship between size and movement distance was linear and related to sex, as in previous studies (Pilliod et. al., 2002) or, as an a priori hypothesis, there was some intermediate size related to greater movement distance. 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; Hosmer and Lemeshow, 2000). We analyzed all data in R (R Core Team, 2014) and used package "lme4" to formulate mixed models.

Results

Capture Data.—We captured 2,599 frogs leaving ponds (i.e., on the inside of drift fences), of which there were four times more in 2014 than in 2013 (2,057 and 542 captures, respectively). The overwhelming majority (95%) of frogs caught in interior pitfall traps were subadults (2,459 captures), compared to only 5% adults (125 captures). We did not record life stage of 15 frogs. We caught frogs on the inside of drift fences more frequently (2,599 captures, 81%) than on the outside of drift fences (594 captures, 19%). Frogs appeared to be preferentially leaving and entering on the side of the pond nearest the creek (2,378 captures, 74%) rather than the side farthest from the creek (815 captures, 26%), although this pattern was more evident at North Seco Well.

The number of frogs moving out of ponds depended on daily rainfall and site (Fig. 2) and was greatest at an intermediate level of rainfall. The relationship between amount of rainfall and emigration differed by site (inferential model included Rain,

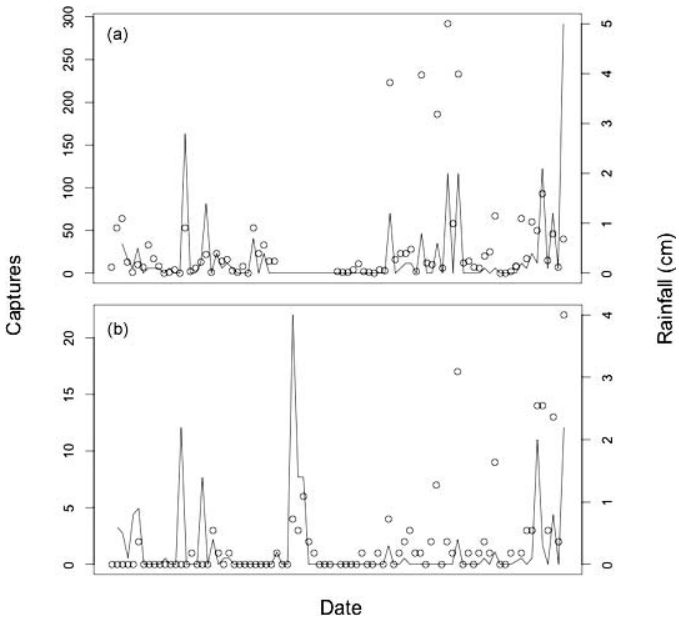

FIG. 2. Daily captures (open circles) and rainfall amounts (lines) at North Seco (a) and Johnson (b) wells, summers 2013 and 2014. Note that dates between the summers of 2013 and 2014 when traps were closed have been removed from the figure.

Site, Rain × Site, and Rain^2; adjusted $R^2 = 0.51$; Table 1). At North Seco Well, daily captures in pitfall traps increased with increasing rainfall, up to a predicted maximum of 154 frogs/day (95% CI = 130–179 frogs/day) with 2.84 cm of rain. After that point, captures were predicted to decline with increasing rainfall (Fig. 3). At Johnson Well, daily captures in pitfall traps increased with increasing rainfall, up to a predicted maximum 36 frogs/day (20–52 frogs/day) with 1.47 cm of rain, and declining after that point (Fig. 3). We found little evidence that water temperature explained the number of frogs in traps, after accounting for rainfall and site differences ($\chi_1^2 = 1.88$, $P = 0.170$).

Radiotelemetry Data.—Frogs that left ponds ($N = 30$ individuals) moved an average of 2,427 m of total daily movements over the tracking periods from July through early September. One individual moved a total of 9,888 m over 36 days with a total displacement between first and last locations of 8,506 m. Frogs moved an average of 97 m/day, but some moved much farther (up to 1,658 m in a day in one case). Movements were related to SUL but not sex or year (inferential model included only SUL, Table 2). Frogs moved 1.46 m/day less for every 1 mm increase in SUL, but uncertainty around this estimate was high (95% CI = −3.34 to 0.41 m/day for every 1 mm increase). We found that movement distances varied greatly among individuals (SD for the random effect = 61 m/day, Fig. 4), suggesting that other individual differences (unrelated to SUL, sex, or year) affect daily movement distances in this frog species. We did not detect evidence that the relationship between distance moved and SUL depended on sex ($\chi_4^2 = 1.71$, $P = 0.789$ for the interaction) or that the distance moved was maximized at some intermediate SUL ($\chi_1^2 = 2.01$, $P = 0.157$ for the quadratic term).

Frogs moved upstream more often than downstream. Of 613 frog movements along Seco Creek, 209 (34%) were downstream (toward the east), whereas 404 movements (66%) were upstream (toward the west).

TABLE 1. Likelihood-ratio tests comparing our final model of Chiricahua Leopard Frog emigration (accounting for Rain, Site, Rain × Site, and Rain^2) to the same model without the specified term.

Variable	χ_1^2	P
Rain	23.65	<0.001
Site	23.78	<0.001
Rain × site	35.93	<0.001
Rain^2	45.24	<0.001

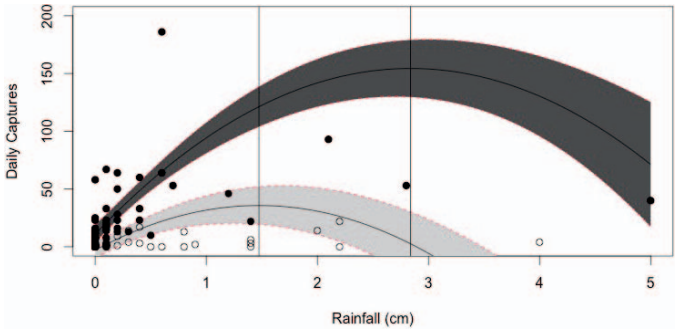

FIG. 3. Predicted changes in daily captures (shaded area is 95% CI) of Chiricahua Leopard Frogs at North Seco Well (dark gray) and Johnson Well (light gray), based on daily rainfall, summers 2013 and 2014, Ladder Ranch, NM. The maximum capture rate is predicted at 2.84 cm of rain at North Seco and 1.47 cm of rain at Johnson (noted by vertical lines). Open circles represent raw capture data from Johnson Well, whereas filled circles are data from North Seco Well.

DISCUSSION

We found that Chiricahua Leopard Frog movements from aquatic to terrestrial habitats are triggered by rain, that they are capable of substantial movements outside of ponds, that movement distances are highly variable among individuals, and that smaller frogs tend to move farthest. Ours is the largest study to examine movement of Chiricahua Leopard Frogs at the level of the individual animal (but see Kruse and Christman, 2005) and provides valuable insights about the ecology of this threatened species.

Water loss by desiccation is the largest limiting factor in the use of terrestrial habitats by amphibians (Thorson, 1955), supporting the idea that precipitation might be an important cue for amphibians leaving water sources in desert environments. Previous research on Northern Leopard Frogs and Chiricahua Leopard Frogs found that movement from ponds were correlated positively with rain events (Dole, 1971; Kruse and Christman, 2005; but see Seburn et al., 1997). We also expected to find a simple positive relationship in our study but instead found the greatest number of frogs captured out of the water at an intermediate level of rainfall. Our findings are somewhat surprising but may be attributable to the specific environmental conditions created during monsoons. We ob-

TABLE 2. Likelihood-ratio tests comparing a model with only the specified term to one without that term. All tested models accounted for individual (random effect). The inferential model only included SUL and individual.

Variable	df	$\chi 2$	P
Sex	2	1.49	0.475
SUL	1	105.77	<0.001
Year	1	1.48	0.224

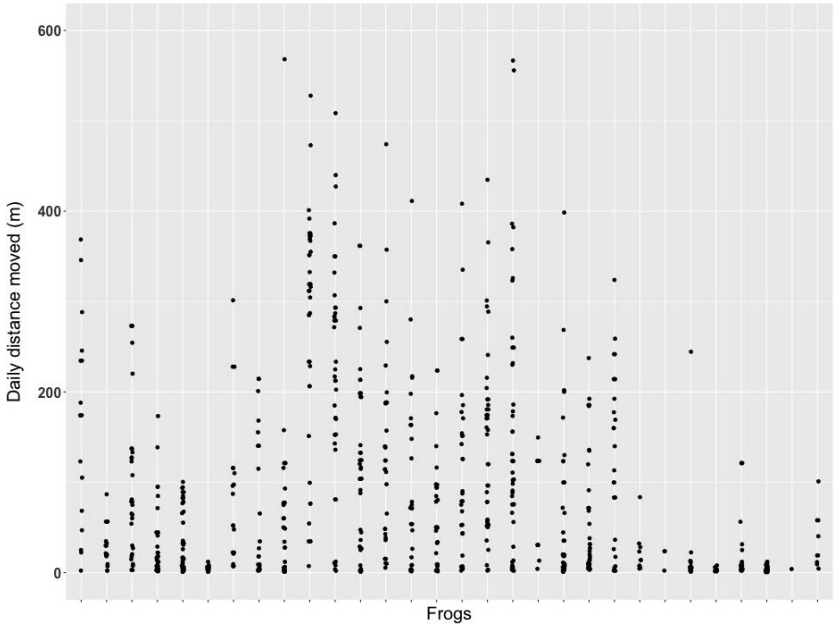

FIG. 4. Variation in daily distances moved by individual Chiricahua Leopard Frogs ($N = 30$ individuals) during summers 2013 and 2014, Ladder Ranch, NM. Columns of points represent individual frogs and each point is a distance that a frog moved in a day. We removed one observation (1,658 m moved in a day) to increase resolution of the remaining points.

served periods of extremely heavy, localized rainfall with high winds during our study (Fig. 2). We hypothesize that these sorts of violent storms may reduce the chances that frogs leave the water if their locomotion or ability to locate habitat features is hampered or chances of injury are increased during travel in storms. Although we did not detect a relationship between water temperatures and trap captures, Kruse and Christman (2005) found the number of frogs leaving ponds was related to water temperature; this study occurred in the same drainage as ours. If water temperature was important during our study, the effect was small enough to be masked by the influence of precipitation.

We found the relationship between rainfall and frogs moving out of the water differed between our study ponds (although uncertainty around these estimates is large), which may be attributable to specific characteristics of the landscapes surrounding each pond. For example, North Seco Well is only 22 m from Seco Creek, whereas Johnson Well is 205 m from the creek. Frogs are more able to detect water sources a short distance away, with navigation to water becoming less direct as distance increases (Mazerolle and Vos, 2006). This difference in proximity may explain why frogs seemed to prefer leaving on the creek side of North Seco Well but did not exhibit such a strong preference at Johnson Well. Johnson Well also is surrounded by fairly open terrain, with little overstory providing shade or understory to retain moisture (Fig. 1). 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. Frogs lose more water when moving across areas of little cover (Mazerolle and Desrochers, 2005); therefore, the chance of a frog successfully reaching the creek channel from North Seco Well is probably higher because of the intervening terrain. If frogs have some sort of innate understanding of the permeability of the surrounding area, they may avoid leaving Johnson Well even when large rainfall events cue more frogs at North Seco Well to leave the water.

While radio-tracking Chiricahua Leopard Frogs moving outside of ponds, we recorded large daily movement distances (average = 97 m/day, maximum = 1,658 m/day). Individuals of the same species moved up to a maximum of 540 m/day in a previous study in the same drainage system with a similar tracking period of 2–8 weeks per frog (Kruse and Christman, 2005). We observed one Chiricahua Leopard Frog that traveled a total of 9,888 m over 36 days with a displacement (difference between first and last location) of 8,506 m over that period. Management recommendations included in the recovery plan for Chiricahua Leopard Frogs are based on maximum displacement distances previously recorded for the species. The maximum distance reported in the recovery plan is 8,047 m (5 miles; U.S. Fish and Wildlife Service, 2007), less than distances we observed even over a relatively short 36-day period. Monsoonal storms continued after the end of tracking in both years, suggesting that frogs may have continued to move after our study ended. This distance is farther than recorded for Red-Legged Frogs (*Rana draytonii*; Bulger et al., 2003) and Wood Frogs (*Lithobates sylvaticus*; Berven and Grudzien, 1990) but shorter than the 34 km over 15 months documented for the semiterrestrial Fowler's Toad (*Anaxyrus fowleri*), possibly the longest recorded distance moved by any anuran (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 exceptional for anuran species, especially for frogs. We also attempted to use individual characteristics of the frogs in our study to more fully explain the variation in distances that frogs traveled and make management recommendations based on those characteristics.

We found that body length and sex did little to explain distances traveled out of water after accounting for variation among individual frogs. Individual heterogeneity in animal behavior is an important factor in population dynamics (Cam et al., 2002; Cote et al., 2010; Vaupel et al., 1979) and large variation in movement distances among individuals also has been found in Wood Frogs (Freidenfelds et al., 2011) and Northern Leopard

Frogs (Dole, 1971). Our findings bolster previous studies and indicate that individual heterogeneity may play a substantial role in amphibian movement patterns. Transfer between habitat patches relies on animals being able to travel intervening distances. Sex, developmental stage, and body size all may influence transfer ability, but relationships differ based on taxon or study (reviewed in Bowler and Benton, 2005). Predicting which Chiricahua Leopard Frogs may move more than others is difficult based on the morphometric data we collected (e.g., sex/age class and body length). Importantly, we were limited to tracking only larger frogs because of transmitter size restrictions and were, therefore, unable to study the movements of small juvenile frogs, which constituted the bulk of trap captures. The distances frogs moved did not differ between sexes in our study, but limitations on assessing sex of subadult frogs in the field may have contributed to this finding. Phenotypic traits and environmental cues such as temperature or local population density may even interact to influence dispersal ability in animals, although this area of research is not well explored (Clobert et al., 2009). For managers 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.

We found that frogs traveled upstream more often than downstream. Other amphibians exhibit a similar bias toward upstream movements (Twitty et al., 1967; Robertson et al., 2008). 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 (RKH, pers. obs.). Upstream movement likely increases the chances that frogs could find reaches suitable for breeding and decreases the chances of desiccation. Assuming that most animals will tend to move upstream if they disperse, managers could focus translocations at sites downstream from other potential habitat patches to increase the chances that dispersing frogs find new colonization sites.

We used the number of frog captures in interior traps as an index of overall movement outside of ponds. Our pitfall trap array was close to the edge of the water (0–5 m), similar to previous studies that have used pitfall traps to quantify numbers of animals entering or leaving a wetland (Gibbons et al., 2006) and timing of seasonal movements out of breeding habitat (Todd and Winne, 2006; Timm et al., 2007). Identifying animals individually would have allowed us to distinguish among animals that only briefly left ponds and returned immediately—after foraging, for example—from frogs that left ponds and never returned and likely emigrated. We observed more frogs leaving ponds than returning to ponds (81% vs. 19% of captures), which seems to indicate that at least some proportion of animals never returned. We speculate that the peak of frogs captured during smaller rainfall events at Johnson Well may reflect those frogs that are predisposed to leaving the water and are waiting for some minimum threshold of rainfall. Performing a similar study to ours on an individually-marked population of animals would be informative, where once a frog leaves the pond it cannot leave again when environmental conditions are even more conducive to overland movement. A more complete understanding of the habitats used by Chiricahua Leopard Frogs during overland travel would also be useful to more efficiently target conservation actions to high-priority habitats important during seasonal movements. Although not discussed here, we also collected and analyzed these data (Hinderer, 2015).

The management and recovery of amphibian populations in the face of continuing biodiversity loss require reliable data about species' movement ecology and metapopulation dynamics (Semlitsch, 2002). Our study and a concurrent study of habitat selection by frogs (Hinderer, 2015) will contribute to the recently growing body of literature regarding ecology and conservation of the Chiricahua Leopard Frog (Chandler et al., 2015; Howell et al., 2016; Jarchow et al., 2016). Developing a better understanding of movement behavior is especially important in fragmented landscapes where the ability of animals to move between habitat patches is fundamental to a species' viability.

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