

Population dynamics of lowland leopard frogs in the Rincon Mountains, Arizona



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Abstract

Amphibians have declined in abundance and distribution worldwide, including populations of ranid frogs in Arizona. Identifying the mechanisms responsible for these declines requires that we distinguish between systematic, long-term declines and natural, short-term fluctuations, which can be challenging for species that inhabit environments where conditions vary markedly, both seasonally and annually.

We leveraged 16 years of survey data for lowland leopard frogs (*Lithobates yavapaiensis*) in montane canyons of southern Arizona—an ecosystem where environmental conditions are highly dynamic—to assess status and trends of frog populations and to identify factors that govern dynamics in distribution and abundance over time. We characterized patterns of occupancy at two geographic scales, drainage ($n = 9$) and pool complex ($n = 71$), which we defined as collection of pools separated by ≥ 120 m; we characterized patterns of abundance at the pool-complex scale for a subset of complexes ($n = 34$).

Between 1996 and 2011, park staff and volunteers completed 470 visual encounter surveys during spring (1 May – 15 July) and fall seasons (1 Oct – 31 Dec). Leopard frogs were observed at least once in $>95\%$ of the drainage reaches and tanks surveyed ($n = 21$), which were chosen because they were known to harbor frogs historically; in general, counts of frogs were highest in south-facing drainages with a high density of pools below 1200 m elevation. Probability of occupancy for adult frogs at both drainage and complex scales increased with the number of pools and as the amount of water available during the previous season increased, and was not associated strongly with distance between local populations. Abundance of adult frogs within complexes varied seasonally, with higher numbers in fall than in spring. Similar to occupancy dynamics, rates of recruitment and survival of populations increased with availability of surface water. We found no evidence of systematic trends in populations of lowland leopard frogs in and near the park. Dynamics and persistence of frog populations in these arid environments, however, depend critically on the amount of surface water available, which is likely to decline in response to increasing pressure from anthropogenic threats, including local withdrawal of groundwater, and changes in climate predicted for this region.

Introduction

Across North America and worldwide, declines in many amphibian populations have been attributed to an array of factors operating across a range of spatial scales, including habitat loss, disease, and climate change (Collins and Storfer 2003, Stuart et al. 2004, Sodhi et al. 2008). Understanding the causes of these declines has become a priority for conservation efforts because they have potential to reduce biodiversity of amphibians on a global scale (Wake and Vredenburg 2008). Without detailed studies of the natural dynamics of amphibian populations, however, differentiating long-term declines that might lead to local extinctions from short-term fluctuations will be impossible, especially for populations that inhabit variable environments (Pechmann et al. 1991). Moreover, understanding factors that govern spatial and temporal dynamics of amphibian populations is necessary to inform effective conservation and management strategies.

Lowland leopard frogs (*Lithobates yavapaiensis*) inhabit ecosystems that provide semi-permanent or permanent surface water throughout southern Arizona, southwestern New Mexico, and northern Mexico (Sredl 2005, Wallace et al. 2010). Like other ranid frogs, many populations of lowland leopard frogs have declined throughout their range (Clarkson and Rorabaugh 1989, Witte et al. 2008). Lowland leopard frogs are classified as a “Species of Greatest Conservation Need” by the Arizona Game and Fish Department because they are vulnerable to multiple environmental threats, including reductions in

groundwater, infection by chytrid fungus, invasions by bullfrogs (*L. catesbeiana*), and probable consequences of climate change (AGFD 2006, Seager et al. 2007).

Riparian areas and their intermittent streams are rare in the desert southwest, yet are ecologically significant because they support a high proportion of the region's biodiversity and are essential for maintaining connectivity of plant and animal populations across arid landscapes (Johnson et al. 1977, Skagen et al. 1998). Ecological function in these riparian areas depends fundamentally on maintaining surface water for both plants and animals (Stromberg et al. 1996). Anthropogenic threats, such as climate change and groundwater withdrawal, are likely to decrease surface water and reduce habitat for wildlife species that inhabit these areas, including lowland leopard frogs (Stromberg et al. 1996).

Populations of lowland leopard frogs in Saguaro National Park (SNP) have been surveyed for more than 16 years, providing a rare opportunity to evaluate dynamics and trends of amphibian populations over a relatively long time-horizon. Assessing trends and identifying factors that govern dynamics of vertebrate populations is challenging because abundance and distribution of many species can vary widely over time and across space in environments that are naturally variable (Pechmann et al. 1991, Sredl et al. 1997, Savage et al. 2011). We used linear models to assess spatial variation in counts of adult leopard frogs in isolated mountain canyons and used hierarchical models (Royle and Dorazio 2008) to relate variation in occupancy, abundance, and population dynamics of frogs to an array of environmental factors to assess status and trends of this threatened species.

Methods

Study areas

The Rincon Mountain District of SNP is bisected by the Tanque Verde Ridge formation, with areas north of the ridge forming the Tanque Verde watershed and areas south of the ridge forming parts of the Rincon Creek and Pantano watersheds. Within these watersheds, leopard frogs primarily inhabit pools along low-order, intermittent streams below 1500 m elevation, but also occasionally inhabit pools at higher elevations and isolated cattle tanks north of SNP on lands managed by the U.S. Forest Service (Fig. 1). Stream flow and connectivity between pools in these mid-elevation streams are highly variable over time, both seasonally and among years (Bogan and Lytle 2007, Wallace et al. 2010, Jaeger and Olden 2012). Pools are often connected by shallow riffles and runs during wet periods (late winter [Jan-Mar], monsoons [Jul-Sep]) and are separated by dry channel beds when areas between pools dry seasonally (Fig. 2).

In 1996, SNP staff surveyed all major drainages and tanks in the park to assess water resources and to identify potential habitat for lowland leopard frogs. Staff selected pools for long-term monitoring that were likely to hold water throughout most of the year, including pools that either were lined by bedrock and ≥ 0.5 m deep or contained cattails (*Typha* spp.) or other perennial aquatic vegetation. Staff numbered pools selected for long-term monitoring uniquely and recorded GPS locations.

Field surveys

Observers used binoculars to survey pools and their terrestrial perimeter for frogs from a distance of 10-20 m or approached pools quietly to scan directly from a distance of <10 m. After an initial scan, observers approached pool edges and counted individuals they observed or heard making a distinctive "plop" when entering the pool (Wallace et al. 2010, D. Swann *pers. comm*). Individuals were not

captured during surveys, but were classified visually into stage classes: adult, juvenile, tadpole, or egg mass. The juvenile stage class included metamorphs in developmental stages 42-46 and froglets (*sensu* McDiarmid and Altig 1999), and the tadpole stage class included individuals in developmental stages 26-41 (Gosner 1960). During each visual encounter survey, observers usually photographed each pool and noted whether or not each pool contained water.

In addition to lowland leopard frogs, observers collected similar data for other aquatic vertebrate species, including canyon treefrogs (*Hyla arenicolor*), black-necked gartersnakes (*Thamnophis cyrtopsis*), and Sonoran mud turtles (*Kinosternon sonoriense*).

Terminology and data structure

Most numbered pools were surveyed periodically for lowland leopard frogs and other aquatic vertebrates since 1996, although the extent and frequency of survey effort has varied substantially over time and space. We restricted analyses to surveys between May 1996 and December 2011 and to areas below 1500 m elevation that were surveyed more than once. We use the term **drainage segment** to identify a collection of pools along a well-defined drainage reach. Therefore, we classified collections of pools in different “forks” (e.g., Loma Verde and Loma Verde South) or in upstream and downstream reaches of the same stream separated by >3 km (e.g., Rincon Proper and Lower Rincon Creek; Fig. 1) as distinct drainage segments. We excluded the few observations of leopard frogs that were not at monitored pools.

Leopard frogs were surveyed primarily during periods when streams were not flowing. We classified survey periods into two primary survey **seasons**: spring (1 May–15 July) and fall (1 October–31 December). Because surveys outside of these periods were often opportunistic and infrequent, we excluded data collected outside of these seasons. Many drainage segments were surveyed more than once per season. For most drainage segments, we considered a **survey** as the set of observations of frogs, other vertebrates, and surface water when most or all pools within a segment were surveyed. Most drainage segments were surveyed in one day, but surveys for segments with a large number of pools sometimes spanned several days within a 30-day period, with a different subset of pools surveyed on each date. When subsets of pools surveyed occasionally overlapped, we used the higher count for analyses.

Pools were often in close proximity (Fig. 3) and therefore could not be considered independent sample units. Because multi-season hierarchical models assume geographic and demographic closure for sample units within a season (Royle and Dorazio 2008, Dail and Madsen 2011), movements of adult leopard frogs between adjacent pools would violate this assumption. To avoid problems associated with spatial autocorrelation, we delineated pool **complexes** as collections of adjacent pools, such that within a season, frogs would likely remain within one complex and would be unlikely to move among complexes. We made no assumptions about movements of frogs between seasons. Because published estimates of home-range sizes and movement distances are unavailable for lowland leopard frogs in mountain canyons, we relied on expert opinion to determine the minimum distance between pool complexes. With one exception, we delineated complexes in each drainage such that >120 m separated adjacent complexes during periods with no flow of surface water between pools. We selected this distance based largely on observations of leopard frogs in Chimenea Canyon, the most extensively studied population in SNP. All pools in Lower Rincon Creek were considered one complex, regardless of the distance between numbered pools because, unlike other drainage segments, pools in Lower Rincon

Creek were often contiguous, even during periods with little or no surface flow. Finally, we considered tanks as independent complexes because they were located outside of surveyed drainages.

Seasonal and spatial variation in counts of adult frogs

We used counts of adult leopard frogs during surveys to assess seasonal and spatial variation in abundance of frogs. For each complex, season, and year, we counted the number of adult leopard frogs observed during each survey when $\geq 50\%$ of pools in a complex were visited; if a complex was surveyed more than once, we used the highest count. We excluded juveniles, tadpoles, and egg masses from counts because the detection process is likely to vary with stage class. For the lower reach of Rincon Creek (Lower Rincon), we included data when ≥ 4 of 11 pools were visited because pools often were contiguous, even during the driest parts of the year.

To quantify seasonal variation in abundance at the complex scale, we compared counts of frogs at each complex during spring surveys to counts during fall surveys averaged across years. To quantify seasonal variation in abundance at the drainage-segment scale, we summed counts in each year and season across all complexes in each segment after excluding drainage-season combinations where $< 50\%$ of complexes were surveyed.

To quantify spatial variation in abundance, we modeled counts of adult leopard frogs in each complex averaged across years and seasons as a function of pool location (tank or drainage), number of pools per complex, elevation, aspect, and distance to the nearest complex. We calculated elevation for each complex as the mean of elevations for each pool in the complex, and evaluated both linear and quadratic terms. For distance to nearest complex, we measured straight-line distances to the nearest drainage for each tank and distances along stream courses for complexes in the same drainage because leopard frogs disperse primarily along drainage courses (Goldberg et al. 2004).

Similarly, we assessed whether counts of adult frogs in each drainage segment varied with pool location, number of pools per segment, elevational range, aspect, watershed area, and stream distance to the nearest drainage known to be inhabited by leopard frogs historically or occupied currently. We calculated watershed area using Automated Watershed Assessment Tools (AGWA; Miller et al. 2007) in ArcGIS 10.0 as total area from the lowest-elevation monitored pool, regardless of whether watersheds of other drainage segments were geographically nested in the same region. For analyses at the scale of both pool complexes and drainage segments, we fit linear models with all subsets of covariates and compared model fit with Akaike's information criterion corrected for small sample sizes (AIC_c).

Occupancy

We used hierarchical models to assess factors explaining variation in occupancy of adult leopard frogs over time while accounting for imperfect detections of frogs during surveys. Dynamic occupancy models include four parameters that can vary as a function of covariates: occupancy in the first season (ψ_1), rates of colonization (γ) and extinction (ϵ), and probability of detecting at least one frog, if present (p ; MacKenzie et al. 2003). We assumed no relationship between rates of colonization and extinction. Because these models require > 1 survey per season in ≥ 1 season, we excluded drainage segments and tanks that were never surveyed multiple times per season or were surveyed in < 3 seasons. Occupancy, or the probability that adult leopard frogs occupy a sample unit, requires detection-nondetection data, so we transformed count data so that any count > 0 was represented with a "1" in analyses. Further, we

excluded detection-nondetection data (count = NA) when <40% of pools in a complex were visited during a survey.

Similar to spatial analyses of frog counts, we modeled occupancy dynamics at two spatial scales. First, we modeled occupancy at the drainage scale, where drainages were comprised of ≥ 1 drainage segments in close proximity that likely represented a single biological population. We treated the lower reach of Rincon Creek as a separate “drainage” because it was separated from all other sample units by >3 km and was downstream from multiple drainages (i.e., Chimenea, Madrona, and various Rincon tributaries). At the complex scale, we modeled occupancy of pool complexes over time.

For analyses at both scales, we modeled variation in parameters as a function of site-, season-, and survey-specific covariates (Table 1). Site-specific covariates, including the number of pools per complex or drainage, mean elevation, elevational range, watershed area, and distance to nearest complex or drainage, were the same as those used in the analyses of mean counts and were standardized for dynamic occupancy models. In addition to site-specific covariates, we modeled temporal variation in occupancy dynamics and detection probability as a function of survey effort and water availability. We quantified effort as the proportion of pools per complex or drainage that were visited by observers during each survey. Because we thought that the amount of water could affect the ability of observers to detect frogs, we calculated a **survey water index** (SWI) as the proportion of pools with water in each complex or drainage during each survey (Table 1). We predicted missing observations (5.4% of surveys) based on a model that related the proportion of pools with water in the spring or fall to official precipitation totals for Tucson, AZ during the previous winter or summer, respectively. We used these data to calculate **water availability**—the minimum proportion of pools with water during each survey season—that we used to explore variation in colonization and extinction rates between each survey season and the subsequent survey season (Table 1). For example, we related extinction rates between spring 1997 and fall 1997 (i.e., during summer 1997) to water availability in spring 1997. Water availability in each survey season likely reflected the minimum amount of surface water available between each survey season and the following season. We used water availability as a proxy for surface water volume, which is likely to affect rates of colonization and extinction.

We used a step-down approach to model occupancy dynamics at both the drainage and complex scales (Lebreton et al. 1992). Generally, we started with a fully parameterized (global) model and decreased the number of covariates for each parameter systematically to identify a parsimonious model. Specifically, we used a four-step process to select a model for inference. First, we evaluated all possible combinations of covariates that we thought had potential to explain variation in detection probability while retaining fully-parameterized models for occupancy in the first season, colonization, and extinction. We considered those covariates with summed AIC model weights ($\sum w_i$) ≥ 0.5 to have substantial explanatory power and retained only these covariates for detection probability in all subsequent models (Burnham and Anderson 2002). Second, we compared models with all possible combinations of covariates that had potential to explain variation in occupancy during the first season while retaining fully-parameterized models for rates of colonization and extinction. Similar to the first step, we retained only those covariates for occupancy with $\sum w_i \geq 0.5$ in subsequent models. In the third and fourth steps, we used the same methods and selection criteria to identify covariates for rates of colonization and rates of extinction in that order.

To model changes in occupancy at the complex scale, we allowed detection probability in the global model to vary with season (spring or fall), SWI, and effort; we retained effort as a covariate in all models regardless of model weights to account for surveys where the entire complex was not surveyed. We

allowed occupancy in the first season to vary with the number of pools per complex, watershed area, and mean elevation. Both colonization and extinction rates were allowed to vary with season, water availability, distance to nearest complex, and number of pools per complex. We assumed that colonization and extinction events occurred between survey seasons, therefore, we used an indicator variable for dynamic parameters, where a value of “1” represented summer (16 Jul – 30 Sep) and “0” represented winter (1 Jan – 30 Apr; Table 1).

At the drainage scale, fewer sample units restricted the number of covariates that we could include in the global model, particularly with respect to occupancy in the first season. Similar to models describing occupancy at the complex scale, we allowed detection probability to vary with season, SWI, and effort, and retained effort as a covariate in all subsequent models. With few drainages, we could not model occupancy in the first season as a function of covariates and therefore restricted first season occupancy to be the same for all drainages. We allowed rates of colonization and extinction to vary with season and water availability. We did not include number of pools or distance to nearest drainage as covariates in models of occupancy at the drainage scale because in both cases one drainage had a value that greatly exceeded values for all other drainages, which caused estimation and convergence problems.

To estimate linear temporal trends in occupancy, we derived estimates of occupancy at both the complex and drainage scale for all seasons after spring 1996 based on estimates of colonization and extinction from the highest-ranking models (MacKenzie et al. 2003). We conditioned projected estimates on the data, thereby restricting inference to sampled sites (Weir et al. 2009), and used non-parametric bootstrap methods to calculate standard errors for seasonal estimates of occupancy. We then fit a generalized least squares regression model that accounted for temporal autocorrelation to seasonal estimates of occupancy and selected a covariance structure based on AIC (Monahan 2008).

Abundance

Similar to occupancy analyses, we used hierarchical models to assess variation in abundance of adult leopard frogs over time while accounting for imperfect detection. Dynamic abundance models use repeated count data to estimate four parameters: abundance in the first season (λ_1), recruitment (γ), apparent survival (ω), and individual-based detection probability (p ; Dail and Madsen 2011). We assumed no relationship between recruitment and survival. Several occupied drainages had few adult leopard frogs (Fig. 4), which can cause convergence problems or yield imprecise estimates. Therefore, we restricted analyses to drainages where the mean number of adult frogs observed across all seasons was >10 . We excluded count data when $<40\%$ of pools in a complex were visited during a survey.

For abundance, we modeled variation in the number of adult frogs per complex, but not per drainage. We used the same general modeling approach and covariates that we used in occupancy analyses with a few exceptions. First, we used AIC from global models to assess whether abundance in the first season was best modeled with Poisson, zero-inflated Poisson, or negative-binomial distributions, and assumed this distribution in all subsequent models. We then evaluated covariates for detection probability, using the same covariates as those used in occupancy analyses (season, SWI, and effort). For abundance in the first season, we used log-transformed number of pools per complex as an offset in all models because it allowed us to (1) account for variation in the amount of habitat per complex, which is likely to affect abundance, and (2) model abundance per pool, rather than total abundance, as a function of covariates. In addition to the offset, we allowed abundance in the first year to vary with watershed area and mean elevation, and included a quadratic term for elevation in a subset of models to determine if the addition of this term improved model fit as measured by AICc. We allowed recruitment in the global

model to vary with season, water availability, number of pools per complex, and distance to nearest complex. We allowed apparent survival, which we modeled last, to vary with season, water availability, and the number of pools per complex. Similar to occupancy models, we assumed that recruitment and mortality events occurred primarily between survey seasons and modeled seasonal effects with an indicator variable that differentiated between summer and winter seasons.

To estimate linear temporal trends in abundance, we used empirical Bayes methods to estimate abundance of frogs in each complex in each season, and summed estimates of abundance across all complexes in each drainage (Royle and Dorazio 2008). We then fit a series of generalized least squares regression models that accounted for temporal autocorrelation within each drainage and evaluated whether abundance in each drainage or across all drainages changed linearly over the 16-year survey period.

Results

A total of 398 pools in 17 drainage segments and 4 tanks were classified as potential habitat for leopard frogs, with 2-118 pools per drainage segment (mean = 23.2, SE = 6.5); each tank was a single pool. Distances between adjacent pools ranged from 0 to 1396 m (mean = 123 m; Fig. 3); we used a minimum distance of 120 m between pools to classify pools into 105 complexes (4 of which were tanks), with 1-17 pools per complex (mean = 3.2, SE = 0.3).

Field surveys

Across the 16-year survey period, there were 257 surveys during spring survey seasons (1 May–15 July) and 213 during fall survey seasons (1 October–31 December). On average, each segment or tank was surveyed in 14.1 seasons (SE = 2.0, range = 2-32), with 1.6 surveys/season in those seasons surveyed at least once (SE = 0.1; range = 1-10). The number of adult lowland leopard frogs observed in each complex during each survey ranged from 0 to 100; other stage classes and other vertebrate species are summarized in Table 2. Adult leopard frogs were absent or undetected at complexes during 72% of surveys, juveniles during 91% of surveys, tadpoles during 85% of surveys, and egg masses during 99% of surveys.

Seasonal and spatial variation in counts of adult frogs

Adult leopard frogs were observed at least once in each of the 17 drainage segments and in 3 of 4 tanks. Where frogs were detected at least once, mean counts across all seasons ranged from 0.2 to 35.2 per drainage segment or tank, with highest counts in Wildhorse Canyon. On average, more frogs were observed in fall (mean = 11.9 adult frogs/season/drainage segment, SE = 3.2) than in spring (5.3 adult frogs/season/drainage segment, SE = 2.1). Based on the highest ranking model for mean counts of adult leopard frogs per drainage segment, counts increased with the number of pools (0.66 adult frogs/pool, SE = 0.12) and decreased as elevational range spanned by a segment increased (-0.03 adult frogs/m, SE = 0.01).

Adult leopard frogs were not observed during any spring or fall survey in 40 of 99 complexes that were surveyed in at least one season (39 of 95 complexes, 1 of 4 tanks). Where adult frogs were observed at least once, mean counts ranged from 0.1 to 23.0 per complex, with the highest counts in the lower portion of Chimenea Canyon (Fig. 5). Similar to total counts per drainage segment, mean counts per

complex were higher during fall surveys (2.7 adult frogs/season/complex, SE = 0.6) than spring surveys (1.2 adult frogs/season/complex, SE = 0.3).

Mean counts of adult frogs per complex varied with all potential covariates that we considered, although distance to the nearest complex was only marginally influential after accounting for the other covariates ($\beta_{\text{distance}} = 0.001$, SE = 0.001; ΔAIC_c of model that excludes distance = 1.13). Distances between complexes ranged from 121 to 1387 m, except for the Lower Rincon complex, which was >3320 m from the nearest complex. With this complex excluded, distance to nearest complex had no explanatory power ($\beta_{\text{dist}} = 0.000$, SE = 0.001). Because the effect of this covariate depended entirely on distance for a single complex, we excluded this covariate from the model used for inference. In the highest ranking model that excluded distance, mean counts were higher in tanks than pool complexes, increased with the number of pools, decreased with elevation, and were higher in south-facing complexes than in north- or west-facing complexes (Table 3).

Occupancy

We included nine drainages in occupancy analyses after combining drainage segments in close proximity (i.e., Loma Verde and Loma Verde South; Rincon Proper and Rincon North) and excluding those drainages and tanks that were surveyed only once per season or were surveyed in <3 seasons. In the highest ranking model for occupancy of frogs at the drainage scale, detection probability was high ($\hat{p} > 0.65$) when $\geq 40\%$ of pools in a drainage were surveyed, increased with survey effort, and was greater in fall than spring (Table 4). All models that included season as a covariate for colonization rates had problems with convergence so they were excluded from further consideration; colonization rates averaged 0.23 per season (95% CI = 0.12-0.38) and did not vary with water availability, the only other covariate we considered (summed AIC model weight [Σw_{water}] = 0.28). Extinction rates decreased as water availability increased, and ranged from 0.10 (95% CI = 0.05-0.20) when only 50% of pools contained water down to 0.02 (95% CI = 0.004-0.12) when all pools contained water (Table 4). There was no evidence that extinction rates varied with season ($\Sigma w_{\text{season}} = 0.28$). Occupancy of drainages varied from 0.55 to 0.95 during the 16-year survey period (Fig. 6), although there was no evidence of a linear trend over time based on a first-order autoregressive model (rate of change per season = -0.002, SE = 0.005, $t_{30} = -0.46$, $P = 0.65$).

We modeled occupancy over time in 71 pool complexes in 9 drainages. Probability of occupancy in the first season was higher in complexes with more pools and did not vary with watershed area ($\Sigma w_{\text{watershed}} = 0.34$; Table 4). Inclusion of elevation as a covariate for occupancy in the first season caused convergence problems, so we eliminated these models from further consideration. Probability of detecting ≥ 1 frog in an occupied pool complex was lower than the probability of detecting ≥ 1 frog in an occupied drainage ($\hat{p} = 0.64$ and 0.80 for complexes and drainages, respectively), but increased similarly with survey effort, and was greater in fall than in spring (Tables 4 and 5; Fig. 7). Detection probability at the complex scale also increased with amount of surface water per survey (Fig. 7). Colonization rates of previously unoccupied complexes were <0.50, higher in larger complexes, and higher in summer than winter (Fig. 8); colonization did not vary with water availability or distance to nearest complex ($\Sigma w_{\text{water}} = 0.43$, $\Sigma w_{\text{distance}} = 0.29$). Extinction rates were generally low (<0.20 for an average-sized complex when $\geq 50\%$ of pools contained water; Table 5), lower in larger complexes, and decreased when more surface water was present (Fig. 9). There was little evidence that extinction rates varied by season or with distance ($\Sigma w_{\text{season}} = 0.42$, $\Sigma w_{\text{distance}} = 0.46$). Occupancy of complexes each season varied from 0.27 to 0.55 during the 16-year study (Fig. 6), but similar to patterns in occupancy at the drainage scale, there was no

evidence of a linear trend over time based on a first-order autoregressive model (rate of change per season = -0.003, SE = 0.008, $t_{30} = -0.38$, $P = 0.70$).

Abundance

For analyses of abundance, we included 34 complexes from 5 drainages after excluding drainages with few adult frogs. Abundance in the first year was represented best with a negative binomial distribution (ΔAIC for other models > 36). In the highest-ranking model, detection probability increased with survey effort and proportion of pools with water, and was greater in fall than spring (Table 6). Detection probability of individuals ($\hat{p} = 0.36$) was considerably lower than site-based detection probabilities in occupancy models ($\hat{p} = 0.64$ at complex level; Tables 5, 7). Abundance in the first season was highest at intermediate elevations (highest predicted mean count at 1124 m elevation; Fig. 10), and did not vary with watershed area ($\Sigma w_{\text{watershed}} = 0.29$). Little to no recruitment of frogs into the adult stage class occurred during summer (i.e., between spring and fall survey seasons; Fig. 11). During winter, however, recruitment in an average-sized complex ranged from 1.2 individuals (95% CI = 0.8-1.9) when only 10% of pools contained water during fall surveys to 9.2 individuals (95% CI = 8.1-10.3) when all pools contained water. Generally, recruitment increased with amount of surface water and number of pools per complex (Fig. 11), and was higher at complexes that were more isolated (Table 6). Apparent survival was higher in summer and increased with water availability in both summer and winter (Fig. 12); apparent survival did not vary with the number of pools per complex ($\Sigma w_{\text{pools}} = 0.27$). Abundance of adult frogs per drainage each season varied from 1 to 367 during the 16-year study, but there was little evidence of a linear trend over time in any of the five drainages or summed across all drainages based on a second-order autoregressive model (Fig. 13; rates of change ranged from -0.42 to 2.80 frogs/season, all P -values > 0.10).

Discussion

Between 1996 and 2011, occupancy and abundance of lowland leopard frogs in the Rincon Mountains varied considerably over time and space. Across the nine drainages where we assessed occupancy, adult leopard frogs were observed in every year surveyed in two drainages (Chimenea, Rincon) and were absent or went undetected between 1 and 5 consecutive years in other drainages. Although this short-term variation complicated efforts to evaluate trends in leopard frog populations over time, we were able to identify several factors that affected spatial and temporal variation in rates of colonization, extinction, recruitment, and survival.

Local extinction rates of frog populations were lower in complexes or drainages with more pools and decreased as water availability increased. In contrast, colonization rates were lower and less variable than extinction rates, and were unaffected by local water availability. Metapopulation theory suggests that colonization rates should be lower for sites that are more isolated (Hanski 1999), but distance to nearest drainage or complex did not affect colonization or extinction rates. This might be expected, however, if colonization rates for leopard frogs in intermittent streams are governed primarily by patterns of stream flow rather than by distances between populations.

The amount of surface water available affected rates of recruitment and survival differently in winter than in summer seasons. Recruitment of adult leopard frogs occurred almost exclusively during winter, prior to spring surveys. Although we are unable to distinguish within-population recruitment (i.e., growth) from immigration of adults, we believe these patterns were driven primarily by reproductive cycles. A previous study of reproduction in lowland leopard frogs in southern Arizona noted that the

majority of egg masses were deposited in spring, with most individuals completing metamorphosis during summer (Sartorius and Rosen 2000). Presumably, these juveniles could transition to the adult stage class during late fall and winter. Interestingly, survival of adults was higher in summer than winter, and in both seasons, survival increased with the amount of surface water available. Lower water temperatures during winter have potential to decrease frog survival via direct and indirect mechanisms. Negative correlations between infection rates of amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) and water temperature have been demonstrated for populations of lowland leopard frogs in Arizona (Forrest and Schlaepfer 2011).

In contrast to other leopard frog populations in the desert southwest, these long-term data suggest that populations of lowland leopard frogs in and near Saguaro National Park are not declining precipitously but are fluctuating widely in response to variation in environmental conditions. Clearly, availability of surface water is integral to population dynamics of lowland leopard frogs, as even with a fairly coarse measure of water availability, we observed strong associations between surface water and rates of extinction, recruitment, and survival. These relationships have implications for persistence of leopard frog populations and other species associated with these aquatic environments given that water levels in riparian areas may decrease in response to climate change or to increased withdrawal of groundwater. Specifically, climate-change scenarios predict increased drought severity and decreased winter precipitation in the desert southwest (Seager et al. 2007, Dominguez et al. 2010). Increased residential development and associated groundwater extraction also will reduce availability of surface water in many low-elevation sites because groundwater and surface water are linked tightly in these systems (Stromberg et al. 1996, Alley et al. 2002).

Chytrid fungus has been implicated in declines of many amphibians, including ranid frogs in Arizona (Bradley et al. 2002, Skerratt et al. 2007). Our ability to assess effect of disease on population dynamics of leopard frogs in and near SNP, however, is limited because water and tissue samples were not collected at all sites over the entire 16-year period. Disease may play a role in dynamics of these populations, but it certainly is not the only factor influencing rates of mortality and local extinction given the associations we observed between surface water and temporal variation in occupancy and abundance of leopard frogs. Moreover, recent studies have demonstrated that some populations of lowland leopard frogs in SNP have persisted while maintaining low rates of infection (Ratzlaff 2012).

In addition to surface water and disease, other factors may affect dynamics of leopard frog populations over time, especially sedimentation events after fire and temperature extremes (e.g., number of days above 35° C or below 0° C per year). Although we plan to pursue these questions in future modeling efforts, one of the covariates we considered—minimum proportion of pools with water—likely reflects sedimentation processes, at least to some extent. Frequently, erosion associated with rainfall events after fire will inundate pools with sediment, reducing the amount and quality of habitat for frogs, although the timing and severity of these events are somewhat unpredictable (Parker 2006). Minimum proportion of pools with water should reflect these changes, at least at the complex scale, as pools that have been partially filled with sediment will hold water for shorter periods of time and pools that have been completely filled in will not hold any water. With a one-year lag, this relationship seemed to hold in the Loma Verde drainage after the Box Canyon fire (Fig. 14). We are in the process of developing tools that will allow us to incorporate observations of multiple stage classes (i.e., adults, juveniles, and tadpoles) into models of population dynamics. All of these future developments will allow us to expand on the analyses described here and provide a more complete understanding of the factors that drive dynamics of lowland leopard frog populations and other similar aquatic species.

Monitoring

The ability to detect long-term trends in populations of lowland leopard frogs is constrained by substantial temporal and spatial variation in rates of survival and recruitment and rates of local extinction and colonization. Given limited resources, a two-level approach to monitoring may be most efficient. Specifically, we suggest monitoring occupancy of adult frogs at a broad spatial scale and monitoring abundance of frogs, which requires more intense survey effort, at a subset of these sites.

Occupancy

Continuing broad-scale surveys in and near SNP will leverage previous survey effort and maximize the ability to detect long-term trends, where power is influenced strongly by duration of the sampling effort (Gibbs et al. 1998). Currently, park scientists attempt to survey each segment multiple times per season, which requires considerable effort and resources. When sites are surveyed ≥ 2 times per season, however, we gain the ability to estimate detection probability to account for those instances where sites are occupied but observers failed to detect frogs. We may be able to reduce this effort and estimate occupancy reliably, however, by surveying a subset of sites only once per season and using sites surveyed ≥ 2 times to estimate detection probability (double or removal sampling; MacKenzie and Royle 2005). Further, we propose that all sites be surveyed at least once during fall, because evidence from this study suggests that abundance and detection probability are higher in fall than spring (Figs. 3 and 6; Tables 4 and 5). Because availability of surface water and survey conditions may be more variable in fall than spring, however, surveys must be scheduled when conditions are amenable to detecting frogs.

Abundance

For this study, we limited our assessment of temporal trends in abundance of frogs to the five drainage segments with highest abundances. It likely would be most efficient to focus estimates of abundance on this subset of sites rather than all drainage segments in and near the park, although the scope of inference would be reduced. To estimate abundance reliably, we propose to survey each site ≥ 2 times per season, with the number of surveys dependent on available resources. Ecologically, these sites are also likely to serve as source populations for other sites where frogs are absent or present in low numbers. Monitoring trends in abundance at these sites could provide insight into the probability of long-term regional persistence assuming local leopard frog populations are connected via occasional dispersal events. If resources permit, studying rates of reproduction, recruitment, and survival in addition to visual encounter surveys at a subset of sites could help identify factors that drive population dynamics and ultimately temporal trends in abundance. Collection of these additional data would also help inform and refine future monitoring efforts.

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Table 1. Site-, season-, and survey-specific covariates used to model variation in initial occupancy (ψ_1), colonization rates (γ), extinction rates (ϵ), and detection probability (p) for lowland leopard frogs in the Rincon Mountains between 1996 and 2011. Spatial resolution indicates whether the covariate applies to a pool complex (c) or drainage (d).

Covariate	Spatial resolution	Parameters	Description
<i>Site-specific</i>			
No. pools	c, d	ψ_1, γ, ϵ	Number of pools per complex or drainage
Mean elevation	c	ψ_1	Mean elevation of each complex (m)
Elevational range	d	ψ_1	Elevational range of each drainage (m)
Watershed area	d	ψ_1	Total watershed area of each drainage from lowest pool (sq. km)
Distance	c, d	γ, ϵ	Distance to nearest complex or drainage (m)
<i>Season-specific</i>			
Season	--	γ, ϵ, p	Indicator for summer (γ, ϵ) or spring season (p)
Water availability	c, d	γ, ϵ	Minimum proportion of pools in each complex or drainage with water in prior survey season
<i>Survey-specific</i>			
Effort	c, d	p	Proportion of pools in each complex or drainage surveyed
Survey water index (SWI)	c, d	p	Proportion of pools in each complex or drainage with water during each survey

Table 2. Total, mean, and maximum number (no./complex/survey) of aquatic vertebrate species observed in the Rincon Mountains during surveys completed between 1996 and 2011.

Species	Stage class	Total no. observations	Mean ^a	SD	Maximum ^a
Lowland leopard frogs	Adults	5148	2.25	8.21	100
	Juveniles	4625	2.30	27.32	995
	Tadpoles	23,234	10.04	81.70	2800
	Egg masses	218	0.09	3.16	130
Canyon treefrogs	Adults	40,107	20.57	70.44	1149
Black-necked gartersnake ^b		626	0.19	0.67	8
Sonoran mud turtle ^b		460	0.23	0.86	10

^a Mean and maximum for observations during spring and fall seasons only, after excluding surveys where <50% of pools in a complex were surveyed.

^b Observations include both juveniles and adults

Table 3. Estimates for covariates in the highest-ranking model describing mean counts of adult leopard frogs per complex across all spring and fall survey seasons in the Rincon Mountains between 1996 and 2011.

Covariate	Estimate	SE
No. pools	0.52	0.08
Pool location ^a	4.72	1.49
Aspect E ^b	-1.98	1.71
Aspect N ^b	-3.34	0.93
Aspect W ^b	-2.70	0.76
Mean elevation (m)	-0.004	0.001

^a Indicator variable established as tank = 1, drainage = 0.

^b Mean counts relative to south-facing complexes.

Table 4. Untransformed estimates and standard errors for covariates in the highest-ranking models describing occupancy of leopard frogs in drainages or pool complexes in the Rincon Mountains between 1996 and 2011.

Parameter	Covariate	Drainage		Complex	
		Estimate	SE	Estimate	SE
Initial occupancy (ψ_1)	No. pools ^a			0.74	0.70
Colonization (γ)	No. pools ^a			0.37	0.17
	Season ^b			0.92	0.63
Extinction (ϵ)	Water availability	-3.07	1.39	-4.09	0.65
	No. pools ^a			-0.97	0.28
Detection probability (p)	Effort	1.03	0.62	0.26	0.68
	Season ^c	-0.98	0.37	-0.76	0.20
	Survey water index			1.63	0.28

^a No. pools was standardized.

^b Indicator variable established as summer = 1, winter = 0.

^c Indicator variable established as spring = 1, fall = 0.

Table 5. Parameter estimates and 95% confidence intervals from the most general dynamic models for occupancy of lowland leopard frogs at the drainage and complex scale in the Rincon Mountains between 1996 and 2011.

Parameter	Drainage		Complex	
	Estimate	95% CI	Estimate	95% CI
Initial occupancy (ψ_1)	0.69	0.16 – 0.96	0.35	0.17 – 0.59
Colonization (γ)	0.22	0.12 – 0.38	0.06	0.04 – 0.09
Extinction (ϵ)	0.08	0.04 – 0.15	0.09	0.06 – 0.14
Detection probability (p)	0.80	0.73 – 0.85	0.64	0.59 – 0.69

Table 6. Untransformed estimates for covariates in the highest-ranking model describing abundance of adult leopard frogs in the Rincon Mountains between 1996 and 2011. The log-transformed number of pools per complex was used as an offset for abundance in the first season.

Parameter	Covariate	Estimate	SE
Initial abundance (λ_1)	Mean elevation ^a	1.51	0.59
	Mean elevation ²	-1.05	0.45
Recruitment (γ)	Season ^b	-2.68	0.35
	Water availability	2.24	0.25
	No. pools ^a	0.63	0.03
	Distance	0.12	0.02
Apparent survival (ω)	Season ^b	1.00	0.22
	Water availability	2.60	0.24
Detection probability (p)	Effort	1.38	0.25
	Season ^c	-1.86	0.09
	Survey water index	1.17	0.11

^a Values for all covariates that were not proportions or indicators (i.e., mean elevation and no. pools) were standardized relative to their means and standard deviations.

^b Indicator variable established as summer = 1, winter = 0.

^c Indicator variable established as spring = 1, fall = 0.

Table 7. Parameter estimates and 95% confidence intervals from the most general dynamic model for abundance of lowland leopard frogs in the Rincon Mountains between 1996 and 2011. Initial abundance is modeled with a negative binomial distribution and is reported as the number of frogs per pool because log-transformed number of pools per complex was used as an offset.

Parameter	Estimate	95% CI
Initial abundance (λ_1)	0.47	0.24 – 0.94
Recruitment (γ)	2.52	2.30 – 2.76
Apparent survival (ω)	0.63	0.59 – 0.67
Detection probability (p)	0.36	0.32 – 0.39

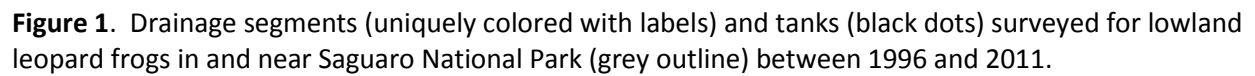




Figure 2. Repeat photographs of two pools in the Rincon Mountains during late spring, when little to no flow occurred between pools (A, C), and summer, when surface water flowed throughout most drainages (B, D).

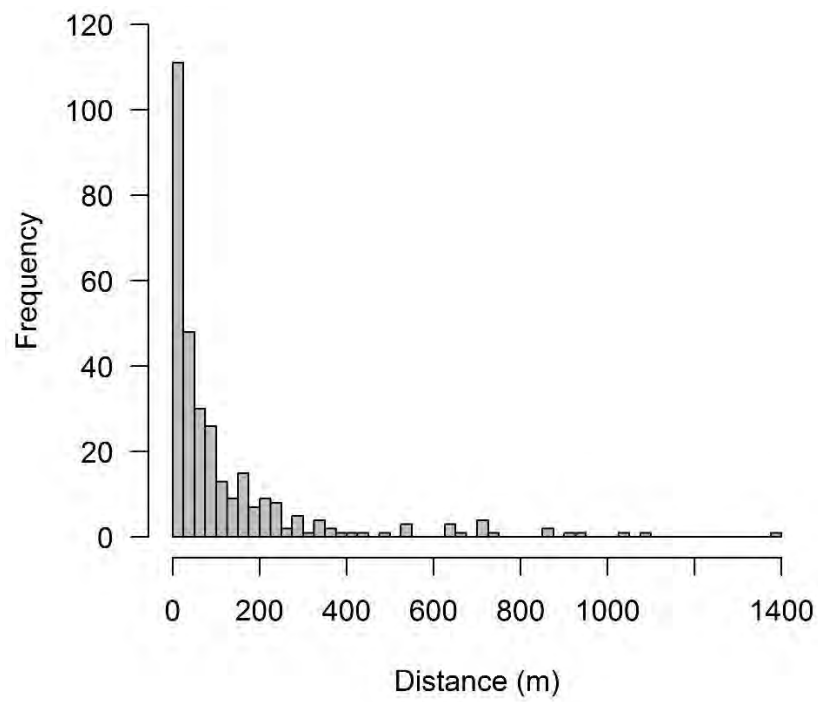


Figure 3. Distances between adjacent monitored pools in drainages surveyed for lowland leopard frogs in the Rincon Mountains between 1996 and 2011.

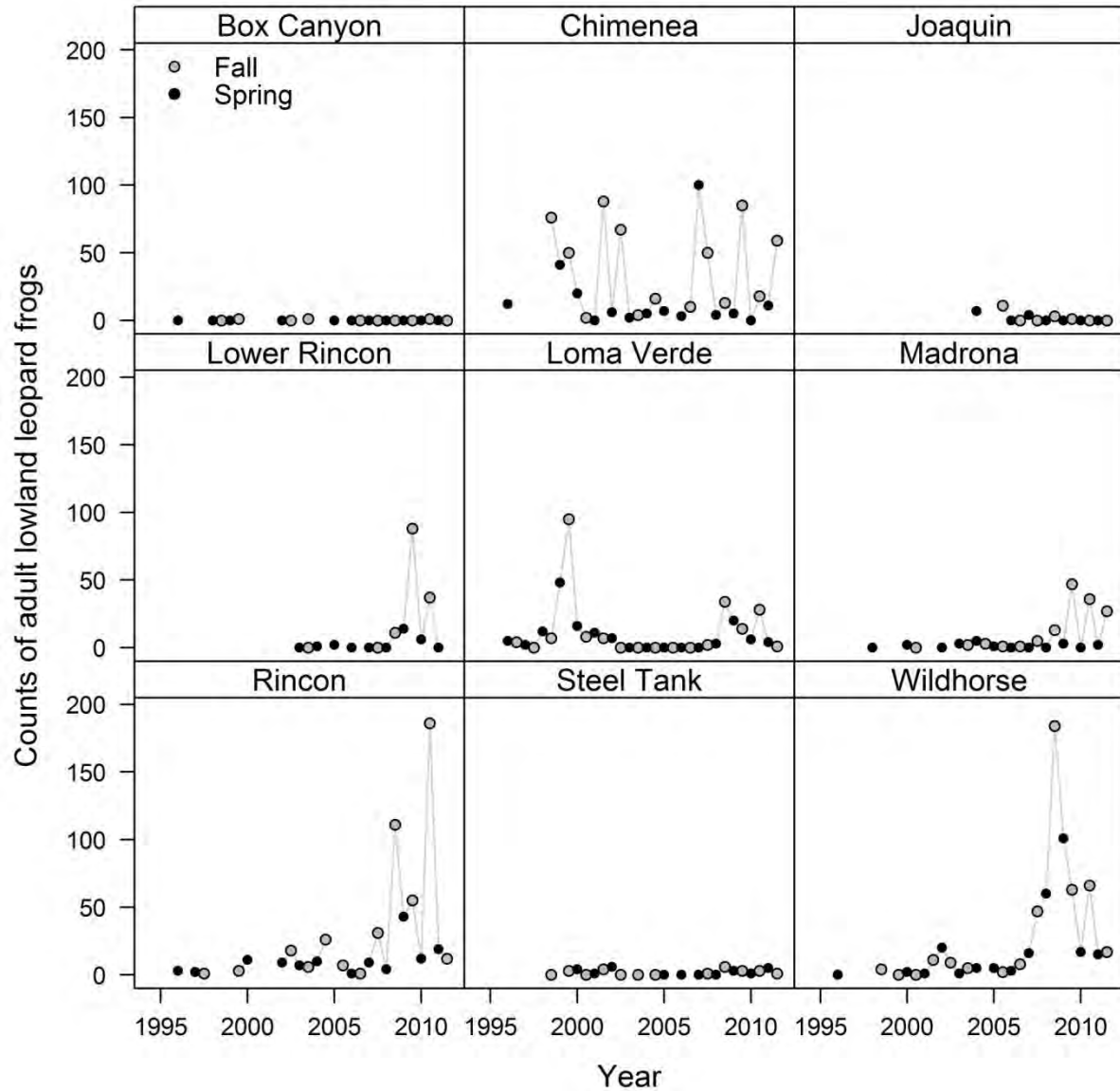


Figure 4. Maximum counts of adult lowland leopard frogs during each spring and fall survey season between 1996 and 2011 for nine drainages in the Rincon Mountains.

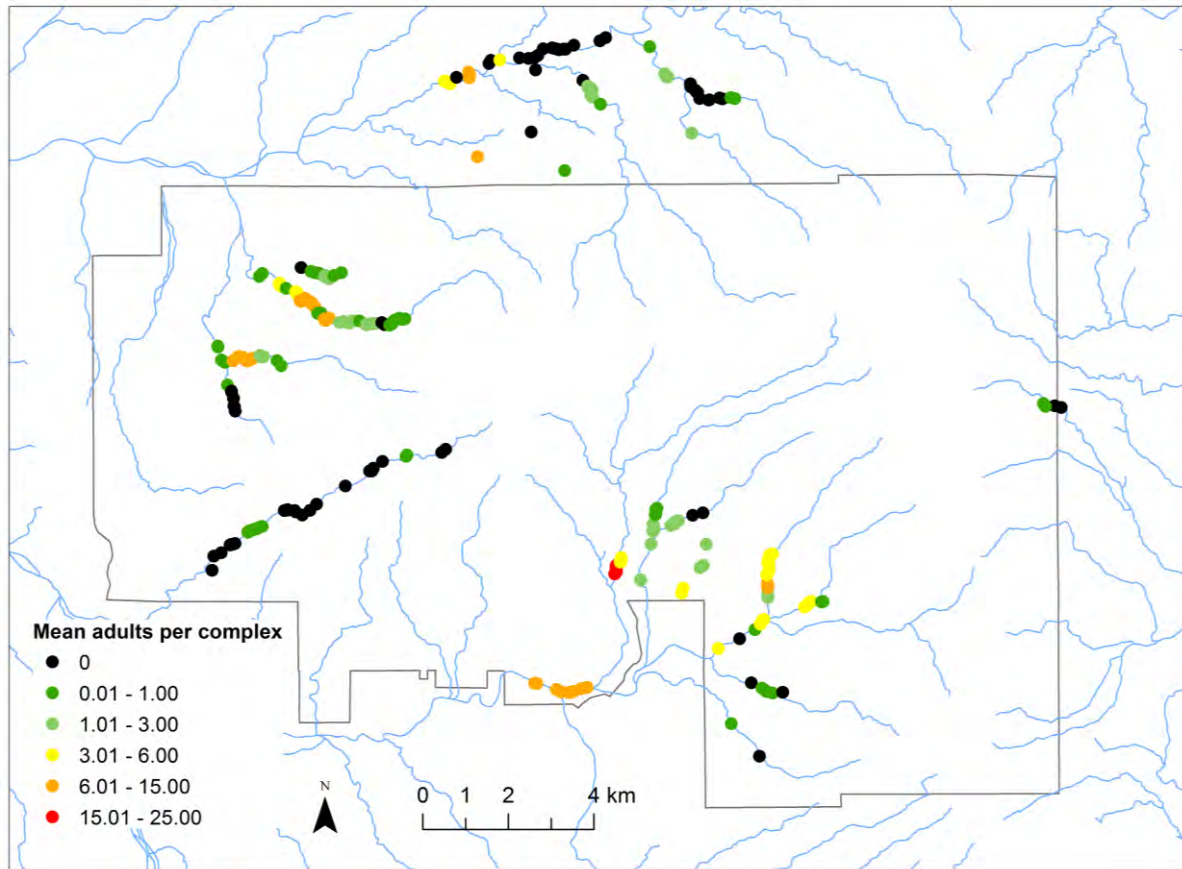


Figure 5. Mean number of adult leopard frog observations in pool complexes in the Rincon Mountains between 1996 and 2011.

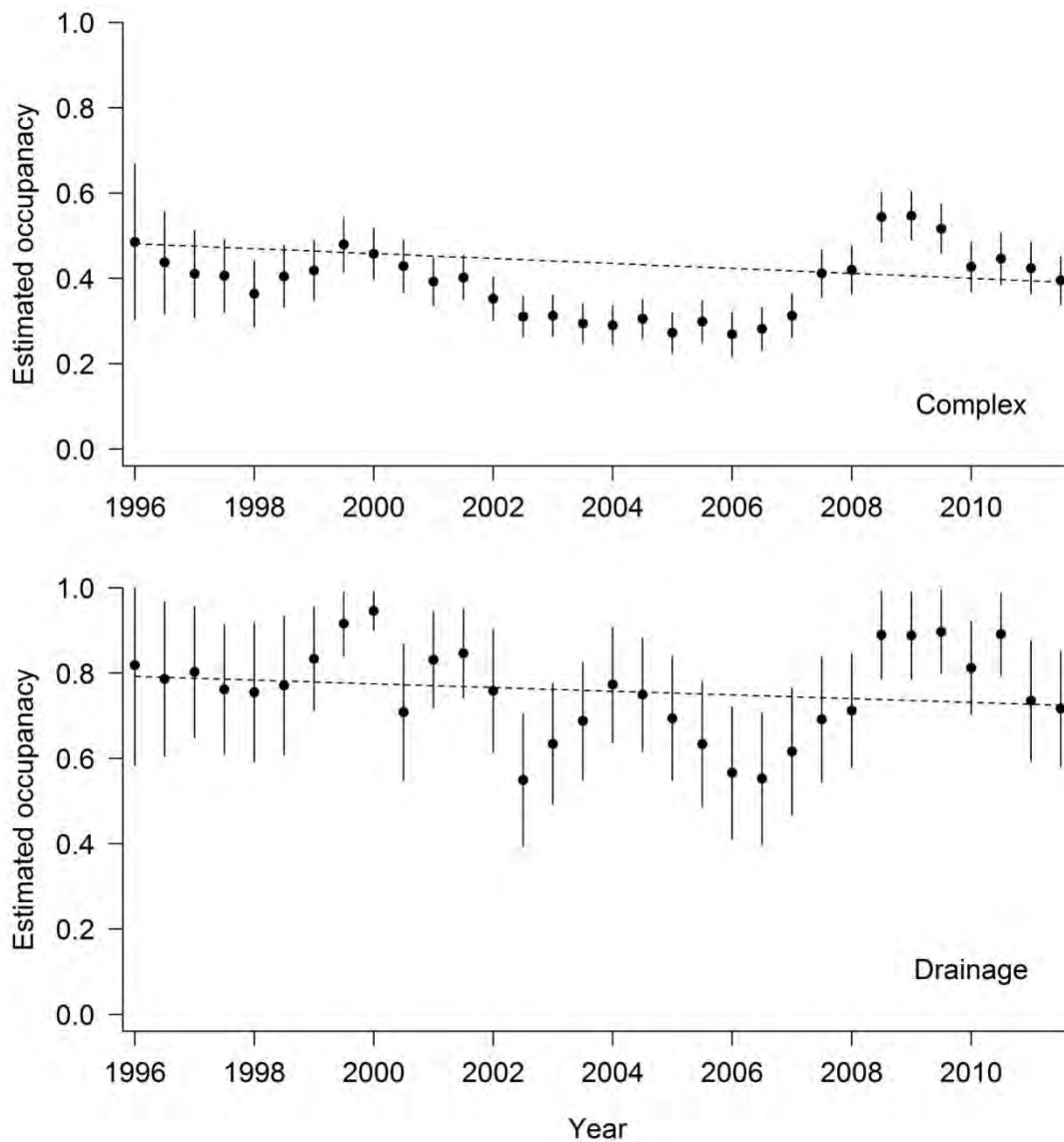


Figure 6. Estimated occupancy (± 1 SE) of pool complexes and drainages in the Rincon Mountains each spring and fall season between 1996 and 2011. Estimated trends in occupancy (dashed lines) were not significant at the complex (P -value = 0.70) or drainage scale (P -value = 0.65).

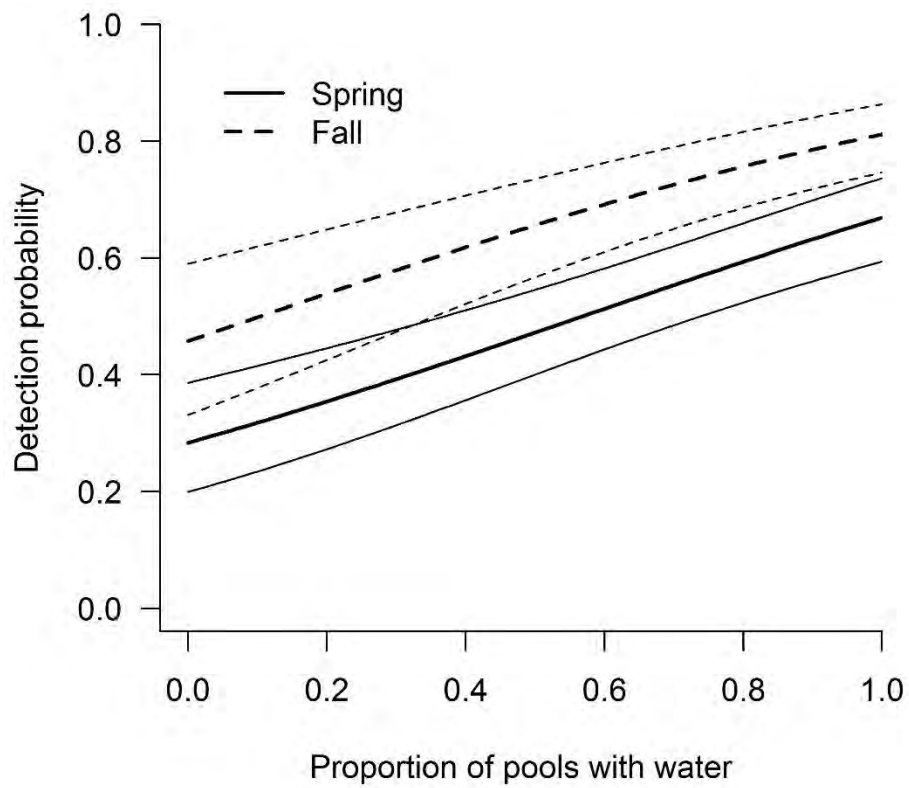


Figure 7. Detection probability (with 95% confidence interval) of adult lowland leopard frogs during spring and fall surveys in the Rincon Mountains as a function of the proportion of pools with water in each pool complex, assuming all pools in the complex were surveyed.

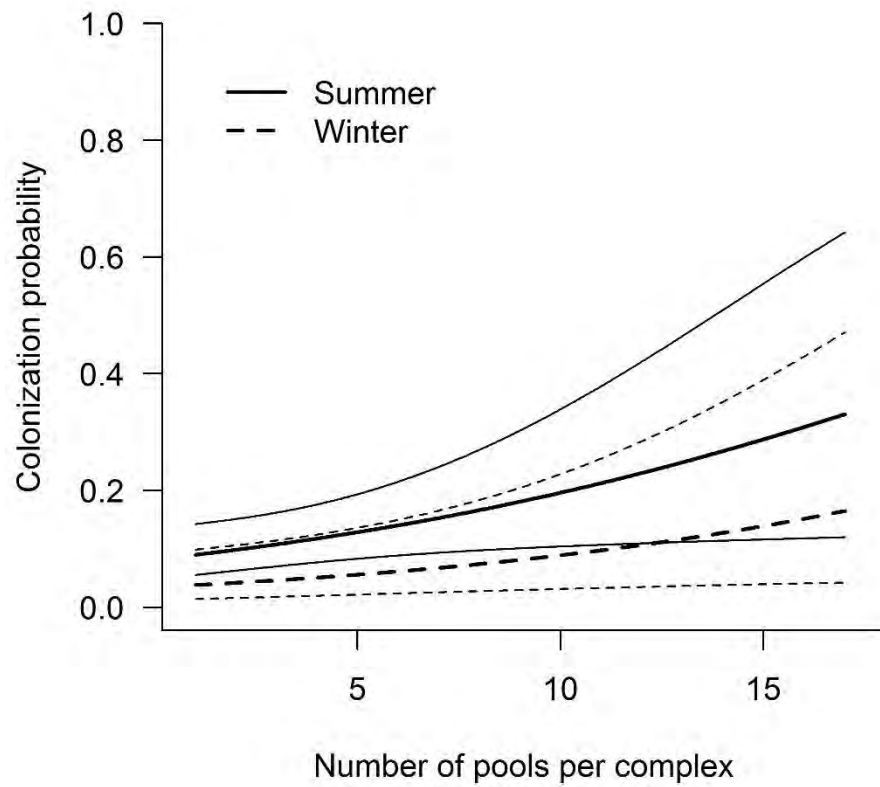


Figure 8. Seasonal probability that lowland leopard frogs colonize a previously unoccupied pool complex (with 95% confidence interval) in the Rincon Mountains as a function of complex size.

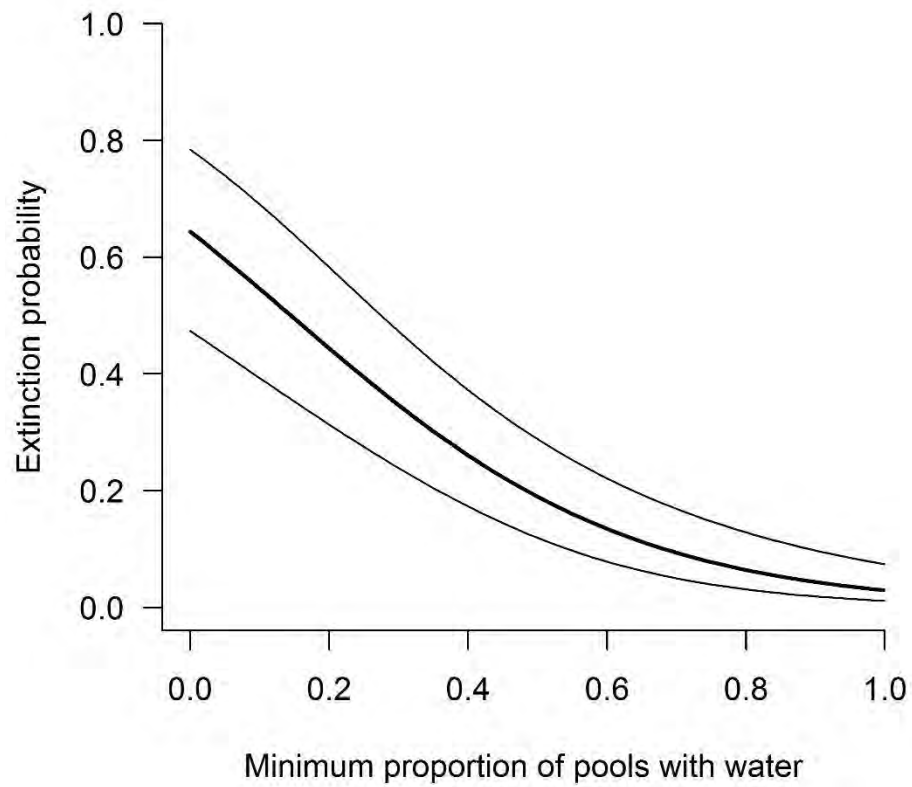


Figure 9. Probability that lowland leopard frogs in an average-sized pool complex go extinct (with 95% confidence interval) as a function of the minimum proportion of pools in the complex with water during the previous survey season.

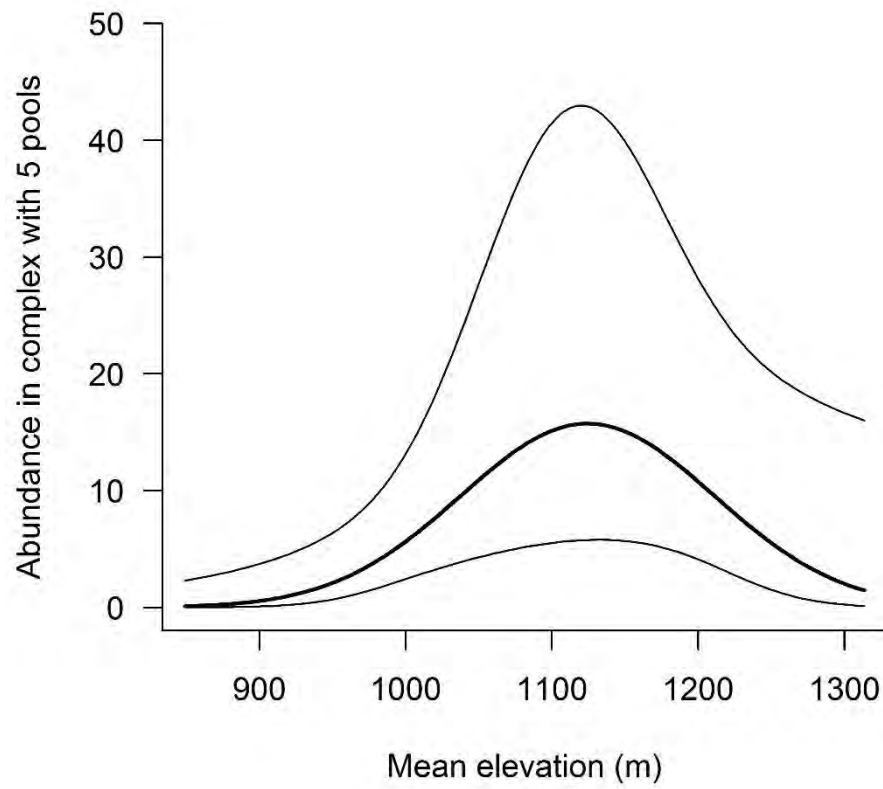


Figure 10. Predicted abundance (with 95% confidence interval) of adult lowland leopard frogs as a function of elevation in an average-sized pool complex in the Rincon Mountains in the spring of 1996.

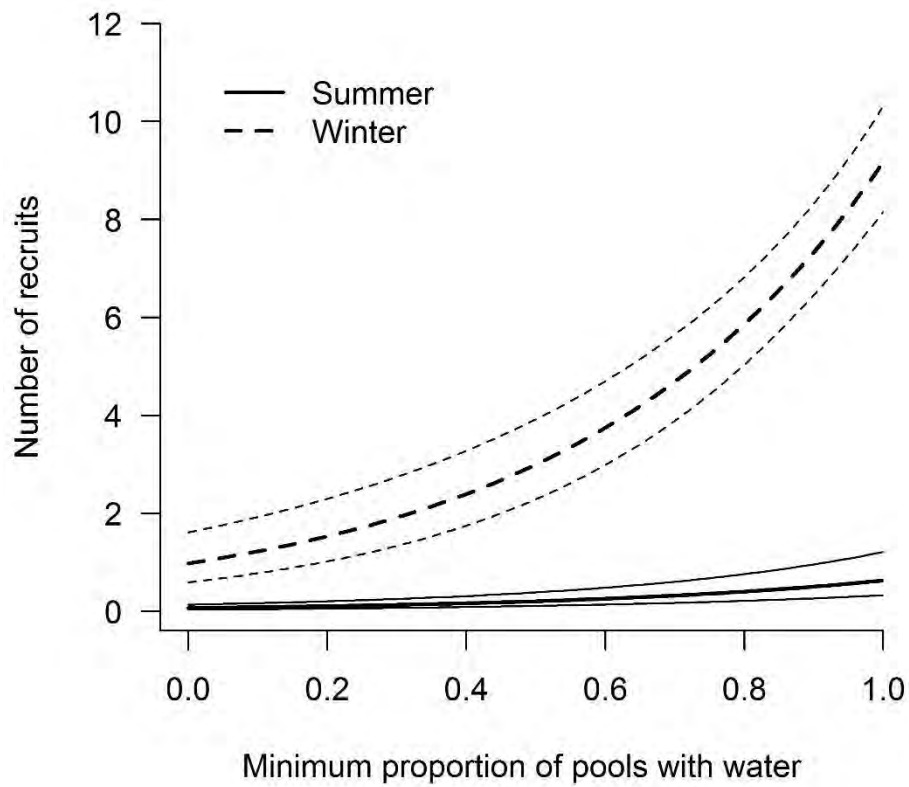


Figure 11. Predicted number of lowland leopard frogs recruited into an adult population (with 95% confidence interval) at a complex of average size and average distance from other complexes in the Rincon Mountains as a function of the minimum proportion of pools in the complex with water during the previous survey season.

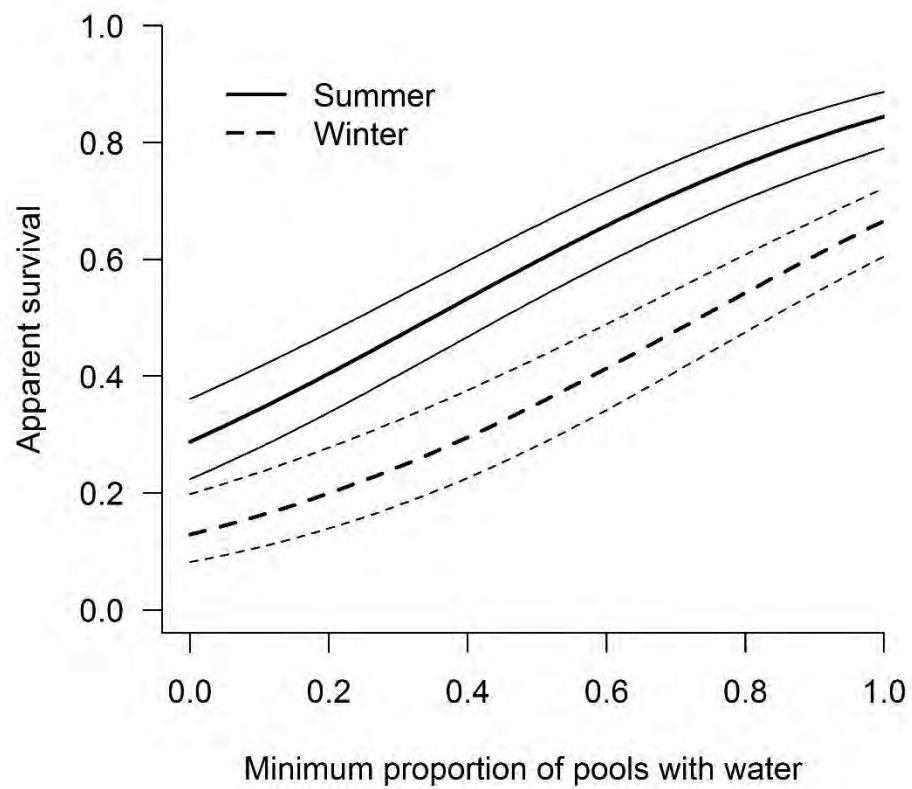


Figure 12. Predicted survival (with 95% confidence interval) of adult lowland leopard frogs in the Rincon Mountains as a function of the minimum proportion of pools in a complex with water during the previous survey season.

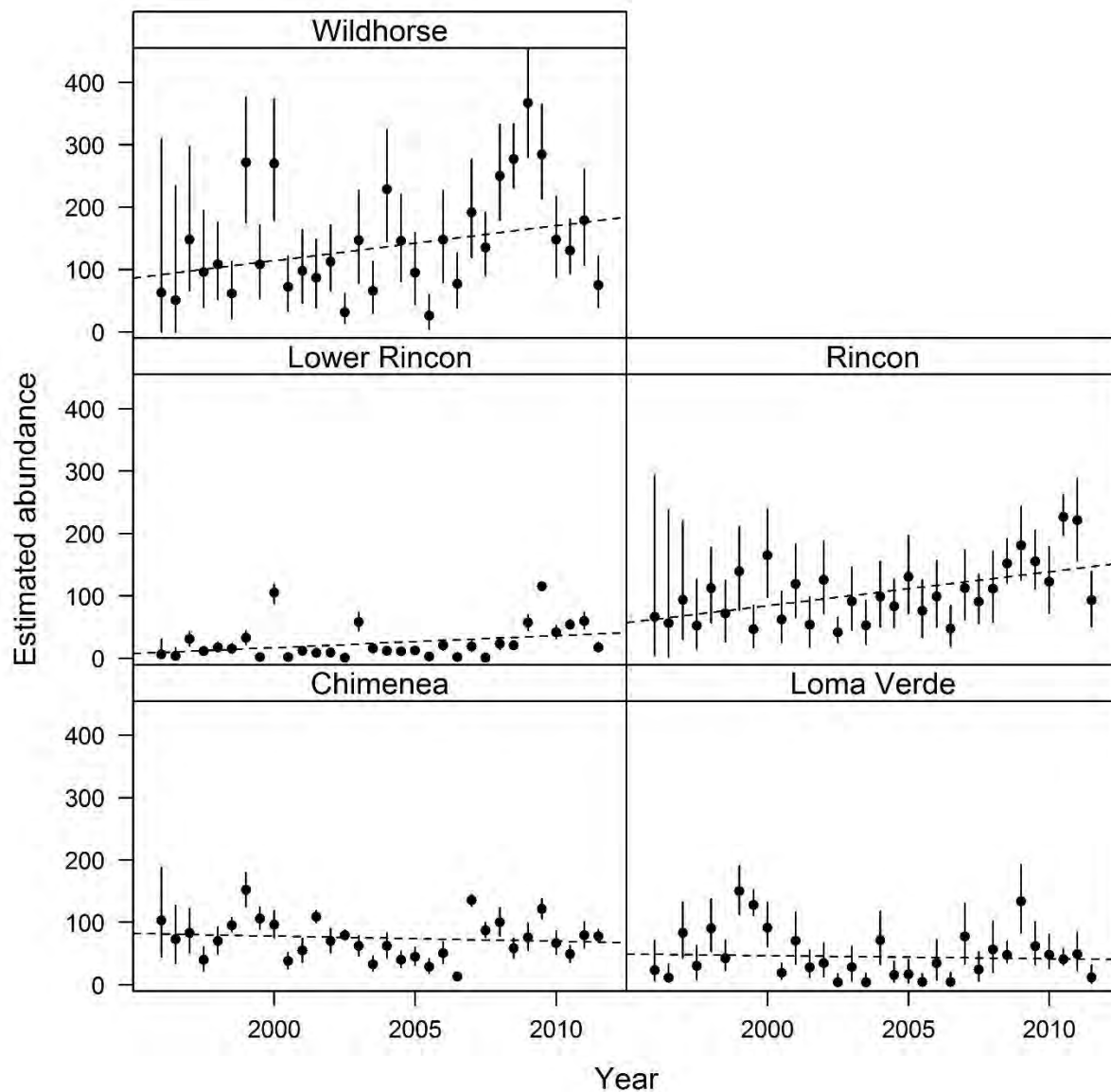


Figure 13. Estimated abundance of adult frogs (with 95% CI) in each of five drainages in the Rincon Mountains during spring and fall seasons between 1996 and 2011. Estimated trends in abundance (dashed lines) were not significant (all P -values > 0.10). The “Rincon” drainage includes pools in Rincon proper and Rincon North; the “Loma Verde” drainage includes pools in Loma Verde proper and Loma Verde South.

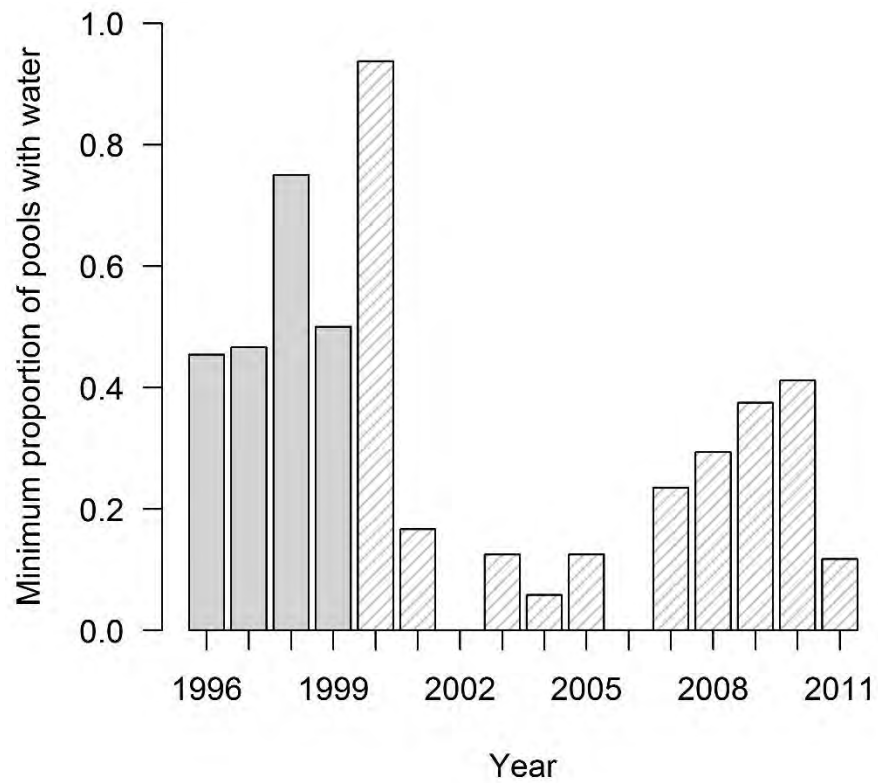


Figure 14. Minimum proportion of pools with water between 1 May and 15 July in the middle reach of Loma Verde drainage before (gray) and after (hatched) the Box Canyon fire.