SPATIALLY EXPLICIT METAPOPULATION MODELS FOR INFORMING CONSERVATION

by

PAIGE ELIZABETH HOWELL

(Under the Direction of Richard B. Chandler)

ABSTRACT

For many species, populations exist as highly fragmented subpopulations linked by dispersal. To manage for long-term metapopulation viability effectively, information is needed about the factors influencing local subpopulation dynamics and connectivity among subpopulations. The objectives of my dissertation were to 1) improve the linkages between metapopulation and landscape ecology by developing spatially-explicit dynamic metapopulation models allowing for inference about local and landscape-level processes, 2) expand on existing metapopulation models by modeling spatio-temporal variation in density, 3) evaluate hypotheses regarding the effects of patch hydroperiod, landscape structure, and density-dependence on metapopulation dynamics using statistical models, and 4) provide management recommendations to enhance the viability of the Chiricahua leopard frog (*Lithobates chiricahuensis*). Colonization rate was influenced by patch hydroperiod, elevation and the spatial distribution of streambeds. Patch-specific growth rates were density-dependent and influenced by hydroperiod. The proportion of occupied ponds increased initially from the reintroduction of tadpoles into three ponds in 2003 to 18 (95% CI; 12, 33) of the 274 available ponds occupied in 2017. Metapopulation extinction risk over a 25-yr time horizon (2018-2043) with static environmental

conditions was predicted to be low (7%) if invasive predator control continues and permanent ponds are maintained. However, under a scenario of increasing drought conditions, extinction risk is substantially higher, particularly in the most pessimistic scenario where some ponds fail and there is no management (40%). Results from my dissertation illustrate the utility of spatiallyexplicit statistical models for understanding the processes underlying metapopulation dynamics and forecasting metapopulation viability, while formally accounting for uncertainty.

INDEX WORDS: Chiricahua leopard frog, Conservation, Metapopulation, Population viability analysis, Spatially-explicit

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PAIGE ELIZABETH HOWELL

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M.S., Michigan State University, 2014

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PAIGE ELIZABETH HOWELL

Major Professor: Committee: Richard B. Chandler John C. Maerz Brian J. Irwin Erin Muths

Electronic Version Approved:

Suzanne Barbour Dean of the Graduate School The University of Georgia May 2018

DEDICATION

This dissertation is dedicated to my husband Ben Ayres and to Perrin Howell Ayres.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

For many taxa, populations exist as highly fragmented subpopulations linked by individuals moving through an inhospitable landscape (Wiens 1997). Increased fragmentation and habitat degradation by anthropogenic activity can reduce successful migration (Thomas 2000), limit gene flow (Epps et al. 2005), and increase metapopulation extinction risk (Fahrig 2007). However, local extinction events are a common characteristic of many metapopulations, and thus metapopulation persistence depends on the ability of individuals to colonize vacant habitat patches (Hanski 1999). To improve long-term metapopulation viability, information is needed about the effects of patch and landscape level factors on patch (e.g., extinction, population growth) and inter-patch dynamics (e.g., colonization). This information can be used in conjunction with hierarchical spatio-temporal models to forecast metapopulation dynamics and viability under uncertain environmental conditions and management alternatives.

Early metapopulation modeling approaches were non-spatial and assumed the landscapes between patches was homogenous, making it impossible to model processes such as connectivity (Levins 1969; Levins 1970; Harrison and Quinn 1989; Gyllenberg and Hanski 1992; Hanski 1994). More recently, metapopulation ecology has focused on spatially-explicit models that account for patch quality and the influence of the spatial arrangements of patches on connectivity (Day and Possingham 1995; Frank and Wissel 1998; Hanski and Ovaskainen 2003; Harrison et al. 2011). To date, such spatially-explicit models have ignored the properties of the intervening habitat matrix (Tischendorf and Fahrig 2001) and only considered distance as the Euclidean distance between habitat patches (Sutherland et al. 2012; Sutherland et al. 2014; Chandler et al. 2015). A limitation of this approach is that animal movement is rarely linear, and more biologically meaningful measures of distance have been developed to acknowledge that habitats may differ in their resistance to movement (Spear et al. 2010). Advances in mark-recapture methods have demonstrated the possibility for directly estimating resistance surfaces and cost distances, but these developments have not been integrated into metapopulation models (Royle et al. 2013). Accounting for resistance to movement in metapopulation models would make it possible to study the landscape factors influencing functional connectivity.

Patch characteristics are also thought to influence the colonization process (Hanski 1999). Emigration rate may be lower from higher quality patches because individuals are able to secure a sufficient amount of resources to survive and reproduce. However, higher quality patches may also contain more conspecifics, which could lead to an increase in intraspecific competition or crowding and increased emigration rate (Denno and Peterson 1995; McCarthy 1999; Matthysen 2005). Additionally, either improved mating success or a reduced predation rate could lead to further increases in the number of individuals per patch (hereafter referred to as density) (Stamps 1991; Matthysen 2005). In these situations, we may expect emigration rate to be lower in higher density patches. Immigration rate is also expected to be influenced by patch quality. Individuals may be more likely to settle in higher quality patches (Moilanen and Hanski 1998). However, if competition increases with density, and density scales with patch quality, our predictions would be reversed (Andreassen and Ims 2001).

Spatio-temporal variation in patch-level extinction risk is also influenced by variation in demographic rates (Wahlberg et al. 2002). For instance, survival or recruitment of new individuals into the population may increase with patch quality (Lambrechts et al. 2004). In this

case, higher quality patches may contribute more potential migrants to colonize empty patches. Patches with larger population sizes, are also less likely to experience an extinction event through stochastic processes, relative to small populations (Lande 1993; Hedrick and Kalinowski 2000). As density increases, growth rates are predicted to decline (Hanski 1998). This population regulation may cause population size to oscillate around a carrying capacity over time, and the amplitude of oscillations depends on the susceptibility of a species to environmental perturbations (Hanski 1999). Most metapopulation models focus on occurrence rather than abundance/density (Sutherland et al. 2012; Sutherland et al. 2014). However, without considering spatio-temporal variation in density it is impossible to model processes such as density-dependent growth or emigration. Moreover, ignoring density-dependence may lead to unreasonably high estimates of patch-specific growth rates and metapopulation level abundance.

For the purposes of conservation, statistical models that can provide probabilistic forecasts of metapopulation dynamics are particularly useful, especially when the models are used to evaluate specific management alternatives and future environmental conditions. However, conventionally, population viability analyses (PVA) have involved a two-step procedure in which demographic parameters are estimated or elicited from experts and then the point estimates are plugged into a stochastic population model (Heinsohn et al. 2004; Olsen et al. 2014; Mortensen and Reed 2016). When future environmental conditions are included in these models, they are often provided as average conditions (Galimberti et al. 2001). However, these conventional practices ignore the uncertainty associated with parameter estimation and future environmental conditions. Bayesian forecasting methods can be used to fully account for uncertainty by computing posterior predictive distributions for future occupancy states and other latent variables, conditional on the observed data.

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Amphibians are a taxonomic group that is especially sensitive to environmental change (Foden et al. 2013). Amphibians in arid environments are particularly sensitive to environmental changes such as increasing drought conditions and catastrophic failure of aquatic breeding habitat (Welch and MacMahon 2005; Walls et al. 2013). In the southwestern USA, all native semi-aquatic frogs (family Ranidae) have declined (Hayes and Jennings 1986), but only the Chiricahua leopard frog (*Lithobates chiricahuensis*) is listed under the US Endangered Species Act (USFWS 2007). The L. chiricahuensis metapopulation that occupied the Altar Valley and the Buenos Aires Wildlife Refuge (BANWR) went locally extinct by 2001, most likely due to the spread of non-native species, including American bullfrog (Lithobates catesbeianus), crayfish and fish (USFWS 2007). After eradication of L. catesbeianus from the refuge in 2001, L. chiricahuensis were reintroduced to three patches in 2003. A monitoring program was established in 2007 and since then, L. chiricahuensis have been observed in cattle tanks other than the release locations, with varying ranges in hydroperiod. Conservation of this species requires information about the influence of patch characteristics and landscape structure on metapopulation dynamics, and predictive models are needed to determine how metapopulation viability is likely to be impacted by future environmental conditions and management options.

The objectives of my dissertation were to 1) improve the linkages between metapopulation and landscape ecology by developing spatially-explicit dynamic metapopulation models allowing for inference about local and landscape-level processes, 2) expand on existing metapopulation models by modeling spatio-temporal variation in density, 3) evaluate hypotheses regarding the effects of patch hydroperiod, landscape structure, and density-dependence on metapopulation dynamics using statistical models, and 4) provide management recommendations for enhancing the viability of the Chiricahua leopard frog (*Lithobates chiricahuensis*).

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Literature Cited

- Andreassen, H. P., and R. A. Ims. 2001. Dispersal in patchy vole populations: role of patch configuration, density dependence, and demography. Ecology **82**:2911-2926.
- Bezy, J. H., Charles, F.; Bahre, Conrad J. 2007. Buenos Aires National Wildlife Refuge, Arizona. University of Arizona.
- Chandler, R. B., E. Muths, B. H. Sigafus, C. R. Schwalbe, C. J. Jarchow, and B. R. Hossack.
 2015. Spatial occupancy models for predicting metapopulation dynamics and viability following reintroduction. Journal of Applied Ecology 52:1325-1333.
- Day, J. R., and H. P. Possingham. 1995. A stochastic metapopulation model with variability in patch size and position. Theoretical Population Biology **48**:333-360.
- Denno, R. F., and M. A. Peterson. 1995. Density-dependent dispersal and its consequences for population dynamics. Population dynamics: new approaches and synthesis:113-130.
- Epps, C. W., P. J. Palsbøll, J. D. Wehausen, G. K. Roderick, R. R. Ramey, and D. R. McCullough. 2005. Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. Ecology Letters 8:1029-1038.
- Fahrig, L. 2007. Non-optimal animal movement in human-altered landscapes. Functional Ecology 21:1003-1015.
- Foden, W. B., S. H. Butchart, S. N. Stuart, J.-C. Vié, H. R. Akçakaya, A. Angulo, L. M. DeVantier, A. Gutsche, E. Turak, and L. Cao. 2013. Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. PLoS One 8:e65427.
- Frank, K., and C. Wissel. 1998. Spatial aspects of metapopulation survival–from model results to rules of thumb for landscape management. Landscape Ecology **13**:363-379.

- Gaines, M. S., and L. R. McClenaghan. 1980. Dispersal in small mammals. Annual review of ecology and systematics **11**:163-196.
- Galimberti, F., S. Sanvito, L. Boitani, and A. Fabiani. 2001. Viability of the southern elephant seal population of the Falkland Islands. Pages 81-88 *in* Animal Conservation forum.Cambridge University Press.
- Gyllenberg, M., and I. Hanski. 1992. Single-species metapopulation dynamics: a structured model. Theoretical Population Biology **42**:35-61.
- Hanski, I. 1994. Patch-occupancy dynamics in fragmented landscapes. Trends in Ecology & Evolution **9**:131-135.
- Hanski, I. 1998. Metapopulation dynamics. Nature 396:41-49.
- Hanski, I. 1999. Metapopulation ecology. Oxford University Press Oxford.
- Hanski, I., A. Moilanen, T. Pakkala, and M. Kuussaari. 1996. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. Conservation biology 10:578-590.
- Hanski, I., and O. Ovaskainen. 2003. Metapopulation theory for fragmented landscapes. Theoretical Population Biology **64**:119-127.
- Harrison, P. J., I. Hanski, and O. Ovaskainen. 2011. Bayesian state-space modeling of metapopulation dynamics in the Glanville fritillary butterfly. Ecological Monographs 81:581-598.
- Harrison, S., and J. F. Quinn. 1989. Correlated environments and the persistence of metapopulations. Oikos:293-298.
- Hayes, M. P., and M. R. Jennings. 1986. Decline of ranid frog species in western North America: are bullfrogs (Rana catesbeiana) responsible? Journal of Herpetology:490-509.

- Hedrick, P. W., and S. T. Kalinowski. 2000. Inbreeding depression in conservation biology. Annual review of ecology and systematics:139-162.
- Heinsohn, R., R. C. Lacy, D. B. Lindenmayer, H. Marsh, D. Kwan, and I. R. Lawler. 2004.
 Unsustainable harvest of dugongs in Torres Strait and Cape York (Australia) waters: two case studies using population viability analysis. Pages 417-425 *in* Animal Conservation forum. Cambridge University Press.
- Howell, P. E., E. Muths, B. R. Hossack, B. H. Sigafus, and R. Chandler. In Press. Increasing connectivity between metapopulation ecology and landscape ecology. Ecology.
- Lambrechts, M. M., S. Caro, A. Charmantier, N. Gross, M.-J. Galan, P. Perret, M. Cartan-Son, P. C. Dias, J. Blondel, and D. W. Thomas. 2004. Habitat quality as a predictor of spatial variation in blue tit reproductive performance: a multi-plot analysis in a heterogeneous landscape. Oecologia 141:555-561.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American naturalist:911-927.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America **15**:237-240.

Levins, R. 1970. Extinction. Lectures on mathematics in the life sciences 2:75-107.

Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. Ecography 28:403-416.

- McCarthy, M. 1999. Effects of competition on natal dispersal distance. Ecological Modelling **114**:305-310.
- Moilanen, A., and I. Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. Ecology **79**:2503-2515.

- Mortensen, J. L., and J. M. Reed. 2016. Population Viability and Vital Rate Sensitivity of an Endangered Avian Cooperative Breeder, the White-Breasted Thrasher (Ramphocinclus brachyurus). PLoS One **11**:e0148928.
- Olsen, M. T., L. W. Andersen, R. Dietz, J. Teilmann, T. Härkönen, and H. R. Siegismund. 2014. Integrating genetic data and population viability analyses for the identification of harbour seal (Phoca vitulina) populations and management units. Molecular ecology 23:815-831.
- Royle, J. A., R. B. Chandler, K. D. Gazenski, and T. A. Graves. 2013. Spatial capture-recapture models for jointly estimating population density and landscape connectivity. Ecology 94:287-294.
- Sarre, S., G. T. Smith, and J. A. Meyers. 1995. Persistence of two species of gecko (Oedura reticulata and Gehyra variegata) in remnant habitat. Biological Conservation **71**:25-33.
- Schtickzelle, N., G. Mennechez, and M. Baguette. 2006. Dispersal depression with habitat fragmentation in the bog fritillary butterfly. Ecology **87**:1057-1065.
- Spear, S. F., N. Balkenhol, M. J. FORTIN, B. H. McRae, and K. Scribner. 2010. Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. Molecular ecology 19:3576-3591.
- Stamps, J. 1991. The effect of conspecifics on habitat selection in territorial species. Behavioral Ecology and Sociobiology 28:29-36.
- Stamps, J. A., V. Krishnan, and M. L. Reid. 2005. Search costs and habitat selection by dispersers. Ecology 86:510-518.
- Stow, A., P. Sunnucks, D. Briscoe, and M. Gardner. 2001. The impact of habitat fragmentation on dispersal of Cunningham's skink (Egernia cunninghami): evidence from allelic and genotypic analyses of microsatellites. Molecular ecology 10:867-878.

- Sutherland, C., D. A. Elston, and X. Lambin. 2012. Multi-scale processes in metapopulations: contributions of stage structure, rescue effect, and correlated extinctions. Ecology 93:2465-2473.
- Sutherland, C., D. A. Elston, and X. Lambin. 2014. A demographic, spatially explicit patch occupancy model of metapopulation dynamics and persistence. Ecology **95**:3149-3160.
- Thomas, C. D. 2000. Dispersal and extinction in fragmented landscapes. Proceedings of the Royal Society of London B: Biological Sciences **267**:139-145.
- Tischendorf, L., and L. Fahrig. 2001. On the use of connectivity measures in spatial ecology. A reply. Oikos **95**:152-155.
- USFWS. 2007. Chiricahua leopard frog (Rana chiricahuensis) recovery plan. Technical report, U.S. Fish and Wildlife Service, Albuquerque, NM.
- Wahlberg, N., T. Klemetti, and I. Hanski. 2002. Dynamic populations in a dynamic landscape: the metapopulation structure of the marsh fritillary butterfly. Ecography **25**:224-232.
- Walls, S. C., W. J. Barichivich, and M. E. Brown. 2013. Drought, deluge and declines: the impact of precipitation extremes on amphibians in a changing climate. Biology 2:399-418.
- Welch, N. E., and J. A. MacMahon. 2005. Identifying habitat variables important to the rare Columbia spotted frog in Utah (USA): an information-theoretic approach. Conservation biology 19:473-481.
- Wiens, J. A. 1997. Metapopulation Dynamics and Landscape Ecology. Pages 43-62 *in* I. Hanski,Gilpin, M. E., editor. Metapopulation biology: ecology, genetics, and evolution.Academic Press, San Diego, California, USA.

CHAPTER 2

INCREASING CONNECTIVITY BETWEEN METAPOPULATION ECOLOGY AND LANDSCAPE ECOLOGY¹

¹ Howell, P.E., Muths, E., Hossack, B.R., Sigafus, B.H., Chandler, R.B. 2017. *Ecology*. Reprinted here with permission of publisher.

<u>Abstract</u>

Metapopulation ecology and landscape ecology aim to understand how spatial structure influences ecological processes, yet these disciplines address the problem using fundamentally different modeling approaches. Metapopulation models describe how the spatial distribution of patches affects colonization and extinction, but often do not account for heterogeneity in the landscape between patches. Models in landscape ecology use detailed descriptions of landscape structure, but often without considering colonization and extinction dynamics. We present a novel spatially-explicit modeling framework for narrowing the divide between these disciplines to advance understanding of the effects of landscape structure on metapopulation dynamics. Unlike previous efforts, this framework allows for statistical inference on landscape resistance to colonization using empirical data. We demonstrate the approach using 11 years of data on a threatened amphibian in a desert ecosystem. Occupancy data for *Lithobates chiricahuensis* (Chiricahua leopard frog) were collected on the Buenos Aires National Wildlife Refuge (BANWR), Arizona, USA from 2007-2017 following a reintroduction in 2003. Results indicated that colonization dynamics were influenced by both patch characteristics and landscape structure. Landscape resistance increased with increasing elevation and distance to the nearest streambed. Colonization rate was also influenced by patch quality, with semi-permanent and permanent ponds contributing substantially more to the colonization of neighboring ponds relative to intermittent ponds. Ponds that only hold water intermittently also had the highest extinction rate. Our modeling framework can be widely applied to understand metapopulation dynamics in complex landscapes, particularly in systems in which the environment between habitat patches influences the colonization process.

Introduction

"...connectivity is a concept and a term that is shared between two ecological disciplines – landscape ecology and metapopulation ecology. The two disciplines measure connectivity at different scales, landscape and patch scale respectively, and use these measures in different ways. Yet, the assumed underlying process – movement of organisms across landscapes – is the same." (Tischendorf and Fahrig 2001)

"Unfortunately, despite parallel interests, landscape ecology... and metapopulation ecology... remain largely separate disciplines..." (Moilanen and Hanski 2001)

Landscape ecology and metapopulation ecology have been described as distinct disciplines that use different approaches to address similar questions about the effects of spatial structure on ecological processes (Hanski and Gilpin 1991; Wiens 1997; Moilanen and Hanski 2001; With 2004). Both branches of ecology aim to understand how habitat fragmentation affects population dynamics and viability, but they differ in their ontogeny and emphasis on the characterization and relative influence of landscape structure (Hanski and Gilpin 1991; Wiens 1997; Moilanen and Hanski 2001; With 2004). Although several authorities have anticipated and advocated for a more comprehensive union of landscape ecology and metapopulation ecology (Hanski and Gilpin 1991; Wiens 1997; With 2004), the two disciplines have not been fully integrated, hindering a synthetic understanding of the role of landscape structure in spatio-temporal population dynamics (Baguette et al. 2013; Driscoll et al. 2013).

The metapopulation approach has a rich theoretical history rooted in a patch-based perspective in which a system is described in terms of the proportion of patches occupied by a

species (Levins 1970; Hanski and Gilpin 1991; Hanski and Simberloff 1997; Hanski 1999; Hanski and Gaggiotti 2004). In the metapopulation context a patch refers to the discrete habitat unit within which a semi-autonomous subpopulation occurs. Early theoretical metapopulation models considered space implicitly (Hanski and Simberloff 1997), but an interest in describing processes such as distance-based colonization and spatially-correlated extinction led to the development of spatially realistic metapopulation theory (Hanski and Ovaskainen 2003). One important concept that arose from spatially realistic metapopulation theory was 'connectivity', defined by the degree to which a patch was isolated from other patches in terms of Euclidean distance (Hanski 1999). Several models that grew out of spatially realistic metapopulation theory, including the incidence function model allowed for statistical inference in some scenarios, which allowed for a powerful way of confronting theoretical predictions with empirical data (Moilanen and Hanski 1998).

In contrast to metapopulation ecology, the field of landscape ecology was catalyzed by efforts to quantify landscape structure and its effects on ecological processes (Turner 1989). In landscape ecology, the focus is on discontinuities in the environment, rather than disjunct aggregations of individuals, that correspond to suitable habitat for the species under consideration. Landscape ecology has advanced knowledge of how population dynamics are influenced by landscape features such as patch edges or boundaries (Schneider-Maunoury et al. 2016), landscape context (Wiens et al. 1993) and habitat corridors (e.g., (Wiens 1997; With 2004). One of the major contributions of landscape ecology is a body of theory proposing that connectivity is defined not by Euclidean distance, but by functional distance determined by the way in which organisms move in response to landscape structure (Wiens et al. 1993). Landscape ecologists have developed innovative non-Euclidean distance metrics for quantifying landscape

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connectivity, such as landscape resistance based on cost-weighted distance functions governed by coefficients describing the degree to which landscape features affect movement (McRae and Beier 2007) and graph theoretic approaches largely rooted in metapopulation theory (Urban and Keitt 2001). One technical challenge facing connectivity modeling is estimating the coefficients that determine the resistance surfaces. Frequently, research in landscape ecology has relied heavily on expert opinion (Spear et al. 2010; Graves et al. 2013; Peterman et al. 2014) and other ad hoc methods to choose, rather than formally estimate, resistance coefficients. Recent approaches have demonstrated how resistance coefficients can be estimated using telemetry or capture-recapture data (Graves et al. 2013; Hanks and Hooten 2013; Royle et al. 2013; Sutherland et al. 2015; Zeller et al. 2015), but not in the context of understanding metapopulation dynamics in complex landscapes.

One of the first attempts to unify concepts from metapopulation ecology and landscape ecology was made by Moilanen and Hanski (1998). However, their modified distance metric assumes that animals move along straight lines between patches, and it can only be calculated in very simple landscapes composed of a small number of habitat types (Baguette et al. 2013). As With (2004) explained in her reflection on metapopulation ecology, there is still a need for spatially realistic metapopulation models to take a more biologically realistic, process-based approach to evaluate the effect of the landscape matrix on colonization (Hanski and Gaggiotti 2004). A process based approach that takes on a species perspective of connectivity, should allow for non-linear movement with habitat-specific resistance coefficients in heterogeneous landscapes that are estimated rather than assigned by expert opinion (Schooley and Branch 2009; Cosentino et al. 2011). As other authors have pointed out, ignoring the effects of the spatial structure of the landscape matrix, particularly when landscapes are complex, heterogeneous, and the remaining amount of suitable habitat is low, negatively affects the ability of patch based models to predict colonization and recolonization rates (e.g., (Bender and Fahrig 2005).

We present an approach for further unifying metapopulation ecology and landscape ecology by combining some of the major concepts and contributions from both fields into a modeling framework for understanding the role of landscape structure on metapopulation dynamics. Our modeling framework is founded on stochastic, spatially-realistic metapopulation theory, and recent statistical developments that have made it possible to fit models to empirical data (Hanski 2001; MacKenzie et al. 2003; Risk et al. 2011; Sutherland et al. 2012; Sutherland et al. 2014; Chandler et al. 2015; Heard et al. 2015). Unlike existing approaches that model colonization as a function of Euclidean distance, we use a least cost path approach and present a method for directly estimating the resistance coefficients. We demonstrate how our model can be used to quantify metapopulation colonization and extinction dynamics using 11 years of occupancy data for *Lithobates chiricahuensis* (Chiricahua leopard frog), an amphibian species listed as threatened under the US Endangered Species Act (USFWS 2007).

Methods: Spatial metapopulation model including landscape resistance:

To understand the effects of landscape features on connectivity, we extended the hierarchical model of Chandler et al. (2015), which treats colonization probability as a function of Euclidean distance among patches. The model consists of three components: a model for patch occupancy in the initial time period, a model for occupancy dynamics in subsequent years, and a model for detection conditional on occupancy. Occupancy probability during the initial time period ($\psi_{i,1}$; i=1, ..., M) can be modeled as a logit-linear function of patch-level covariates. Importantly, *M* is the number of patches within the entire metapopulation network, not the number of sampled patches. While data need only be collected at a subset of patches, the entire metapopulation

network must be modeled because a focal patch can be colonized by individuals from any other patch, not just the patches in the sample.

The ecological process model describes patch occupancy $(z_{i,k})$ in years k>1 as a function of colonization (γ) and extinction (ε) dynamics:

$$\psi_{i,k} = \gamma_{i,k-1} (1 - z_{i,k-1}) + (1 - \varepsilon_{i,k-1} (1 - \gamma_{i,k-1}))(z_{i,k-1})$$

$$z_{i,k} \sim \text{Bernoulli}(\psi_{i,k})$$
(1)

such that an unoccupied patch *i* is colonized in year *k* with probability $\gamma_{i,k-1}$, and an occupied patch becomes extinct with probability $\varepsilon_{i,k-1}(1 - \gamma_{i,k-1})$, which accounts for the rescue effect (Hanski 1999). Spatially-realistic metapopulation models regard colonization probability as a function of the occupancy state of every other patch in the metapopulation network and the distances among patches. One formulation uses a Gaussian kernel to describe the pairwise probabilities of patch *i* being colonized by at least one disperser from patch *m*:

$$\rho_{i,m,k-1} = \rho_0 \exp(-d_{i,m}^2 / 2\sigma^2)$$
(2)

where ρ_0 is the baseline colonization probability, $d_{i,m}$ is the Euclidean distance between patches *i* and *m*, and σ is the scale parameter that determines the rate of decay in colonization probability as a function of distance. The cumulative probability of a colonization event is given by:

$$\gamma_{i,k-1} = 1 - \{\prod_{m=1}^{M} 1 - \rho_{i,m,k-1} z_{m,k-1}\}$$
(3)

Similar to Chandler et al. (2015), patch-level extinction rate can be modeled as a logit-linear function of patch-level habitat features. This is a spatially explicit model of the colonization and extinction processes, but as with previous metapopulation models, it is based on Euclidean distance and does not explicitly account for the influence of landscape structure.

Drawing on contributions from landscape ecology, we extended the biological realism of the model by replacing Euclidean distance with a more functional connectivity measure: least cost distance. A least cost path (LCP) is defined as the path with the lowest cost-weighted distance between two locations (Dijkstra 1959). Least cost paths can be modeled by imposing a grid over the spatial region of interest such that landscape attributes and a set of coefficients that determine the resistance of each landscape attribute can be associated with each grid cell. The cost-weighted distance between any two locations is the accumulation of costs of moving from a focal to adjacent cell along the entire path between two locations.

To explicitly estimate resistance coefficients in a metapopulation context, we begin with a model describing the effects of one or more landscape covariates, $\mathbf{c}(\mathbf{x})$, on the cost of moving between adjacent cells *x* and *x'*. Covariates can be continuous (e.g., percent forested area) or discrete (e.g., specific landcover classes) variables. In the case of a single covariate, the cost function is:

$$cost(x, x') = \frac{\exp(\alpha_1 * c_1(x)) + \exp(\alpha_1 * c_1(x)))}{2}$$
(4)

where α_1 is the resistance coefficient. Conditional on the cost model, cost-weighted distance between patches *i* and *m* ($d_{i,m}^{cost}$) can be computed by summing the products of costs along a path defined by line segments $x_1, x_2, ..., x_L$ and the Euclidean distance among patches:

$$d_{i,m}^{cost} = \sum_{l=1}^{L-1} cost(x_l, x_{l+1}) \|x_l - x_{l+1}\|$$
(5)

where $||x_l - x_{l+1}||$ is the Euclidean distance between patches *i* and *m*. The LCP is the path with the lowest $d_{i,m}^{\text{cost}}$ among all possible paths between the two locations, and the length of the leastcost path is denoted by $d_{i,m}^{\text{LCP}}$. By replacing this alternative, more process-based distance metric into Eq 2, we can more formally unite principles (i.e., connectivity and colonization dynamics) of landscape ecology and metapopulation ecology in a single hierarchical model that can be fitted to data from empirical studies. Information about α_1 and hence $d_{i,m}^{LCP}$ comes from variation in colonization events among sites with different intervening landscapes. As a technical matter, covariates should be transformed to ensure that the cost function crosses 1 for any value of α_1 . This can be accomplished by centering or standardizing continuous covariates, and by coding categorical variables with Q levels as Q-1 dummy variables. Such transformations facilitate estimation and ensure that cost distance can be interpreted relative to Euclidean distance.

To draw inferences from data collected at a subset of patches where the species may go undetected when present, we model the observed detection/non-detection data $(y_{i,j,k})$ conditional on the latent state of the system:

$$y_{i,j,k} \sim \text{Bernoulli}(p_{i,j,k} \times z_{i,k})$$
 (6)

where $p_{i,j,k}$ is the probability of detecting a species that is present at patch *i* during primary sampling occasion *k* and secondary sampling occasion *j*. This model assumes that colonization and extinction occur between, but not within, primary occasions. Variation in detection probability can be modeled as a logit-linear function of covariates or random effects. CASE STUDY: CHIRICAHUA LEOPARD FROG: Chiricahua leopard frogs occur in the southwestern United States and northern Mexico (USFWS 2007). One of the largest metapopulations is located in the Altar Valley of Arizona, which includes the Buenos Aires National Wildlife Refuge (BANWR, Figure 2.1) where this research was conducted. The Altar Valley is primarily semiarid grassland desert with mesquite trees (*Prosopis spp.*), riparian/wetland areas, and foothills (Bezy 2007). Within the Altar Valley there is moderate spatial variation in topography, with elevation ranging between 784 and 2,352m. Annual average rainfall is approximately 413mm, with most rainfall occurring during the monsoon season (late June - late September) (Bezy 2007). Summer temperature and precipitation vary across BANWR, with lower elevations characterized by lower precipitation and higher temperatures while higher elevations are characterized by higher precipitation and lower temperatures (Whittaker 1975). Most natural amphibian habitat has been lost due to human alteration of the landscape and suitable habitat is now almost exclusively stock tanks (APPENDIX A). Stock tanks (hereafter referred to as patches) are small (mean=0.15ha, range=0.0084-7.7ha), earthen, man-made water bodies originally built to provide water for livestock (Jarchow et al. 2016).

In 2001, Chiricahua leopard frogs were extirpated within BANWR, most likely due to drought and the spread of non-native *Lithobates catesbeianus* (American bullfrog) (Jarchow et al. 2016). After eradication of bullfrogs from the refuge, Chiricahua leopard frogs were reintroduced to three patches in 2003 (Jarchow et al. 2016). A monitoring program was established in 2007 and since then, leopard frogs have expanded from the initial reintroduction sites (Jarchow et al. 2016), demonstrating their ability to navigate the terrestrial matrix and successfully colonize suitable habitat patches (Chandler et al. 2015).

DATA COLLECTION AND HYPOTHESES: In total, 47 patches were surveyed on BANWR and adjoining State Trust land to the west, over a period of 11 years (2007-2017), with a maximum of 44 patches surveyed in a given year (i.e., 47 unique patches of M=274 available patches). At each patch in each year, two or three visual surveys were conducted in June, prior to the monsoon rains that often trigger dispersal. Binary data were recorded indicating if at least one individual was detected. Because surveys were conducted during the pre-monsoon season, prior to the emergence of most metamorphs and juveniles, the majority of detections were of adults. Patch hydroperiod was expected to influence colonization and extinction dynamics, so each

patch in the metapopulation was characterized as permanent (PERM; holds water every year, all year), semi-permanent (SEMI; holds water each year, but only part of the year), or intermittent (INTER; holds water during some years, only part of the year).

Because leopard frogs were reintroduced into three patches, the initial occupancy status for each patch $z_{i,1}$ was known and used as data rather than regarded as a latent variable to be estimated. Local extinction probability $\varepsilon_{i,k-1}$ and the baseline colonization probability ρ_{0_i} were modeled as hydroperiod-specific. Detection probability was modeled as a logit-linear function of wind speed and ambient temperature.

We addressed several hypotheses regarding the influence of landscape features of the intervening terrestrial matrix and patch-specific characteristics on leopard frog colonization and extinction dynamics. Intermittent stream beds between patches (landscape-level habitat characteristic) were hypothesized to increase colonization probability because of the potential for moisture in streambeds to decrease frog desiccation rates and increase the probability of successful colonization (i.e., reaching a habitat patch; Bull 2009, Westgate et al. 2012). Spatial information on intermittent stream beds was obtained from the National Hydrography Dataset and used to calculate the distance to nearest streambed for each pixel across our study area. Elevation was hypothesized to impede movement and reduce colonization (landscape-level habitat characteristic) because elevation is a proxy for ruggedness (correlation with slope, r=0.70), and because soil moisture is lower at higher elevations, effectively limiting frog rehydration rates (Tracy 1976). An elevation dataset was obtained from the National Elevation Dataset digital elevation model (DEM). Both spatial data layers were standardized (i.e., mean zero and unit variance) and reclassified to a pixel size of 900m x 900m to improve computational efficiency without sacrificing predominant variation in the landscape. We fit four models that

differed with respect to the covariates hypothesized to influence landscape resistance (i.e., no covariate, elevation, distance to nearest streambed, and elevation + distance to nearest streambed). Pearson correlation between elevation and streambed rasters was 0.19.

For inference, we used Bayesian methods and a custom Metropolis-within-Gibbs sampler that used the R package 'gdistance' to compute least-cost paths (van Etten 2012). We sampled from posterior distributions using 3 Markov chains each of length 15,000, and we discarded the first 1000 iterations as burnin. We compared models using effect sizes, credible intervals, and posterior deviance statistics, but other Bayesian model selection techniques could have been considered (Hooten and Hobbs 2015). Vague priors were used for all parameters (see APPENDIX B). R code is provided in the online version of this manuscript in APPENDIX C. A description of the joint posterior and full conditional distributions are provided in APPENDIX D. **Results:** We detected frogs at 19 of the 47 sampled ponds over the 11 year survey period. The observed occupancy rate provided evidence of initial metapopulation expansion after reintroduction into three ponds in 2003 (seven ponds occupied in 2011), followed by contraction (three ponds occupied in 2012) and expansion again in more recent years (eight ponds occupied in 2017). We detected frogs at ponds as far as 15.4 km from the reintroduction locations.

Convergence diagnostics (trace plots) for all parameters for our model with elevation influencing landscape resistance are included in APPENDIX E. Landscape resistance, and hence colonization probability, were affected by landscape structure. Landscape resistance increased as elevation among patches increased (mean α_1 =0.94, 95% CI [0.20, 1.84], Table 2.1). There was a slightly weaker effect of distance to nearest streambed (mean α_1 =0.79, 95% CI [0.11, 1.36]), indicating that resistance was lower closer to streams than further away. When we included both elevation and distance to nearest streambed, the effects of both covariates decreased and there was no decrease in the deviance, suggesting that the simpler models were more parsimonious (APPENDIX F). The influence of elevation on colonization can be seen in the posterior distribution of the least cost path between pairs of patches (Figure 2.2 A). The least cost path with the highest posterior probability bends around the mountains (Figure 2.2 A). The effect of cost distance on colonization probability along each path is illustrated by the fading shades of grey (Figure 2.2).

In addition to inference on the effects of landscape structure on connectivity and colonization probabilities, our model yielded estimates of the influence of patch-specific habitat characteristics on metapopulation dynamics. Local extinction probability was influenced by patch-specific covariates. Patches that hold water permanently had much lower extinction risk than patches that hold water semi-permanently or intermittently (Table 2.1). The probability of a focal patch being colonized by any neighbor (baseline colonization probability) was influenced by patch hydroperiod. Semi-permanent (mean γ_2 = 0.23, 95% CI [0.09, 0.41]) and permanent patches (mean γ_3 = 0.22, 95% CI [0.05, 0.67]) had a much greater contribution to focal patch colonization probability relative to intermittent patches (mean γ_1 = 0.02, 95% CI [0.01, 0.05]), Table 2.1).

All four of our models yielded similar predictions about spatio-temporal occupancy dynamics, and there were minimal differences in the annual number of occupied patches when comparing a model with landscape resistance to a model without landscape resistance (Table 2.1, APPENDIX F). Our model including elevation effects on landscape resistance predicted lower mean number of occupied patches relative to our model without including landscape structure, however the credible intervals overlapped (Table 2.1, APPENDIX F). The proportion of occupied patches increased rapidly following the reintroduction event in 2003 (Figure 2.3, Table
2.1). Expansion occurred primarily within the low to intermediate elevations in the study area (Figure 2.1 and Figure 2.3), and disproportionately into permanent and semi-permanent ponds.

Detection probability was not affected strongly by either wind speed or air temperature (Table 2.1). The probability of detecting leopard frogs after three visits ranged from 0.94-0.99, and thus failure to account for imperfect detection would have resulted in only a small amount of upward bias in estimates of extinction probability and downward bias in estimates of colonization probability. The more important reason for modeling the latent ecological process at all patches in the metapopulation network, and not just in the sampled patches, was that it allowed us to account for colonization by emigrants from unsampled patches. Failure to do so would underestimate patch-specific and metapopulation level connectivity.

Discussion: The model we developed represents another step forward in efforts to unify metapopulation and landscape ecology. It can be used to directly model the processes governing spatio-temporal variation in occupancy in terms of both patch-level habitat variables and landscape structure. In addition, it is possible to estimate least cost paths between any two patches, and produce resistance surfaces for entire landscapes, while accounting for uncertainty arising from sampling and observation error. Our approach addresses some of landscape ecologists' criticisms of metapopulation ecology (Wiens 1997; With 2004) by integrating a more process-based characterization of the matrix (i.e., least cost path modeling) when estimating the influence of landscape structure on colonization probability. In accordance with metapopulation theory, our model describes how colonization and extinction processes determine spatial and temporal variation in occupancy dynamics (Hanski and Gaggiotti 2004).

Ecological theory predicts, and empirical evidence supports the concept that matrix composition and configuration (Ricketts 2001, Driscoll et al. 2013) are important factors

influencing connectivity and population dynamics. The modeling framework we presented makes it possible to test theoretical predictions regarding the effects of the landscape matrix on metapopulation colonization and extinction dynamics. We found evidence in our Chiricahua leopard frog system that colonization rate was influenced by elevation among patches. Leopard frogs appear to avoid routes that go through high elevations, instead favoring areas of lower elevation, even if the Euclidean distance is greater. Elevation can be a good proxy for climatic conditions (e.g., temperature, rainfall) and habitat features (e.g., ruggedness, soil moisture) that are important determinants of colonization rate (Fan and Van den Dool 2008). Colonization rate was also influenced by the distribution of streambeds, providing evidence that dispersing leopard frogs may preferentially move through wetter areas where dehydration rates are relatively low.

In addition to providing more unification between two ecological disciplines, our model increases the potential for using ecological theory in applied contexts. Resistance surfaces are frequently used as the basis of planning efforts to increase connectivity, but until now, were largely based on expert opinion (Spear et al. 2010; Zeller et al. 2012) and were rarely accompanied by confidence intervals or other measures of uncertainty. Recently, methods have been developed for formally estimating resistance coefficients using capture-recapture, landscape genetic or telemetry data (Graves et al. 2013; Hanks and Hooten 2013; Royle et al. 2013; Sutherland et al. 2015; Zeller et al. 2015), but not in the context of understanding metapopulation dynamics. In heterogeneous systems composed of complex mosaic landscapes, particularly when suitable habitat represents a relatively small fraction of the landscape (Hanski and Gaggiotti 2004), modeling approaches based on simple Euclidean distance or simplistic measures of landscape structure, are likely to overestimate pairwise colonization probability. A "mosaic management" (Wiens 1997) approach may be most effective, whereby the landscape context in

which patches are arranged and the influence of matrix structure on metapopulation dynamics is considered during conservation decision making.

In addition to quantifying the influence of the landscape matrix and patch quality on metapopulation dynamics, we used our modeling framework to test predictions regarding the effect of variation in patch quality on colonization and local, patch-level extinction rate. We found evidence that intermittent ponds contribute very little to the colonization of neighboring ponds, relative to semi-permanent or permanent ponds. We also found evidence that annual extinction risk was influenced by patch-level characteristics, with local extinction probability decreasing with increasing hydroperiod. Taken together, these results suggest that intermittent ponds contribute very little to metapopulation-level viability, even if they are located near other occupied patches. In spite of an apparent dependence on permanent water bodies, such wetlands were historically rare in our study system and are prone to invasion by non-native species such as bullfrogs, which require permanent hydroperiod habitat to persist (Rosen et al. 1994). Metapopulation viability will therefore require continued invasive species management of ponds surrounding BANWR that could act as sources of invaders. These actions include bullfrog removal and the maintenance of ephemeral wetlands (e.g., semi-permanent ponds) resembling more natural conditions.

The issue of scale is ubiquitous in landscape ecology, with estimation of landscape resistance being no exception. For computational efficiency, we began by using a resolution (pixel area) of 900 x 900m for our raster covariates (elevation and distance to nearest streambed). Nevertheless, we were still able to document evidence for the effect of landscape structure on landscape resistance (Table 2.1, APPENDIX F). We expected the effect of both landscape features on resistance would likely increase with increasing resolution, and so we subsequently

investigated several other raster resolutions (720x720m, 360x260m; APPENDIX G). However, the credible intervals for the effect of landscape structure on landscape resistance overlapped substantially for all resolutions that we considered, so we included results from our original analysis based on 900x900m resolution rasters (APPENDIX G). In general, researchers should be cautious when generating raster covariates, particularly with rare and/or linear landscape features.

Our work draws on contributions from both metapopulation ecology and landscape ecology and hopefully will assist in efforts to unite these fields. In particular, our modeling framework provides a way to explicitly estimate matrix effects on connectivity and metapopulation colonization dynamics using empirical data. The ability to do so opens up opportunities for testing theoretical predictions (e.g., matrix effects on recolonization rates) and making more informed conservation decisions (e.g., managing the matrix to decrease patch isolation). In addition to the future avenues of research mentioned already, another potential extension of our work would be to make use of an abundance-based and/or stage-structured formulation (Sutherland et al. 2014). Given sufficient data, our model could be extended to estimate patch-specific and metapopulation-level abundance over time and space. Doing so would allow for researchers to test predictions regarding the effect of heterogeneity in the landscape matrix on density-dependent emigration and immigration (Hanski and Gaggiotti 2004). Future extensions of our work could also integrate individual-based movement models developed from tracking animals moving through the matrix (Harrison et al. 2011) or through experimental studies of animal movement (Stevens et al. 2005). Data collected on individual movement behavior (e.g., distance, direction, rate) through different habitat types could improve precision in our parameter estimation (Harrison et al. 2011), predictability regarding population

persistence (Aben et al. 2014) and provide a more mechanistic understanding of the effect landscape structure has on the process of colonization. Each of these extensions would allow for a more comprehensive understanding of the effects of spatial structure on the dynamics of metapopulations in complex landscapes.

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Literature Cited

- Aben, J., D. Strubbe, F. Adriaensen, S. C. Palmer, J. M. Travis, L. Lens, and E. Matthysen. 2014. Simple individual-based models effectively represent Afrotropical forest bird movement in complex landscapes. Journal of Applied Ecology 51:693-702.
- Baguette, M., S. Blanchet, D. Legrand, V. M. Stevens, and C. Turlure. 2013. Individual dispersal, landscape connectivity and ecological networks. Biological Reviews 88:310-326.
- Bender, D. J., and L. Fahrig. 2005. Matrix structure obscures the relationship between interpatch movement and patch size and isolation. Ecology 86:1023-1033.
- Bezy, J. H., Charles, F.; Bahre, Conrad J. 2007, Buenos Aires National Wildlife Refuge, Arizona, University of Arizona.
- Chandler, R. B., E. Muths, B. H. Sigafus, C. R. Schwalbe, C. J. Jarchow, and B. R. Hossack.
 2015. Spatial occupancy models for predicting metapopulation dynamics and viability following reintroduction. Journal of Applied Ecology 52:1325-1333.
- Cosentino, B. J., R. L. Schooley, and C. A. Phillips. 2011. Spatial connectivity moderates the effect of predatory fish on salamander metapopulation dynamics. Ecosphere 2:1-14.
- Dijkstra, E. W. 1959. A note on two problems in connexion with graphs. Numerische mathematik 1:269-271.
- Driscoll, D. A., S. C. Banks, P. S. Barton, D. B. Lindenmayer, and A. L. Smith. 2013. Conceptual domain of the matrix in fragmented landscapes. Trends in ecology & evolution 28:605-613.
- Fan, Y., and H. Van den Dool. 2008. A global monthly land surface air temperature analysis for 1948–present. Journal of Geophysical Research: Atmospheres 113.

- Graves, T. A., P. Beier, and J. A. Royle. 2013. Current approaches using genetic distances produce poor estimates of landscape resistance to interindividual dispersal. Molecular ecology 22:3888-3903.
- Hanks, E. M., and M. B. Hooten. 2013. Circuit theory and model-based inference for landscape connectivity. Journal of the American Statistical Association 108:22-33.

Hanski, I. 1999, Metapopulation ecology, v. 312, Oxford University Press Oxford.

- —. 2001. Spatially realistic theory of metapopulation ecology. Naturwissenschaften 88:372-381.
- Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain.Biological journal of the Linnean Society 42:3-16.
- Hanski, I., and O. Ovaskainen. 2003. Metapopulation theory for fragmented landscapes. Theoretical population biology 64:119-127.
- Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation biology. Metapopulation Biology, Academic Press, San Diego, California:5.
- Hanski, I. A., and O. E. Gaggiotti. 2004, Ecology, genetics and evolution of metapopulations, Academic Press.
- Harrison, P. J., I. Hanski, and O. Ovaskainen. 2011. Bayesian state-space modeling of metapopulation dynamics in the Glanville fritillary butterfly. Ecological Monographs 81:581-598.
- Heard, G. W., C. D. Thomas, J. A. Hodgson, M. P. Scroggie, D. S. Ramsey, and N. Clemann.
 2015. Refugia and connectivity sustain amphibian metapopulations afflicted by disease.
 Ecol Lett 18:853-863.

Jarchow, C. J., B. R. Hossack, B. H. Sigafus, C. R. Schwalbe, and E. Muths. 2016. Modeling habitat connectivity to inform reintroductions: a case study with the Chiricahua Leopard Frog. Journal of Herpetology.

Levins, R. 1970. Extinction. Lectures on mathematics in the life sciences 2:75-107.

- MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200-2207.
- McRae, B. H., and P. Beier. 2007. Circuit theory predicts gene flow in plant and animal populations. Proceedings of the National Academy of Sciences 104:19885-19890.
- Moilanen, A., and I. Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. Ecology 79:2503-2515.
- —. 2001. On the use of connectivity measures in spatial ecology. Oikos 95:147-151.
- Peterman, W. E., G. M. Connette, R. D. Semlitsch, and L. S. Eggert. 2014. Ecological resistance surfaces predict fine-scale genetic differentiation in a terrestrial woodland salamander. Molecular ecology 23:2402-2413.
- Risk, B. B., P. De Valpine, and S. R. Beissinger. 2011. A robust-design formulation of the incidence function model of metapopulation dynamics applied to two species of rails. Ecology 92:462-474.
- Rosen, P. C., C. R. Schwalbe, D. Parizek, P. A. Holm, and C. H. Lowe. 1994. Introduced aquatic vertebrates in the Chiricahua region: Effects of declining native ranid frogs. Biodiversity and management of the Madrean Archipelago: the sky islands of the southwestern United States and northwestern Mexico:251-261.

- Royle, J. A., R. B. Chandler, K. D. Gazenski, and T. A. Graves. 2013. Spatial capture-recapture models for jointly estimating population density and landscape connectivity. Ecology 94:287-294.
- Schneider-Maunoury, L., V. Lefebvre, R. M. Ewers, G. F. Medina-Rangel, C. A. Peres, E. Somarriba, N. Urbina-Cardona et al. 2016. Abundance signals of amphibians and reptiles indicate strong edge effects in Neotropical fragmented forest landscapes. Biological Conservation 200:207-215.
- Schooley, R. L., and L. C. Branch. 2009. Enhancing the area–isolation paradigm: habitat heterogeneity and metapopulation dynamics of a rare wetland mammal. Ecological Applications 19:1708-1722.
- Spear, S. F., N. Balkenhol, M. J. FORTIN, B. H. McRae, and K. Scribner. 2010. Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. Molecular ecology 19:3576-3591.
- Stevens, V. M., E. Polus, R. A. Wesselingh, N. Schtickzelle, and M. Baguette. 2005. Quantifying functional connectivity: experimental evidence for patch-specific resistance in the Natterjack toad (Bufo calamita). Landscape ecology 19:829-842.
- Sutherland, C., D. A. Elston, and X. Lambin. 2012. Multi-scale processes in metapopulations: contributions of stage structure, rescue effect, and correlated extinctions. Ecology 93:2465-2473.
- Sutherland, C., D. A. Elston, and X. Lambin. 2014. A demographic, spatially explicit patch occupancy model of metapopulation dynamics and persistence. Ecology 95:3149-3160.

- Sutherland, C., A. K. Fuller, and J. A. Royle. 2015. Modelling non-Euclidean movement and landscape connectivity in highly structured ecological networks. Methods in Ecology and Evolution 6:169-177.
- Tischendorf, L., and L. Fahrig. 2001. On the use of connectivity measures in spatial ecology. A reply. Oikos 95:152-155.
- Tracy, C. R. 1976. A model of the dynamic exchanges of water and energy between a terrestrial amphibian and its environment. Ecological Monographs:293-326.
- Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. Annual review of ecology and systematics:171-197.
- Urban, D., and T. Keitt. 2001. Landscape connectivity: a graph-theoretic perspective. Ecology 82:1205-1218.
- USFWS. 2007. Chiricahua leopard frog (Rana chiricahuensis) recovery plan. Albuquerque, NM, Technical report, U.S. Fish and Wildlife Service.
- van Etten, J. 2012. gdistance: Distances and routes on geographical grids. R package version 1.1–4.
- Whittaker, R. H. N., W. A. 1975. Vegetation of the Santa Catalina Mountains, Arizona. V.Biomass, Production, and Diversity along the Elevation Gradient. Ecology 56:19.
- Wiens, J. A. 1997. Metapopulation Dynamics and Landscape Ecology, Pages 43-62 *in* I. Hanski,Gilpin, M. E., ed. Metapopulation biology: ecology, genetics, and evolution. San Diego,California, USA, Academic Press.
- Wiens, J. A., N. Chr, B. Van Horne, and R. A. Ims. 1993. Ecological mechanisms and landscape ecology. Oikos:369-380.

- With, K. 2004. Metapopulation Dynamics: Perspectives from Landscape Ecology *in* I. Hanski, and O. E. Gaggiotti, eds. Ecology, Genetics, and Evolution of Metapopulations. San Diego, California, Academic Press.
- Zeller, K. A., K. McGarigal, S. A. Cushman, P. Beier, T. W. Vickers, and W. M. Boyce. 2015. Using step and path selection functions for estimating resistance to movement: pumas as a case study. Landscape Ecology:1-17.
- Zeller, K. A., K. McGarigal, and A. R. Whiteley. 2012. Estimating landscape resistance to movement: a review. Landscape Ecology 27:777-797.

Table 2.1. Estimates of the posterior mean, standard deviation and 95% credible intervals for detection and occupancy parameters for our spatially explicit model of the influence of elevation on landscape resistance and metapopulation dynamics.

Parameter	Description	Mean	SD	2.5	97.5
sigma	Scale parameter of colonization function	2.52	0.69	1.48	4.16
gamma1	Baseline colonization probability at intermittent patches	0.02	0.01	0.01	0.05
gamma2	Baseline colonization probability at semi- permanent patches	0.23	0.08	0.09	0.41
gamma3	Baseline colonization probability at permanent patches	0.22	0.16	0.05	0.67
eps1	Extinction probability at intermittent patches	0.84	0.12	0.57	0.99
eps2	Extinction probability at semi-permanent patches	0.79	0.15	0.47	0.99
eps3	Extinction probability at permanent patches	0.15	0.13	0.02	0.55
beta0	Intercept of logit-linear detection model	2.07	0.27	1.57	2.62
beta1	Effect of temperature on logit(p)	0.29	0.36	-0.31	1.1
beta2	Effect of wind on logit(p)	-0.15	0.32	-0.78	0.47
alpha1	Linear effect of elevation on landscape resistance	0.94	0.44	0.2	1.88
z2003	Number of occupied patches in 2003	3	0	3	3
z2004	Number of occupied patches in 2004	4.22	1.26	2	7
z2005	Number of occupied patches in 2005	5.26	1.71	2	9
z2006	Number of occupied patches in 2006	6.31	1.94	3	11
z2007	Number of occupied patches in 2007	7.58	1.92	5	12
z2008	Number of occupied patches in 2008	9.41	2.2	6	15
z2009	Number of occupied patches in 2009	9.13	2.49	6	15
z2010	Number of occupied patches in 2010	9.65	2.59	6	16
z2011	Number of occupied patches in 2011	12.22	2.62	8	18
z2012	Number of occupied patches in 2012	10.18	2.7	6	16
z2013	Number of occupied patches in 2013	12.82	2.7	8	19
z2014	Number of occupied patches in 2014	16.26	2.73	12	23
z2015	Number of occupied patches in 2015	21.42	2.88	17	28
z2016	Number of occupied patches in 2016	18.26	3.25	13	26
z2017	Number of occupied patches in 2017	17	3.77	11	26
Deviance	Deviance	142.35	9.82	131.37	165.43



Figure 2.1. Potential breeding patches for *Lithobates chiricahuensis* (Chiricahua leopard frog) in the Altar Valley of Arizona. Black outline indicates the boundaries of the Buenos Aires National Wildlife Refuge (BANWR). Square symbols indicate permanent patches, triangles indicate intermittent patches, and pentagons indicate semi-permanent patches. Colored symbols indicate patches that are sampled annually and red indicates the three reintroduction patches. Dots within symbols indicate patches where leopard frogs were detected at least one time



Figure 2.2 A, B. Posterior distribution of the least cost path between two pairs of patches (red and blue circles) chosen to represent how both elevation and distance influence colonization probability. Each transparent path was computed from a sample of the posterior distribution of the resistance coefficient for elevation. The transparency of the line segments is proportional to colonization probability, which declines as cost distance from the focal patch (blue) increases. Black polygon indicates the boundary of the Buenos Aires National Wildlife Refuge (BANWR). Open circles indicate 274 potential breeding patches for *Lithobates chiricahuensis* (Chiricahua leopard frog). Elevation (m) across the study area is shown in the background of each figure.



Figure 2.3. The estimated spatiotemporal occupancy dynamics of *Lithobates chiricahuensis* (Chiricahua leopard frog) from 2003 to 2017 within the Altar Valley of Arizona. Large green dots are occupied patches and small black crosses are unoccupied patches. Estimates of patch occupancy are posterior modes. Cost (log scale) associated with each pixel (900x900m) based on elevation in each pixel and the mean resistance coefficient from our model is shown in the background of each figure.

CHAPTER 3

A STATISTICAL FRAMEWORK FOR MODELING DENSITY DEPENDENT

METAPOPULATION DYNAMICS 1

¹ Howell, P.E., Muths, E., Hossack, B.R., Sigafus, B.H., Chandler, R.B. To be submitted to *Ecology*.

<u>Abstract</u>

In metapopulations, dispersal and population growth rates are influenced by patch quality and local density. Recently developed spatial metapopulation models have made it possible to account for distance effects on dispersal, but these models typically focus on patch occupancy rather than abundance. This simplification makes it impossible to study demographic processes such as density-dependent population growth, emigration and immigration. Without being able to model demographic processes, it is difficult to quantify how changes in patch and landscape scale characteristics will influence metapopulation viability through changes in population growth rates and dispersal. Our objective was to develop an integrated abundance-based metapopulation model to draw inferences about spatiotemporal variation in density using count and presence-absence data. We applied the model to data from an 11-year study of the federallythreatened Chiricahua leopard frog (Lithobates chiricahuensis) in the Buenos Aires National Wildlife Refuge (BANWR), Arizona, USA. Our results indicate that pond-specific population growth was influenced by pond hydroperiod and density, such that permanent and semipermanent patches with low densities of adult frogs experienced the highest annual population growth. Emigration rate was not influenced by pond hydroperiod and immigration rate declined as the distance among patches increased. Metapopulation-level abundance increased until 2015, when it has appeared to stabilize around 1225 adult frogs (95% CI, 1001-1526). Our study extends existing statistical models of metapopulation dynamics by focusing on abundance and making it possible to test hypotheses regarding the influence of patch quality and density on local dynamics and colonization.

Introduction

Many populations exist as spatially-segregated subpopulations that persist through the movement of individuals from occupied, to vacant, but suitable patches. Metapopulation theory has provided a framework for predicting changes in occupancy and for understanding the underlying processes of colonization and extinction that affect occupancy dynamics (Hanski and Gilpin 1991). Early research in metapopulation ecology considered space implicitly and assumed suitable patches were homogeneous (Hanski and Gaggiotti 2004). These simplifying assumptions make it impossible to model processes such as connectivity or the influence of spatial variation in patch quality on metapopulation dynamics. The development of spatially-realistic metapopulation theory, makes it possible to consider hypotheses regarding the effect of variation in patch characteristics (e.g., patch area) and the spatial distribution of patches on colonization and extinction.

The majority of spatially-explicit metapopulation models arising from spatially-realistic metapopulation theory deal with quantifying spatio-temporal changes in occurrence (Hanski 1999). Traditionally the focus has been on distilling the processes of birth, death, immigration and emigration into patch extinction and inter-patch colonization (Hanski and Gaggiotti 2004). While trends in occurrence inform us about metapopulation persistence, abundance is a better predictor of extinction risk (Morris and Doak 2002, Payne et al. 2011). Not all patches within a metapopulation network are equivalent, and occupancy status alone may not accurately reflect the contribution of each patch to metapopulation persistence. Patches with a high number of expected migrants may be important for re-colonizing patches that become temporarily extinct, or colonizing new, vacant patches within the network. In addition, patches with large population sizes are less likely go extinct through stochastic processes that disproportionately affect small

populations (Lande 1993, Hedrick and Kalinowski 2000). In systems where metapopulation dynamics are less dependent on patch quality relative to demographic processes occurring within patches (Matthysen 1999), a focus on occurrence could result in inaccurate forecasts of metapopulation extinction risk.

In metapopulations, local dynamics and dispersal are likely influenced by patch quality and density (Hanski 1999). However, focusing on occurrence precludes testing hypotheses that assess the role of demographic processes occurring within patches. For example, survival or recruitment of new individuals into the population may be influenced by patch quality, including the density of conspecifics (Lambrechts et al. 2004). In this case, higher quality patches may contribute more potential migrants to colonize empty patches. Density may indicate favorable habitat conditions, in which case individuals would remain in high density patches or immigrate into high density patches (Stamps 1988). Alternatively, density may facilitate increased intraspecific competition relative to other patches in the metapopulation (Andreassen and Ims 2001; De Meester and Bonte 2010), and predictions regarding dispersal would be reversed. However, without considering spatio-temporal variation in density it is impossible to model processes such as density-dependent growth, emigration, or immigration.

Recent advancements in statistical techniques have demonstrated methods for using repeated count data with imperfect detection to estimate abundance (Chandler and King 2011; Dail and Madsen 2011). These advances still consider space implicitly and are therefore similar to earlier metapopulation modeling approaches (Levins 1969; Levins 1970; Gyllenberg and Hanski 1992; Hanski 1994) in their inability to model fundamental processes such as connectivity. At the inter-patch scale, the movement of individuals among local populations is influenced by distance among patches and the quality of the intervening habitat matrix (Hanski 2001; Hanski and Ovaskainen 2003; Ovaskainen and Hanski 2004). Recent advancements to metapopulation modeling have allowed for the direct estimation of connectivity among habitat patches (Sutherland et al. 2012; Sutherland et al. 2014; Chandler et al. 2015). However, there is a need for a general statistical framework based on spatially realistic metapopulation theory that allows for testing hypotheses regarding both local demographic processes and the spatial distribution of suitable patches on metapopulation abundance.

We developed a spatially-explicit integrated metapopulation model based on spatially realistic metapopulation theory (Hanski 2001). In keeping with the tradition of spatially-realistic metapopulation theory, our modeling framework allows for testing the influence of patch quality and the spatial distribution of patches on metapopulation dynamics. Our model allows for testing hypotheses about the influence of patch density on patch-level growth and dispersal. We can quantify trends in metapopulation size, rather than simply occurrence by integrating count and presence absence data collected in the field. Integrated population models (IPM) that incorporate empirical data collected using multiple sampling processes are at the forefront of ecological modeling. Often logistical or financial constraints necessitate collecting more valuable data (e.g., count data) at only a subset of sites or in a subset of years. When less informative data (e.g., presence-absence data) are collected at other, perhaps broader, spatial or temporal scales, an integrated model provides enough flexibility to combine data sets to estimate parameters of interest (Besbeas et al. 2002; Brooks et al. 2004). In some cases, IPMs have the added benefit of improving precision around parameter estimates (Zipkin and Saunders 2018). While the use of IPMs has proliferated in population ecology (Zipkin and Saunders 2018), there are far fewer examples of integrated metapopulation models (Harrison et al. 2011).

We demonstrated our approach using data collected for the federally-threatened Chiricahua leopard frog (*Lithobates chiricahuensis*) on the Buenos Aires National Wildlife Refuge (BANWR), AZ, USA. Previous modeling approaches developed in this system have quantified how colonization rate is influenced by the spatial distribution of patches (Chandler et al. 2015) and the landscape matrix in which patches are embedded (Howell et al. In Press). These previous approaches also allowed us to quantify the influence of habitat covariates on local patch level extinction risk while formally accounting for imperfect detection (Chandler et al. 2015; Howell et al. In Press). However, previous modeling efforts focused on occurrence and do not consider the effect of density on metapopulation dynamics.

Methods: SPATIALLY-EXPLICIT INTEGRATED METAPOPULATION MODEL: We developed a dynamic, spatially-explicit integrated metapopulation model based on spatially realistic metapopulation theory (Hanski 2001). Our modeling framework extends the spatially-explicit metapopulation occupancy model of Chandler et al. (2015) by estimating spatio-temporal variation in density and making it possible to test hypotheses regarding the influence of patch quality and density on population growth, emigration and immigration. Our model includes five components describing i) initial abundance, ii) local population dynamics, iii) emigration probability, iv) immigration rates and v) the observed data conditional on abundance and as a function of detection probability.

Abundance in the first time point is described by the following condition:

$$N_{i,1} \sim \text{Poisson}(\psi_{i,1}) \tag{1}$$

Where $N_{i,1}$ is the number of individuals at patch *i* during year one and depends on the expected initial abundance, $\psi_{i,1}$. In our system, we know the location of reintroduction events, but not the exact number of individuals released (see CASE STUDY: CHIRICAHUA LEOPARD FROG). We therefore treated abundance as zero at non-reintroduction patches, and at the reintroduction ponds we used a $N_{i,1}$ ~ Poisson(3) prior to describe our uncertainty about initial abundance. Abundance in subsequent years, *t*, at each patch *i*, is dependent on local population dynamics, emigration, and immigration. We used a simple geometric growth model and a Poisson assumption to describe the number of individuals $N_{i,t}^*$ resulting from local population dynamics:

$$N_{i,t}^* \sim \text{Poisson}(N_{i,t} * \lambda_{i,t}) \tag{2}$$

However, any standard model of population dynamics could be used, including separate models for describing the respective contribution of fecundity and survival to population growth. We modeled the patch-specific population growth rates $\lambda_{i,t}$ as a function of pond hydroperiod and pond density (area = pond area in square meters) on the log -linear scale:

$$\log(\lambda_{i,t}) = \alpha_1 * \text{INTER}_i + \alpha_2 * \text{PERM}_i + \alpha_3 * \text{SEMI}_i + \alpha_4 * (N_{i,t} / \text{area}_i)$$
(3)

Emigration was modeled as the proportion of $N_{i,t}^*$ that left a focal patch, using a binomial model where $\rho 0$ is the probability of emigration:

$$E_{i,t} \sim \text{Binomial}(N_{i,t-1}^*, \rho 0_i) \tag{4}$$

We tested the influence of patch level covariates (pond hydroperiod; PERM=permanent pond, SEMI=semi-permanent pond, INTER=intermittent pond) on the probability of emigration:

$$\rho 0_i = \rho 0_1 * \text{INTER}_i + \rho 0_2 * \text{SEMI}_i + \rho 0_3 * \text{PERM}_i$$
(5)

Immigration into a focal patch was quantified as the sum of the successful migrants from all the neighboring patches. Successful immigration was modeled with a multinomial distribution:

$$I_{i,1,t} \dots I_{i,M,t} \sim \text{Multinomial}(E_{i,t}, \pi_{i,m})$$
(6)

Where *M* is the number of patches in the metapopulation and $\pi_{i,m}$ is the probability of individuals immigrating into patch *i* from neighboring patch *m*. We then summed the *I*s over all

neighboring patches to calculate the number of immigrants into a focal patch. The probability of immigration, $\pi_{i,m}$, was modeled as a log-linear function of the Euclidean distance among all neighboring patches:

$$\log(\pi_{i,m}) = -\rho_1 * \mathbf{d}_{i,m} \tag{7}$$

The above description is the full model, however it can be simplified. If the multinomial size is Poisson, the realized abundance *N* comes from a Poisson distribution, since the sum of multinomial outcomes is also Poisson. Here, the multinomial size is $Poisson(N_{i,t} * \lambda_{i,t})$. Thus we modeled realized *N* as coming from a Poisson model: $N_{i,t} \sim Poisson(EN_{i,t})$ Where $EN_{i,t}$ is the expected number of individuals and is a function of the sum of the expected number of migrants *EM* to each site *i* from all *M* neighboring sites in time *t*:

$$EN_{i,t} = \sum_{m=1\dots M}^{M} EM_{m,i,t} \tag{8}$$

The expected number of migrants to each site *i* in time *t* is a function of the probability of individuals immigrating to site *i* from neighboring sites $m(\pi_{i,m})$ as well as the local population growth $(\lambda_{i,t})$:

$$EM_{i,m,t} = N_{i,t-1} * \lambda_{i,t-1} * \pi_{i,m}$$
(9)

CASE STUDY: CHIRICAHUA LEOPARD FROG: The Chiricahua leopard frog is a federally-threatened amphibian that occurs within the southwestern United States and portions of northern Mexico (Bezy 2007). We studied the metapopulation occupying the BANWR in the Altar Valley, southern Arizona (Figure 3.1). The Altar Valley is primarily used for grazing cattle and is characterized by semiarid grassland desert along with some riparian/wetland areas, foothills and mesquite trees (Bezy 2007). The majority of existing amphibian habitat patches are artificial cattle tanks (Bezy 2007). Cattle tanks in our study area are earthen, man-made water bodies that range in size (mean=0.15ha, range=0.0084-7.7ha) and were originally built to provide water for livestock (Jarchow et al. 2016). Within BANWR, leopard frogs were extirpated by 2001, most likely due to the spread of non-native *Lithobates catesbeianus* (American bullfrog) (Jarchow et al. 2016). Between 2001 and 2003, bullfrogs were eradicated from the refuge and Chiricahua leopard frogs were reintroduced to three cattle tanks in 2003 (Jarchow et al. 2016). We based our assumption of the extirpation of leopard frogs in BANWR on unpublished data, reporting extensive surveys (VES and seining) where leopard frogs were targeted and had occurred on BANWR prior to the reintroduction (USGS unpublished, BH Sigafus, pers. communication). Further, bullfrogs are known predators of leopard frogs and were common in all water bodies at the refuge (USGS unpublished, BH Sigafus and C. Schwalbe, pers. communication). Because of these surveys and reports from US Fish and Wildlife Service, we are confident in our assumption of no other reintroduction sites. A monitoring program collecting presence-absence data was established in 2007, and beginning in 2013 count data were collected at the same subset of patches.

Forty-seven patches were surveyed on BANWR and adjoining State Trust land, over 11 years (2007-2017). The maximum number of patches surveyed during a single year was 44 and 47 unique patches, of a possible M=274, were surveyed during the course of our study. From 2007-2012, we visited each of the surveyed patches K=3 times during the pre-monsoon period when the population was assumed to be closed (e.g., no birth, death, immigration, emigration). Visual encounter surveys were conducted between 21:00 and 03:00 (Crump and Scott). Two observers would each start at the same location on the edge of a pond and walk away from one another, until they reached a point directly across from their starting location. If any leopard frog was detected, we recorded $y_{i,k,t} = 1$ for patch i (i=1,...n) during survey k (k=1,...K) and year t

(t=1,...,T), or $y_{i,k,t} = 0$ if no frogs were detected (presence-absence data). During 2013-2017, we collected count data by visiting a patch K=2 or K=3 times during the pre-monsoon season. To collect count data, we conducted visual surveys using the dependent double observer method (Nichols et al. 2000). Observer one counted the number of frogs observed and recorded the life-stage (adult, juvenile, metamorph, tadpole) of each individual. Observer two conducted a survey immediately following observer one. For this analysis we only considered the counts of adult frogs.

We also characterized each of the M=274 available breeding locationspond (patch) hydroperiod as holding water permanently (40 patches, PERM), semi-permanently (10 patches, SEMI), and intermittently (224, INTER). We measured the area of each pond in ArcGIS using 2015 NAIP imagery (USDA-FSA-APFO Aerial Photography Field Office, 2015). For three of the ponds, we were unable to effectively determine the pond area, because the boundaries of the pond were unclear. For these ponds, we assigned pond area as the maximum area for all other ponds in the metapopulation. Wind speed (WIND, range: 0-17.3 kilometers/hour) and ambient temperature (TEMP, range: 9.2-41.2 degrees Celsius) were recorded because they can influence amphibian detection probability (Weir et al. 2005). All research was conducted under AGFD Scientific Collecting Permits SP695065, SP740593 and SP561283; BANWR Special Use Permits 2003-6 and 2007-12; and USFWS Permit TE081509.

MODEL FOR THE SAMPLING PROCESS: For years when we had only presence-absence data (2007-2012), we modeled the observed data conditional on local abundance and detection probability. $y_{i,tk} \sim \text{Bernoulli}(p_{i,t,k})$ (10)

$$p_{i,t,k} = 1 - (1 - r_{i,t,k})^{N_{i,t}}$$
(11)

Where *r* is the probability of detection in patch *i*, in primary period *t*, and secondary sampling occasions *k* for a particular individual (i.e., frog). $(1 - r_{i,t,k})^{N_{i,t}}$ describes the probability of not detecting any of the *N* individuals in patch *i*, during primary period *t*. The probability of detecting at least one individual is described by $1 - (1 - r_{i,t,k})^{N_{i,t}}$. In other words, detection *p* is related to abundance *N* through *r*, the binomial sampling probability that a particular individual is detected (Royle and Nichols 2003).

We modeled the influence of temperature and wind on detection probability using a logit-linear model.

$$logit(r_{i,t,k}) = \beta_0 + \beta_1 TEMP_{i,t,k} + \beta_2 WIND_{i,t,k}$$
(12)

For years in which we had count data (2013-2017), we modeled the observed data conditional on the latent abundance and as a function of detection probability. We included the influence of temperature and wind on detection probability in a logit-linear model. Because a dependent double observer method for sampling was used, there are two detection models, one specific to each observer:

$$y1_{i,tk} \sim \text{Binomial}(r1_{i,t,k}, N_{i,t})$$
(13)

$$logit(r1_{i,t,k}) = \beta_0 + \beta_1 TEMP_{i,t,k} + \beta_2 WIND_{i,t,k}$$
(14)

$$y2_{i,tk} \sim \text{Binomial}(r2_{i,t,k}, N_{i,t} - y1_{i,tk})$$
(15)

$$logit(r2_{i,t,k}) = \beta_0 + \beta_1 TEMP_{i,t,k} + \beta_2 WIND_{i,t,k}$$
(16)

Here the β parameters in the models of detection probability are regression coefficients to be estimated.

We used a Bayesian approach and performed MCMC sampling using rjags (Plummer 2003) called from R (Team 2014) to analyze the model (JAGS model code provide in APPENDIX H).

For all parameters, we used vague priors

 $(\alpha_1 \sim \text{Norm}(0, 0.1), \alpha_2 \sim \text{Norm}(0, 0.1), \alpha_3 \sim \text{Norm}(0, 0.1), \alpha_4 \sim \text{Uniform}(-20, 0),$ $\rho 0_1 \sim \text{Uniform}(0, 1), \rho 0_2 \sim \text{Uniform}(0, 1), \rho 0_3 \sim \text{Uniform}(0, 1),$ $\rho_1 = 1/2\sigma^2, \sigma \sim \text{Gamma}(0.001, 0.001), \beta_0 \sim \text{Norm}(0, 0.1), \beta_1 \sim \text{Norm}(0, 0.1),$ $\beta_2 \sim \text{Norm}(0, 0.1)).$ We sampled posterior distributions using 3 Markov chains of length 15000. Convergence was assessed visually by inspecting trace plots (APPENDIX I). **Results:** Following reintroduction into three patches in 2003, leopard frogs have colonized other ponds and expanded the network of occupied patches within the BANWR metapopulation (Figure 3.1, Figure 3.2.). Metapopulation level abundance increased steadily from 2004-2013 (Table 3.1, Figure 3.3). Between 2013 and 2014, average metapopulation abundance more than doubled, from an estimated 862 to 2,083 individuals (Table 3.1, Figure 3.3). Following the dramatic increase from 2013-2014, there was a decline in metapopulation abundance to 2017 (Table 3.1, Figure 3.3). In general, the metapopulation spread from the initial reintroduction locations in a northwest direction into permanent ponds on State Trust Land (Figure 3.1, Figure 3.2).

Colonization was influenced by the spatial distribution of patches and patch density. As the distance between patches increased, the immigration rate decreased (Table 3.1, Figure 3.4) and the expected number of migrants from a given patch immigrating into neighboring patches declined (Figure 3.4). Isolated patches with a low number of potential migrants and few occupied neighbors are unlikely to be colonized naturally by dispersing individuals and currently contribute little to metapopulation persistence. The probability of individuals leaving a focal patch (i.e., emigration rate) did not vary by pond hydroperiod (Table 3.1). Patch-specific population growth (adult survival from time t-1 to t and growth to the adult life stage in time t of individuals recruited into the population through births in t-1) was influenced by pond hydroperiod and the patch-specific density of the adult breeding population (Table 3.1, Figure 3.5). In general, pond-level dynamics played a larger role in the changes in abundance/density relative to the movement of individuals among ponds (Figure 3.2). Semipermanent ponds had the highest annual growth followed by permanent and then intermittent patches (Table 3.1, Figure 3.5). Lower quality patches contributed very minimally to population growth and could be considered a demographic sink (e.g., growth rate less than one; Table 3.1, Figure 3.5). Population growth was also strongly negatively density-dependent (Table 3.1), with annual growth rate decelerating, as local population size increased (Figure 3.5).

For count surveys, detection probability was influenced by both wind speed and ambient temperature (Table 3.1). Although the effect was small, the probability that a frog was detected increased with decreasing temperature and decreasing wind speed (Table 3.1).

Discussion: The model we developed expands on existing spatially-explicit metapopulation models by estimating patch-specific population density and metapopulation level abundance, rather than simply occurrence. By accommodating both count and presence-absence data, we tested hypotheses regarding the influence of patch characteristics, including density, on local dynamics and the spatial distribution of patches on colonization. In the Chiricahua leopard frog system, we showed that population growth was influenced not only by patch characteristics but also the density of conspecifics. In addition, patch characteristics did not influence emigration rate and patches that were more isolated from neighboring patches experienced lower immigration rates. We documented negative density-dependence in our system, with growth rate decelerating as population size increased. This result is consistent with previous empirical studies of density-dependence in metapopulations (Hanski 1990) Intermittent ponds generally had growth rates less than 1, regardless of density, and could be considered demographic sinks. Permanent ponds had growth rates greater than 1 (i.e., demographic source) at low pond level densities while semi-permanent ponds had the largest range of pond densities at which growth rates were greater than 1. Intermittent patches currently make up the vast majority of patches within the metapopulation network (n=224/274). In the southwestern United States, rainfall is expected to decrease while ambient temperatures are expected to rise as the climate becomes more arid (Seager et al. 2007). Lower precipitation could mean that ponds dry out (i.e., are not permanent) during the summer. Multiple, consecutive years of drought may lead to ponds going from permanent or semi-permanent to intermittent. This type of scenario may necessitate managers to intervene. For example, tank restoration may be necessary to provide water long enough to support a breeding population.

Patch hydroperiod affected population growth, but did not influence emigration rate. This result is in contrast to other metapopulation studies of the influence of patch quality on emigration rate (White and Levin 1981; Kuussaari et al. 1996; Gundersen et al. 2001). For , in the Glanville Fritillary butterfly system, lower emigration rates were documented from patches with a greater abundance of food resources (White and Levin 1981; Kuussaari et al. 1996). However, the strength of the relationship varied by sex, with the effect of patch quality being much weaker for females (Kuussaari et al. 1996). We did not investigate stage-specific emigration rates in our study and it is possible that emigration rate in the Chiricahua leopard frog varies by age, sex or body condition. Similar to the Glanville Fritillary butterfly, female leopard

frogs may have a greater tendency to emigrate regardless of patch quality. In other amphibians, females have been shown to leave breeding ponds shortly after depositing eggs (Muths et al. 2010) and there is evidence that dispersal may be female-biased in other anurans (Austin et al. 2003; Palo et al. 2004). After successfully breeding, female leopard frogs may leave the breeding pond to avoid continued harassment by males (Sztatecsny et al. 2006). We also only considered adult frogs in our study, and it may that juvenile frogs constitute the majority of dispersing individuals (Funk et al. 2005). Any effect of patch quality on emigration rate could be more pronounced in this age class relative to adults. Although emigrate ration may be lower at higher quality patches, because they produce so many potential migrants, highly productive patches may still be the primary source of dispersers.

We did not consider the impact of density on emigration rate, other metapopulation studies suggest emigration rate increases with increasing density if the population exceeds local carrying capacity (Dethier and MacArthur 1964). In other cases, emigration rate has been found to decrease with increasing density, possibly because of a higher number of potential mates at higher density patches (Gilbert and Singer 1973). Chorusing behavior, where males form lek-like aggregations and call to females, has been observed in other ranids (Wells 1977). Leopard frogs may exhibit similar behavior, leading to a decrease in emigration rate and increase in immigration rate with increasing density. If emigration or immigration rate are influenced by density, but not pond hydroperiod, this would provide evidence that the presence of potential mates could be indicative of the importance of chorusing behavior.

A widely held contention in anuran ecology is that anurans exhibit high site fidelity and natal philopatry. Several mark-recapture studies have demonstrated that a majority of recaptured individuals (both juveniles and adults) were recaptured at the pond where they were initially captured (Berven and Grudzien 1990; Waldman and McKinnon 1993). However, it is possible that in mark-recapture studies, many of the marked individuals that were not recaptured could have dispersed and were never recaptured again. It is also possible that individuals do not disperse because conditions in their natal pond are favorable to reproduction and growth. Dispersal propensity has been shown to be linked to body condition and environmental conditions. During the time of a field study, environmental conditions may not promote dispersal (e.g., insufficient rainfall) (Dole 1971) or individuals may be less likely to emigrate depending on their internal and external state (Barbraud et al. 2003).

Expansion from the initial reintroduction patches occurred primarily in a northwestern direction and immigration rate declined as distance among patches increased. We were not able to fit a model with immigration rate varying by hydroperiod, however the majority of colonized patches were permanent hydroperiod ponds. Although there have been fewer studies investigating the factors affecting immigration rate using empirical data, available evidence suggests that immigration rate increases with patch size and patch quality (Kuussaari et al. 1996). The density of neighboring patches could also influence immigration rate in the Chiricahua leopard frog. If density of conspecifics indicates favorable habitat, frogs may be more likely to settle in high density ponds (Stamps 1988). Alternatively, frogs may avoid higher density ponds in favor of less crowded patches where intra-specific competition for resources may be lower (Andreassen and Ims 2001; De Meester and Bonte 2010).

The Chiricahua leopard frog metapopulation increased steadily until 2014, at which point the level of abundance of the metapopulation began to decline. In more recent years (2015-2017), the metapopulation appears to be oscillating around 1200 adult frogs. This metapopulation level trend may be explained, in part, by the local pond level density-dependence we documented in our system. Focusing on the transition from 2013-2014 (increase in metapopulation abundance) and then 2014-2015 (decrease in metapopulation abundance), we found that from 2013-2014 36 patches increased, 1 decreased, and 96 patches had no change in density (85 of these patches remained unoccupied). From 2014-2015, although there was a large decline in metapopulation abundance, only four patches had a decrease in population size (n=2)permanent, n=1 intermittent, n=1 semi-permanent pond). Changes in the density of only a few ponds seemed to be sufficient to cause substantial changes in metapopulation-level abundance. All four occupied ponds that declined in density from 2014-2015 also had some of the highest densities during 2014, relative to other occupied ponds in the metapopulation. One hypothesis is negative density-dependence (e.g., intraspecific competition for food resources, space; Skogland 1985, Petranka and Sih 1986): once these ponds exceeded their carrying capacity, local population sizes declined, irrespective of any abiotic changes to the system. Another hypothesis is declining habitat quality: rainfall in desert ecosystems is often highly localized and could have led to a decline in quality of available habitat (e.g., pond depth, amount of submergent vegetation) and subsequently lowered the carrying capacity of these ponds (Noy-Meir 1973). The patches that declined in population size from 2014-2015 may have received a disproportionately small amount of the summer monsoon precipitation. PRISM data over the course of our study (2003-2017) indicate that the refuge as a whole experienced lower than average summer precipitation from 2010-2012 (data not shown). However, not all ponds declined in population size from 2014-2015 and we do not have data on pond-level trends in precipitation. Future research focused on pond-level habitat characteristics and climate will help elucidate the mechanisms behind the density dependence we observed in our system.

Our modeling framework extends existing spatially-explicit metapopulation models by quantifying spatio-temporal variation in patch density as well as incorporating multiple data sets collected across different temporal scales. By estimating patch density rather than focusing on occurrence, we incorporated density-dependence into our model of local population dynamics. While we did not consider the influence of density on emigration and immigration rates, our modeling framework is sufficiently flexible to allow for testing hypotheses regarding the influence of density on these processes. Integrated population models are at the forefront of ecological modelling and provide practical benefits to conservation efforts. The flexibility of integrated models allow researchers to incorporate multiple datasets that may otherwise have been discarded because of previous constraints. Our efforts address one of these constraints and our model could be further extended to incorporate additional types of data sets including markrecapture data. Including this kind of data set would allow us to estimate vital rates such as survival and fecundity within a spatially-explicit metapopulation model. Our abundance-based metapopulation dynamic model can be applied to other taxa and systems, where researchers are interested in understanding the influence of demographic processes on metapopulation dynamics. Acknowledgements: All research was conducted under AGFD Scientific Collecting Permits SP616031, SP674249, and SP713908; BANWR Special Use Permits 2013-013, 2017-008, and 2015-016; and USFWS Permit TE08548B. Research was conducted under approved IACUC procedure 12-334 and A2014 01-028-Y2-A2. Funding was provided by a grant from the U.S. Geological Survey. This is contribution number 5xx of the U.S. Geological Survey Amphibian Research and Monitoring Initiative. Use of trade, product, or firm names are descriptive and do not imply endorsement by the U.S. Government. This software has been approved for release by the U.S. Geological Survey (USGS). Although the software has been subjected to rigorous

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Literature Cited

- Andreassen, H. P., and R. A. Ims. 2001. Dispersal in patchy vole populations: role of patch configuration, density dependence, and demography. Ecology 82:2911-2926.
- Austin, J. D., J. A. Davila, S. C. Lougheed, and P. T. Boag. 2003. Genetic evidence for femalebiased dispersal in the bullfrog, Rana catesbeiana (Ranidae). Molecular Ecology 12:3165-3172.
- Barbraud, C., A. R. Johnson, and G. Bertault. 2003. Phenotypic correlates of post-fledging dispersal in a population of greater flamingos: the importance of body condition. Journal of Animal Ecology 72:246-257.
- Berven, K. A., and T. A. Grudzien. 1990. Dispersal in the wood frog (Rana sylvatica): implications for genetic population structure. Evolution:2047-2056.
- Besbeas, P., S. N. Freeman, B. J. Morgan, and E. A. Catchpole. 2002. Integrating mark– recapture–recovery and census data to estimate animal abundance and demographic parameters. Biometrics 58:540-547.
- Bezy, J. H., Charles, F.; Bahre, Conrad J. 2007, Buenos Aires National Wildlife Refuge, Arizona, University of Arizona.
- Brooks, S., R. King, and B. Morgan. 2004. A Bayesian approach to combining animal abundance and demographic data. Animal Biodiversity and Conservation 27:515-529.
- Chandler, R. B., and D. I. King. 2011. Habitat quality and habitat selection of golden-winged warblers in Costa Rica: an application of hierarchical models for open populations. Journal of Applied Ecology 48:1038-1047.

- Chandler, R. B., E. Muths, B. H. Sigafus, C. R. Schwalbe, C. J. Jarchow, and B. R. Hossack.
 2015. Spatial occupancy models for predicting metapopulation dynamics and viability following reintroduction. Journal of Applied Ecology 52:1325-1333.
- Crump, M., and J. Scott. NJ., 1994. Visual encounter surveys. Standard methods for amphibians (WR Heyer, MA Donnely, RW Mc Diarmid, LAC Hayek & MS Foster, eds).Smithsonian Institution Press, Washington:84-92.
- Dail, D., and L. Madsen. 2011. Models for estimating abundance from repeated counts of an open metapopulation. Biometrics 67:577-587.
- De Meester, N., and D. Bonte. 2010. Information use and density-dependent emigration in an agrobiont spider. Behavioral Ecology:arq088.
- Dethier, V., and R. H. MacArthur. 1964. A field's capacity to support a butterfly population. Nature 201:728-729.
- Dole, J. W. 1971. Dispersal of recently metamorphosed leopard frogs, Rana pipiens. Copeia:221-228.
- Funk, W. C., A. E. Greene, P. S. Corn, and F. W. Allendorf. 2005. High dispersal in a frog species suggests that it is vulnerable to habitat fragmentation. Biology Letters 1:13-16.
- Gilbert, L. E., and M. C. Singer. 1973. Dispersal and gene flow in a butterfly species. The American Naturalist 107:58-72.
- Gundersen, G., E. Johannesen, H. Andreassen, and R. Ims. 2001. Source–sink dynamics: how sinks affect demography of sources. Ecology Letters 4:14-21.
- Gyllenberg, M., and I. Hanski. 1992. Single-species metapopulation dynamics: a structured model. Theoretical Population Biology 42:35-61.
- Hanski, I. 1990. Density dependence, regulation and variability in animal populations.Philosophical Transactions of the Royal Society of London B: Biological Sciences 330:141-150.
- Hanski, I. 1994. Metapopulation dynamics: from concepts and observations to predictive models. Metapopulation biology: ecology, genetics, and evolution. Academic Press, New York, New York, USA:69-91.
- Hanski, I. 1999, Metapopulation ecology, v. 312, Oxford University Press Oxford.
- —. 2001. Spatially realistic theory of metapopulation ecology. Naturwissenschaften 88:372-381.
- Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain.Biological journal of the Linnean Society 42:3-16.
- Hanski, I., and O. Ovaskainen. 2003. Metapopulation theory for fragmented landscapes. Theoretical population biology 64:119-127.
- Hanski, I. A., and O. E. Gaggiotti. 2004, Ecology, genetics and evolution of metapopulations, Academic Press.
- Harrison, P. J., I. Hanski, and O. Ovaskainen. 2011. Bayesian state-space modeling of metapopulation dynamics in the Glanville fritillary butterfly. Ecological Monographs 81:581-598.
- Howell, P. E., E. Muths, B. R. Hossack, B. H. Sigafus, and R. Chandler. In Press. Increasing connectivity between metapopulation ecology and landscape ecology. Ecology.
- Jarchow, C. J., B. R. Hossack, B. H. Sigafus, C. R. Schwalbe, and E. Muths. 2016. Modeling habitat connectivity to inform reintroductions: a case study with the Chiricahua Leopard Frog. Journal of Herpetology.

- Kuussaari, M., M. Nieminen, and I. Hanski. 1996. An experimental study of migration in the Glanville fritillary butterfly Melitaea cinxia. Journal of animal Ecology:791-801.
- Lambrechts, M. M., S. Caro, A. Charmantier, N. Gross, M.-J. Galan, P. Perret, M. Cartan-Son et al. 2004. Habitat quality as a predictor of spatial variation in blue tit reproductive performance: a multi-plot analysis in a heterogeneous landscape. Oecologia 141:555-561.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237-240.

—. 1970. Extinction. Lectures on mathematics in the life sciences 2:75-107.

- Matthysen, E. 1999. Nuthatches (Sitta europaea: Aves) in forest fragments: demography of a patchy population. Oecologia 119:501-509.
- Muths, E., R. D. Scherer, and B. A. Lambert. 2010. Unbiased survival estimates and evidence for skipped breeding opportunities in females. Methods in Ecology and Evolution 1:123-130.
- Nichols, J. D., J. E. Hines, J. R. Sauer, F. W. Fallon, J. E. Fallon, and P. J. Heglund. 2000. A double-observer approach for estimating detection probability and abundance from point counts. The Auk 117:393-408.
- Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual review of ecology and systematics 4:25-51.
- Ovaskainen, O., and I. Hanski. 2004. Metapopulation Dynamics in Highly Fragmented Landscapes-4.
- Palo, J., D. Lesbarreres, D. Schmeller, C. Primmer, and J. Merilä. 2004. Microsatellite marker data suggest sex-biased dispersal in the common frog Rana temporaria. Molecular Ecology 13:2865-2869.

- Plummer, M. 2003, JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling Proceedings of the 3rd international workshop on distributed statistical computing 124:125.
- Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence-absence data or point counts. Ecology 84:777-790.
- Stamps, J. A. 1988. Conspecific attraction and aggregation in territorial species. The American Naturalist 131:329-347.
- Sutherland, C., D. A. Elston, and X. Lambin. 2012. Multi-scale processes in metapopulations: contributions of stage structure, rescue effect, and correlated extinctions. Ecology 93:2465-2473.
- Sutherland, C., D. A. Elston, and X. Lambin. 2014. A demographic, spatially explicit patch occupancy model of metapopulation dynamics and persistence. Ecology 95:3149-3160.
- Sztatecsny, M., R. Jehle, T. Burke, and W. Hödl. 2006. Female polyandry under male harassment: the case of the common toad (Bufo bufo). Journal of Zoology 270:517-522.
- Team, R. C. 2014. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2012. Open access available at: <u>http://cran</u>. rproject. org.
- Waldman, B., and J. S. McKinnon. 1993. Inbreeding and outbreeding in fishes, amphibians, and reptiles. The natural history of inbreeding and outbreeding: theoretical and empirical perspectives:250-282.
- Weir, L. A., J. A. Royle, P. Nanjappa, and R. E. Jung. 2005. Modeling anuran detection and site occupancy on North American Amphibian Monitoring Program (NAAMP) routes in Maryland. Journal of Herpetology 39:627-639.

Wells, K. D. 1977. The social behaviour of anuran amphibians. Animal Behaviour 25:666-693.

- White, R. R., and M. P. Levin. 1981. Temporal variation in vagility: implications for evolutionary studies. American Midland Naturalist:348-357.
- Zipkin, E. F., and S. P. Saunders. 2018. Synthesizing multiple data types for biological conservation using integrated population models. Biological Conservation 217:240-250.

Parameter	Description	Mean	SD	2.5	97.5
	Linear effect of Euclidean distance on				
rho1	emigration rate	0.12	0.06	0.02	0.24
$rho0_1$	Emigration rate of intermittent patches	0.96	0.04	0.85	1.00
	Emigration rate of semi-permanent				
rho0 ₂	patches	0.99	0.01	0.97	1.00
rho0 ₃	Emigration rate of permanent patches	0.98	0.00	0.97	0.99
	Local population growth at intermittent				
alpha1	patches	0.06	0.11	-0.16	0.28
	Local population growth at permanent				
alpha2	patches	0.57	0.02	0.52	0.61
	Local population growth at semi-				
alpha3	permanent patches	0.66	0.04	0.58	0.74
	Effect of population density on local				
alpha4	population growth	-1.89	0.13	-2.14	-1.63
	Intercept of logit-linear detection				
beta0	model	-1.30	0.07	-1.45	-1.17
beta1	Effect of temperature on detection	0.11	0.02	0.07	0.16
beta2	Effect of wind on detection	0.30	0.03	0.24	0.36
Ntotal[2004]	Metapopulation abundance in 2004	13.44	2.91	8.00	19.00
Ntotal[2005]	Metapopulation abundance in 2005	27.27	5.72	17.00	40.00
Ntotal[2006]	Metapopulation abundance in 2006	53.31	10.43	36.00	76.03
Ntotal[2007]	Metapopulation abundance in 2007	97.91	17.24	68.00	135.03
Ntotal[2008]	Metapopulation abundance in 2008	163.48	26.16	116.00	219.00
Ntotal[2009]	Metapopulation abundance in 2009	251.16	35.22	185.00	326.03
Ntotal[2010]	Metapopulation abundance in 2010	360.80	41.60	283.00	446.03
Ntotal[2011]	Metapopulation abundance in 2011	494.05	43.27	412.98	582.03
Ntotal[2012]	Metapopulation abundance in 2012	643.97	43.51	565.00	732.03
Ntotal[2013]	Metapopulation abundance in 2013	862.46	47.98	777.00	963.00
Ntotal[2014]	Metapopulation abundance in 2014	2083.41	56.54	1985.00	2209.00
Ntotal[2015]	Metapopulation abundance in 2015	1186.97	76.79	1054.00	1356.03
Ntotal[2016]	Metapopulation abundance in 2014	927.66	96.29	768.00	1139.00
Ntotal[2017]	Metapopulation abundance in 2015	1225.51	135.38	1001.00	1526.00

Table 3.1. Estimates of the posterior mean, standard deviation and 95% credible intervals for detection and abundance parameters for our spatially explicit integrated metapopulation model.



Figure 3.1. Potential breeding patches for Chiricahua leopard frogs in the Altar Valley, Arizona, USA (Buenos Aires National Wildlife Refuge [BANWR] and State Trust Land). Black outline indicates the boundaries of BANWR. Square symbols indicate permanent patches, triangles indicate intermittent patches, and pentagons indicate semi-permanent patches. Colored symbols indicate patches that are sampled annually and orange indicates the three reintroduction patches. Dots within symbols indicate patches where leopard frogs were detected at least one time.



Figure 3.2. Illustration of metapopulation dynamics from 2013-2015. A) Realized abundance in 2013, B) Local dynamics (abundance after local population growth and before movement), C) Movement (net number of individuals gained or lost via movement at each patch), D) Expected abundance in 2014 and E) Realized abundance in 2014 for Chiricahua leopard frogs in the Buenos Aires National Wildlife Refuge and nearby State Trust Land within the southern Altar Valley of Arizona, USA. Local patch level growth represents survival from time t-1 to t and growth to the adult life stage of individuals recruited into the population. Immigration is quantified as the sum of all contributions of individuals moving from neighboring patches (n=274) to a given patch within the metapopulation.



Figure 3.3. Metapopulation realized abundance over time for Chiricahua leopard frogs in the Buenos Aires National Wildlife Refuge and nearby State Trust Land within the southern Altar Valley of Arizona, USA from 2004-2017. Circles indicate mean abundance and lines indicate the upper and lower limit of the 95% credible interval.



Figure 3.4. Example of the expected number of migrants (EM) and number of individuals expected to remain in a focal pond (n) for a subset of ponds on the Buenos Aires National Wildlife Refuge. In this example, n=528 adults are expected to remain within the focal pond from 2015-2016, while a total of 8 individuals are expected to immigrate into other ponds within the Refuge. The number of expected migrants declines with distance from the focal pond.



Figure 3.5. Local population growth as a function of pond hydroperiod and patch-specific density (adult frogs/square meter) for Chiricahua leopard frogs in the Buenos Aires National Wildlife Refuge and nearby State Trust Land within the southern Altar Valley of Arizona, USA. Solid, colored lines indicate mean, dashed lines indicate upper and lower limits of 95% credible intervals. Solid black line indicates no change in local population growth.

CHAPTER 4

SPATIALLY EXPLICIT METAPOPULATION VIABILITY ANALYSIS¹

¹ Howell, P.E., Muths, E., Hossack, B.R., Sigafus, B.H., Chandler, R.B. To be submitted to *Conservation Biology*

<u>Abstract</u>

Successful conservation of at-risk species requires reliable models for projecting the consequences of environmental change and management actions on population viability. Conventional population viability analysis (PVA) involves a two-step process in which parameters are estimated, or elicited from expert opinion, and then used in a stochastic population model without accounting for statistical uncertainty. Recently-developed statistical PVAs differ because projections are made conditional on empirical data. This allows for inference about quantities such as extinction risk, while accounting for parameter uncertainty and standard sources of uncertainty arising from demographic and environmental stochasticity. We conducted a statistical metapopulation viability analysis using a spatio-temporal occupancy model fitted to 11 years (2007-2017) of data on the federally-threatened Chiricahua leopard frog (Lithobates chiricahuensis). We considered models of no environmental change and increasing drought conditions over 25 years. Based on historical data on pond failure, we included the probability that human-made breeding ponds would fail, changing habitat from suitable to unsuitable. Additionally, we evaluated management actions involving the restoration of 1, 3, or 6 ponds, and calculated the marginal gains associated with each level of pond restoration, under each model of future environmental change. Projections over a 25-yr time horizon indicated that under current environmental conditions, metapopulation extinction risk is low (7%), even when no additional ponds are restored. However, under a scenario of increasing drought conditions, extinction risk is substantially higher (40%), particularly in the most pessimistic scenario where ponds are allowed to fail and there is no management. Active management may be necessary to maintain permanent breeding habitat and decrease extinction risk as drought conditions are expected to increase over time. Our study illustrates the utility of biologically-realistic statistical

models for forecasting viability to inform conservation planning for species and populations at risk of extinction.

Introduction

Biodiversity is declining worldwide at an alarming rate in response to rapid environmental change (Fischlin et al. 2007). In some cases, highly mobile species may be able to respond to environmental change by tracking suitable habitat and climate conditions via dispersal (Peterson 2003; Last et al. 2011). Other species may respond through plasticity in the timing of important life history events or by adapting to novel environmental conditions (Joshi et al. 2001). However, if adaptation is too slow, or dispersal is limited by environment or demography, animals may be unable to move to suitable habitats (Schloss et al. 2012; Bay et al. 2018). Without human intervention, this scenario can result in extirpations or extinctions.

Population viability analysis (PVA) (Beissinger and McCullough 2002; Morris and Doak 2002) has been developed as a framework for predicting the impacts of environmental change and identifying the best conservation actions for reducing extinction risk. In general, PVAs involve determining the current status of a population or species and then identifying conservation options to enhance long-term persistence (Beissinger 2002). As PVAs have grown in popularity as a conservation tool, so has the recognition of their potential pitfalls. Conventional PVAs involve estimating parameters with empirical data or eliciting them from expert opinion, and then inserting point estimates into stochastic population models without formally accounting for statistical uncertainty in parameter estimates (Heinsohn et al. 2004; Olsen et al. 2014; Mortensen and Reed 2016). Ignoring parameter uncertainty can result in overestimation of the precision associated with predictions of extinction risk. When management decisions are made based on erroneously high confidence in projections, there can be negative

consequences. For many species of conservation concern, there is a paucity of data available with which to conduct a PVA (Morris and Doak 2002; Trenham and Shaffer 2005). When data are sparse, accounting for parameter uncertainty is especially important because uncertainty around parameter estimates is likely to be high, and should be reflected in the confidence intervals around our predictions. Another criticism that has been levied against PVAs is the omission of uncertainty about future environmental variation and catastrophic events (Beissinger and McCullough 2002; Morris and Doak 2002). When anticipated future conditions are included in PVAs, these scenarios are often represented as averages without any measure of uncertainty (but see (Oppel et al. 2014; McElderry et al. 2015).

Recently developed statistical PVAs have made it possible to account for parameter uncertainty by fitting biologically-realistic hierarchical models to empirical data (Heard et al. 2013; Green and Bailey 2015). A statistical framework makes it possible to propagate parameter uncertainty, uncertainty arising from the sampling process (MacKenzie et al. 2003), and uncertainty surrounding future environmental conditions when making projections of extinction risk. In the case of metapopulations, persistence depends on colonization of vacant habitat patches, and the spatial distribution of patches affects colonization rates (Hanski et al. 1996). Predicting the consequences of management actions on metapopulations, including reintroductions and habitat restoration, can be accomplished using spatially-explicit statistical models that explicitly estimate the influence of space on metapopulation connectivity (Tischendorf and Fahrig 2001).

Not all animal taxa are equally vulnerable to environmental change, and some groups, such as amphibians, are especially sensitive (Foden et al. 2013). Although multiple stressors may act in concert, habitat loss has been implicated as the most important factor in amphibian declines (Stuart et al. 2004). Recent estimates suggest that a third of all amphibian species are threatened globally (Stuart et al. 2004), and this number is likely to increase in the near future if habitat loss and degradation continue. Amphibians require water during a portion of their life cycle and increasing drought conditions can result in result in a decline in reproduction (Semlitsch 1987; Dodd Jr 1993) and local extinction events (Blair 1957). For amphibians that are able to persist in the terrestrial habitat for multiple seasons, drought events may cause them to forgo breeding (Dodd Jr 1993). If adults are able to breed in aquatic habitat, drought conditions may cause ponds to dry before metamorphs emerge, resulting in catastrophic reproductive failure (Semlitsch 1987; Taylor et al. 2006; Amburgey et al. 2012; Amburgey et al. 2014). Unless individuals are able to colonize other available aquatic habitat, declines in survival and reproduction will lead to extinction of local populations and ultimately a decline in metapopulation viability. These facets of amphibian ecology make them a pressing conservation challenge and require development of accurate predictive models to evaluate management alternatives.

Aquatic and semi-aquatic animals in arid environments face a range of threats from increasing drought conditions and potential catastrophic breeding failure due to reduced or lacking aquatic habitat (Welch and MacMahon 2005; Walls et al. 2013). In the southwestern USA, all native semi-aquatic frogs (family Ranidae) have declined (Hayes and Jennings 1986), but only the Chiricahua leopard frog (*Lithobates chiricahuensis*) is listed under the US Endangered Species Act (USFWS 2007). The metapopulation of Chiricahua leopard frogs in the Altar Valley, Arizona, USA was extirpated in 2001, likely because of invasion by the non-native American bullfrog (*Lithobates catesbeianus*) (Jarchow et al. 2016). Following eradication of bullfrogs, Chiricahua leopard frog tadpoles were reintroduced into three ponds on the refuge in 2003 (Jarchow et al. 2016). Since then, leopard frogs have expanded to colonize additional ponds in the region (Chandler et al. 2015). The USFWS recovery plan for this species requires that a PVA be conducted (USFWS 2007). In 2004, a PVA was carried out, however the models were not spatially-explicit, many parameters were based on expert-opinion, parameter uncertainty was ignored, and specific management alternatives were not explicitly integrated into projections (USFWS 2007).

Our objective was to develop spatially-explicit models to predict the consequence of potential management actions and environmental change on metapopulation extinction risk. Similar to other desert-dwelling amphibians, increasing drought may be one of the biggest threats to Chiricahua leopard frog viability (Semlitsch 2000; Semlitsch 2002; Walls et al. 2013). We projected extinction risk 25 years into the future under two models of future environmental conditions, a Static model where environmental conditions do not change and a Drought model with changing drought conditions. We organized two workshops with BANWR managers and identified potential management actions to increase long-term metapopulation persistence, with the most feasible management option being restoration of existing ponds to increase hydroperiod. We quantified the tradeoff over time between metapopulation persistence and the marginal gains of restoring additional ponds.

Methods: SPATIAL OCCUPANCY MODEL: To quantify metapopulation occupancy dynamics, we extended the spatially-explicit occupancy model developed by Chandler et al. (2015) to accommodate environmental variation and potential management actions. The model contains several components: 1) occupancy in the first year, 2) inter-patch colonization rate, 3) patch-specific extinction rate, and 4) a model for the observed data, conditional on the latent occupancy dynamics. In our system, the occupancy state of each pond in the first year ($z_{i,1}$) was treated as

known because the population had been reintroduced (see STUDY PONDS AND DATA COLLECTION BELOW).

In subsequent years, the occupancy state z for each pond for t = 2, ..., T was modeled as:

$$\psi_{i,t-1} = \gamma_{i,t-1} (1 - z_{i,t-1}) + (1 - \varepsilon_{i,t-1} (1 - \gamma_{i,t-1})) z_{i,t-1}$$
(1)
$$z_{i,t} \sim \text{Bernoulli}(\psi_{i,t-1})$$

Where γ is the probability that a patch is colonized and ε is the probability of local extinction. The model for persistence (the inverse of local extinction probability) is $1 - \varepsilon_{i,t-1} (1 - \gamma_{i,t-1})$, which accounts for the rescue effect (Hanski 1999).

We used a Gaussian model to describe the probability of site *i* being colonized by at least one individual from a neighboring site *j*:

$$\rho_{i,j,t} = \rho_{0,j} \exp\left(\frac{-d_{i,j}^2}{2\sigma^2}\right) z_{j,t-1} \tag{2}$$

$$logit(\rho_{0,j}) = \rho_1 * Inter_j + \rho_2 * Semi_j + \rho_3 * Perm_j$$
(3)

where ρ_0 is the baseline colonization probability (i.e., colonization probability of ponds if they were found at the same spatial location), $d_{i,j}$ is the Euclidean distance between two ponds, σ is the scale parameter that determines how quickly colonization probability declines as a function of distance between ponds, and $z_{j,t-1}$ is the occupancy state of the neighboring site at the previous time point. We allowed baseline colonization probability to vary based upon hydroperiod (Inter=Intermittent, Semi=Semi-permanent, Perm=Permanent(Howell et al. In Press).

The cumulative probability of colonization for pond *i* in year *t* is then defined as:

$$\gamma_{i,t} = 1 - \left(\prod_{j=1}^{M} 1 - \rho_{i,j,t}\right)$$
(4)

where M is the total number of ponds in the metapopulation.

In our first model of extinction rate, site-specific extinction $\varepsilon_{i,t-1}$ was modeled as a logit-linear function of pond hydroperiod (Model 1: Static). For our second model we assumed drought also influenced pond-level extinction risk (Model 2: Drought):

logit
$$(\varepsilon_{i,t-1}) = \varepsilon_1 * \text{Inter}_i + \varepsilon_2 * \text{Semi}_i + \varepsilon_3 * \text{Perm}_i + \varepsilon_4 * \text{PDSI}_{t-1}$$
 (5)
As our metric of drought, we used the Palmer Drought Severity Index (PDSI) calculated from
surface air temperature and precipitation (Dai et al. 2004). PDSI data were available from 2003-
2014, so we predicted PDSI for 2015-2017 using a simple linear model with PDSI varying by

We modeled the observed presence-absence data conditional on true site occupancy and

detection probability.

year.

$$y_{i,t,k} \sim \text{Bernoulli}(z_{i,t} \ge p_{i,t,k})$$
 (6)

$$logit(p_{i,t,k}) = \beta_0 + \beta_1 TEMP_{i,t,k} + \beta_2 WIND_{i,t,k}$$
(7)

where TEMP is ambient temperature WIND is wind speed.

We used Bayesian methods and a custom Metropolis-within-Gibbs sampler for inference (See APPENDIX J for R code). For all parameters we used vague priors ($\varepsilon_1 \sim \text{Beta}(1,1)$, $\varepsilon_2 \sim$ Beta(1,1), $\varepsilon_3 \sim \text{Beta}(1,1)$, $\varepsilon_4 \sim \text{Beta}(1,1)$, $\rho_1 \sim \text{Unif}(0, 100)$, $\rho_2 \sim \text{Unif}(0, 100)$, $\rho_3 \sim \text{Unif}(0, 100)$, $\sigma \sim \text{Gamma}(0.001, 0.001)$, $\beta_0 \sim \text{Norm}(0, 10)$, $\beta_1 \sim \text{Norm}(0, 10)$, $\beta_2 \sim \text{Norm}(0, 10)$. For our Static model we sampled from posterior distributions using 3 Markov chains of length 15000, and we discarded the first 100 samples as burn-in. For our Drought model we sampled from posterior distributions of length 8000, and we discarded the first 100 samples as burn-in. For our Drought model we sampled from posterior evaluations of length 8000, and we discarded the first 100 samples as burn-in. We reported posterior means and credible intervals for all point estimates.

FORECASTING METAPOPULATION VIABILITY: We used Bayesian forecasting methods to project metapopulation dynamics 25 years into the future. Bayesian forecasting involves computing the posterior predictive distributions of the future occupancy states. Posterior predictive distributions are conditional on the observed data and therefore naturally incorporate parameter uncertainty into predictions of future metapopulation viability. Posterior predictive distributions can be easily computed as part of the MCMC procedure by treating future values of the occupancy states as unknown random variables. When occupancy depends on time-varying covariates, a model is also needed to predict the future covariate values. For example, in our model in which extinction rate varied with hydroperiod and drought (Model 2: Drought), we used a simple linear model to describe the relationship between our drought index (PDSI) and time (years):

$$E(PDSI_t) = \alpha_0 + \alpha_1 * Year_t$$

 $PDSI_t \sim Norm(E(PDSI_t), \sigma^2)$

where α_0, α_1 , and σ^2 were estimated from the data. This allowed us to compute posterior predictions of occupancy while accounting for uncertainty about drought.

In addition to environmental conditions, we incorporated the effect of management into the models: restoration of 0, 1, 3, or 6 ponds or allowing ponds to fail, under each climate model. Ponds were chosen for restoration based on three criteria: 1) ponds with the highest probability of colonization from 2017-2018, 2) ponds characterized as semi-permanent or intermittent, and 3) ponds that were occupied infrequently (i.e., 8 years, or less than half of the study period). The pond-specific probability of colonization and occupancy were taken from posterior distributions of γ and *z* from our models fit to empirical data. During our study (2003-2017) three ponds failed structurally (i.e., catastrophic weather events such as flooding destroyed the tank or caused it to fill completely with sediment) over the course of 11 years out of the 47 ponds surveyed. Extrapolating to all 274 ponds, each pond has approximately a 0.0058% chance of failing in a given year (3 ponds/(47 ponds surveyed x 11 survey years)). For each year, whether or not a pond *i* failed was estimated with a Bernoulli model:

*Blow Out*_{*i*} ~ Bernoulli(0.0058)

For this scenario, any pond that failed in a given year remained unusable for all subsequent years in our projections. Similar to how we treated drought in our projections, we calculated the probability of tank failure for each MCMC iteration. Under each model of environmental conditions and management action, we conducted simulations forward in time 25 years. We computed extinction risk as the proportion of MCMC iterations that resulted in metapopulation extinction in each year.

EVALUATING TRADEOFF BETWEEN EXTINCTION RISK AND MANAGEMENT COST: We quantified the tradeoff between the benefits of reducing metapopulation extinction risk and the costs of pond restoration using the formula for marginal gains (Conroy and Peterson 2013) to provide an objective way for managers to evaluate the effect of pond restoration on metapopulation extinction risk:

$$G_x = \frac{\phi_x - \phi_0}{x} \tag{10}$$

where ϕ_0 is the metapopulation extinction risk (i.e., proportion of MCMC iterations where metapopulation went extinct) with no management and ϕ_x is the metapopulation extinction risk assuming x ponds are restored to permanent. In this formula, x can be thought of as the cost of restoring a pond, and we assumed that the cost of restoring a pond was the same for all ponds in the metapopulation.

STUDY SITE AND DATA COLLECTION: Eleven years (2007-2017) of occupancy data and habitat covariates were collected for the Chiricahua leopard frog from the Buenos Aires National Wildlife Refuge (BANWR) and surrounding public and private land in the Altar Valley of southern Arizona, USA (Figure 4.1). This region is used primarily for grazing cattle and is characterized by semiarid grassland desert along with some riparian/wetland areas, foothills and mesquite trees. This species depends on water bodies that hold water all year for self-sustaining populations (USFWS 2007). The majority of permanent water bodies within their range contain populations of invasive fish and American bullfrogs (USFWS 2007). Consequently, Chiricahua leopard frogs are relegated to man-made habitat (i.e., ponds) constructed to provide water for livestock, most of which hold water only intermittently (Figure 4.1). From 2007-2017, 47 ponds were surveyed on BANWR and adjoining State Trust land to the west, with a maximum of 44 ponds surveyed in a given year (47 unique ponds out of M=273 available ponds). Each pond was visited a maximum of K=3 times per year for T=11 years during the pre-monsoon period during 2100 and 0300 hr. We recorded $y_{i,t,k} = 1$ if at least one frog was detected, and $y_{i,t,k} = 0$ if no frogs were detected. In addition to presence-absence data, information on hydroperiod was assigned. Hydroperiod was assigned as one of three dummy categorical variables: PERM, SEMI, and INTER. Of the M total available ponds, 40 ponds held water permanently (PERM), 9 semipermanently (SEMI) and 224 intermittently (INTER). We also recorded wind speed (WIND) and ambient temperature (TEMP) during each survey. All research was conducted under AGFD Scientific Collecting Permits SP616031, SP674249, and SP713908; BANWR Special Use Permits 2013-013, 2017-008, and 2015-016; and USFWS Permit TE08548B. Research was conducted under approved IACUC procedure 12-334 and A2014 01-028-Y2-A2.

Results: From 2003 to 2017, our Static and Drought models yielded similar estimates of occupancy trends and covariate effects. The percent of occupied ponds increased from three in 2003 to 23 (95% CI; 18, 33) in 2015 followed by a decline to 18 (95% CI; 12, 33) in 2017 (Table 4.1, Figure 4.2). Ponds that held water permanently or semi-permanently during the year had higher baseline colonization rates than ponds that only held water intermittently, and as the distance among ponds increased, colonization rate declined (Table 4.1). Extinction rate was high for intermittent ponds and declined as pond hydroperiod changed to semi-permanent and permanent (Table 4.1). There was a small, negative effect of drought on extinction rate, but credible intervals for all extinction rate parameters were wide (Table 4.1). There was minimal influence of drought on metapopulation dynamics, as evidenced by similar occupancy estimates for the Static and Drought model (Table 4.1, Figure 4.2). As wind speed and ambient temperature increased, detection probability decreased (Table 4.1).

The 25-yr projections from the Static and Drought models indicated a qualitatively similar increase in proportion of ponds occupied and increase in extinction risk (Figure 4.2, Figure 4.3). The most pessimistic scenario was when drought increased over time and ponds were allowed to fail structurally (Figure 4.3). In this scenario, extinction risk increased to ~40% by 2043 (Figure 4.3). Restoring additional ponds to permanent hydroperiod increased the mean proportion of occupied ponds and lowered extinction risk relative to no management action (Figure 4.3). However, credible intervals for proportion of occupied sites under each management scenario (restoration of 0, 1, 3, 6) overlapped substantially in both the Static and Drought models (Figure 4.4). Based on the estimates of extinction risk from both models (Figure 4.2), the marginal gain of restoring additional ponds was highest when only a single pond was restored (Drought model 1 pond = 0.011, 3 ponds = 0.008, 6 ponds = 0.008; Static model 1 pond

= 0.013, 3 ponds = 0.009, 6 ponds = 0.007), given the current number of permanent ponds in the metapopulation (n=40).

Discussion: Projections of Chiricahua leopard frog metapopulation viability 25 years into the future were optimistic under a future scenario of a static climate. In the absence of increasing drought, high projected metapopulation viability can most likely be attributed to the low extinction rate of permanent hydroperiod ponds, an absence of invasive predators, and high functional connectivity. The high density of permanent ponds near the reintroduction locations and the dispersal capabilities of the Chiricahua leopard frog have allowed them to colonize additional ponds from the initial sites of reintroduction. Once permanent ponds are colonized, there is low turnover in subsequent years. Invasive competitors/predators (e.g., American bullfrog, *Lithobates catesbeianus*) that also rely on permanent hydroperiod ponds have been removed and continue to be monitored so that they can be prevented from re-colonizing permanent ponds on the refuge (personal communication Brent Sigafus). However, in a more likely scenario where drought conditions continue to worsen, metapopulation extinction risk will continue to increase regardless of functional connectivity and continued removal of invasive species. In this case, pond maintenance and restoration may be necessary to reduce extinction risk and improve long-term metapopulation viability.

Similar to previous studies of Chiricahua leopard frog metapopulation dynamics (Chandler et al. 2015; Howell et al. In Press), we demonstrated a strong influence of distance on inter-pond colonization rate, with colonization declining as distance among neighboring ponds increased. We also demonstrated a strong influence of pond characteristics on extinction and colonization rate in both the Static and increasing Drought models. Permanent ponds are less prevalent in our study system (n=40 of 274 pond) relative to ponds with reduced hydroperiods.

However, they also had the lowest extinction rates and contributed more to the colonization of neighboring ponds. This evidence suggests that permanent hydroperiod ponds are essential to maintaining a viable metapopulation of Chiricahua leopard frog. Estimates of metapopulation occupancy were similar in the Static and increasing Drought models. This is likely because of the variation around the temporal trend in drought from 2003-2014, resulting in a minimal influence of drought on pond-level extinction rate and consequently, the proportion of occupied ponds.

Amphibians face numerous stressors and in the desert southwest, one of the biggest threats to their continued persistence is increasing drought conditions (Welch and MacMahon 2005; Walls et al. 2013). Indeed, during the years of our study (2003-2017) there was a general trend of decreasing PDSI, indicative of increasingly severe drought conditions (Figure 4.5). In the desert southwest, temperatures are expected to increase, precipitation is expected to decrease and both are likely to become more variable leading to suitable breeding habitat becoming more unpredictable and sparse (Archer and Predick 2008). Ponds receive some rain in the winter, but are reliant primarily on summer monsoon rains to stay full throughout the year (Bezy 2007). If summer monsoon rains decrease and continue to occur later in the summer, ponds that historically remained full may dry up. Frogs occupying these ponds will either die or be forced to attempt dispersal through dry, harsh terrestrial landscapes. Projections over a 25-yr time frame suggest that drought substantially increases metapopulation extinction risk to nearly 40% when ponds also have a chance of catastrophically failing (e.g., flash flooding causing structural failure or complete filling with sediment), relative to when environmental conditions are static over time. With the current number of permanent ponds in the network (n=40), management is limited in terms of the marginal gain associated with restoring any additional ponds. However, in more

realistic scenarios (e.g., consecutive years of severe drought, catastrophic weather events) additional management may become necessary.

Our model of drought was based on PDSI and changes in PDSI influences all ponds equally. Although PDSI provides a measure of drought in our study area, the ability to estimate the size/depth of each pond and to correlate changes in size with changes in climate would provide pond-specific estimates of the influence of drought on pond-level extinction risk. The management scenarios we considered in this study are pond-specific and involve targeted restoration of individual semi-permanent, or intermittent ponds, so that they will hold water year round. However, it may be possible to restore multiple ponds at the same time by removing or altering structures, such as dams and floodplain water spreaders, associated with the man-made ponds. Water control structures and diversion channels have altered natural runoff pathways and affect how ponds fill with water. For example, a concrete water control structure may be built after a stock tank, preventing it from filling with runoff after rainfall when it previously would have filled. In some cases, it may be possible for managers to remove or alter some of the structures associated with ponds to improve the hydroperiod of multiple ponds, rather than restoring ponds individually. Targeting the landscape rather than individual ponds could make restoration efforts more cost-effective.

We used a spatially-explicit metapopulation model, to forecast occupancy dynamics and extinction risk under different environmental scenarios and management alternatives. Our modeling framework accounted for uncertainty in the sampling process, parameter estimation and future environmental conditions. Our projections over 25 years suggest that if there is no increase in drought conditions, extinction risk is very low. However, current conditions are unlikely to remain static, with projections for the Southwestern United States suggesting an increase in severity and extent of drought (Gutzler and Robbins 2011). With a combination of increasing drought conditions and a change of ponds failing structurally the extinction risk is expected to increase to nearly 40%. Restoring ponds to permanent hydroperiod increased the proportion of occupied ponds and decreased metapopulation extinction risk, in both the Static and increasing Drought model, suggesting that as drought conditions increase, pond restoration may be necessary to ensure availability of permanent hydroperiod ponds and a higher probability of persistence of Chiricahua leopard frogs in the Altar Valley, Arizona, USA.

Literature Cited

- Amburgey, S., L. Bailey, M. Murphy, E. Muths, and W. Funk. 2014. The effects of hydropattern and predator communities on amphibian occupancy. Canadian Journal of Zoology 92:927-937.
- Amburgey, S., W. C. Funk, M. Murphy, and E. Muths. 2012. Effects of hydroperiod duration on survival, developmental rate, and size at metamorphosis in boreal chorus frog tadpoles (Pseudacris maculata). Herpetologica 68:456-467.
- Archer, S. R., and K. I. Predick. 2008. Climate change and ecosystems of the southwestern United States. Rangelands 30:23-28.
- Bay, R., R. Harrigan, V. Underwood, H. Gibbs, T. Smith, and K. Ruegg. 2018. Genomic signals of selection predict climate-driven population declines in a migratory bird. Science 359:83-86.
- Beissinger, S. R. 2002. Population viability analysis: past, present, future. Population viability analysis:5-17.
- Beissinger, S. R., and D. R. McCullough. 2002, Population viability analysis, University of Chicago Press.
- Bezy, J. H., Charles, F.; Bahre, Conrad J. 2007, Buenos Aires National Wildlife Refuge, Arizona, University of Arizona.
- Blair, W. F. 1957, Changes in vertebrate populations under conditions of drought Cold Spring Harbor Symposia on Quantitative Biology 22:273-275.
- Chandler, R. B., E. Muths, B. H. Sigafus, C. R. Schwalbe, C. J. Jarchow, and B. R. Hossack.
 2015. Spatial occupancy models for predicting metapopulation dynamics and viability following reintroduction. Journal of Applied Ecology 52:1325-1333.

- Conroy, M. J., and J. T. Peterson. 2013, Decision making in natural resource management: a structured, adaptive approach, John Wiley & Sons.
- Dai, A., K. E. Trenberth, and T. Qian. 2004. A global dataset of Palmer Drought Severity Index for 1870–2002: relationship with soil moisture and effects of surface warming. Journal of Hydrometeorology 5:1117-1130.
- Dodd Jr, C. K. 1993. Cost of living in an unpredictable environment: the ecology of striped newts Notophthalmus perstriatus during a prolonged drought. Copeia:605-614.
- Fischlin, A., G. F. Midgley, L. Hughs, J. Price, R. Leemans, B. Gopal, C. Turley et al. 2007. Ecosystems, their properties, goods and services.
- Foden, W. B., S. H. Butchart, S. N. Stuart, J.-C. Vié, H. R. Akçakaya, A. Angulo, L. M.DeVantier et al. 2013. Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. PloS one 8:e65427.
- Green, A. W., and L. L. Bailey. 2015. Using Bayesian Population Viability Analysis to Define Relevant Conservation Objectives. PloS one 10:e0144786.
- Gutzler, D. S., and T. O. Robbins. 2011. Climate variability and projected change in the western United States: regional downscaling and drought statistics. Climate Dynamics 37:835-849.
- Hanski, I. 1999, Metapopulation ecology, v. 312, Oxford University Press Oxford.
- Hanski, I., A. Moilanen, T. Pakkala, and M. Kuussaari. 1996. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. Conservation Biology 10:578-590.
- Hayes, M. P., and M. R. Jennings. 1986. Decline of ranid frog species in western North America: are bullfrogs (Rana catesbeiana) responsible? Journal of herpetology:490-509.

- Heard, G. W., M. A. McCarthy, M. P. Scroggie, J. B. Baumgartner, and K. M. Parris. 2013. A Bayesian model of metapopulation viability, with application to an endangered amphibian. Diversity and Distributions 19:555-566.
- Heinsohn, R., R. C. Lacy, D. B. Lindenmayer, H. Marsh, D. Kwan, and I. R. Lawler. 2004, Unsustainable harvest of dugongs in Torres Strait and Cape York (Australia) waters: two case studies using population viability analysis Animal Conservation forum 7:417-425.
- Howell, P. E., E. Muths, B. R. Hossack, B. H. Sigafus, and R. Chandler. In Press. Increasing connectivity between metapopulation ecology and landscape ecology. Ecology.
- Jarchow, C. J., B. R. Hossack, B. H. Sigafus, C. R. Schwalbe, and E. Muths. 2016. Modeling habitat connectivity to inform reintroductions: a case study with the Chiricahua Leopard Frog. Journal of Herpetology.
- Joshi, J., B. Schmid, M. Caldeira, P. Dimitrakopoulos, J. Good, R. Harris, A. Hector et al. 2001. Local adaptation enhances performance of common plant species. Ecology Letters 4:536-544.
- Last, P. R., W. T. White, D. C. Gledhill, A. J. Hobday, R. Brown, G. J. Edgar, and G. Pecl. 2011. Long-term shifts in abundance and distribution of a temperate fish fauna: a response to climate change and fishing practices. Global Ecology and Biogeography 20:58-72.
- MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200-2207.
- McElderry, R. M., M. H. Salvato, and C. C. Horvitz. 2015. Population viability models for an endangered endemic subtropical butterfly: effects of density and fire on population dynamics and risk of extinction. Biodiversity and conservation 24:1589-1608.

- Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology. Sinauer, Sunderland, Massachusetts, USA.
- Mortensen, J. L., and J. M. Reed. 2016. Population Viability and Vital Rate Sensitivity of an Endangered Avian Cooperative Breeder, the White-Breasted Thrasher (Ramphocinclus brachyurus). PloS one 11:e0148928.
- Olsen, M. T., L. W. Andersen, R. Dietz, J. Teilmann, T. Härkönen, and H. R. Siegismund. 2014. Integrating genetic data and population viability analyses for the identification of harbour seal (Phoca vitulina) populations and management units. Molecular ecology 23:815-831.
- Oppel, S., G. Hilton, N. Ratcliffe, C. Fenton, J. Daley, G. Gray, J. Vickery et al. 2014. Assessing population viability while accounting for demographic and environmental uncertainty. Ecology 95:1809-1818.
- Peterson, A. T. 2003. Projected climate change effects on Rocky Mountain and Great Plains birds: generalities of biodiversity consequences. Global Change Biology 9:647-655.
- Schloss, C. A., T. A. Nuñez, and J. J. Lawler. 2012. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. Proceedings of the National Academy of Sciences 109:8606-8611.
- Semlitsch, R. D. 1987. Relationship of pond drying to the reproductive success of the salamander Ambystoma talpoideum. Copeia:61-69.
- —. 2000. Principles for management of aquatic-breeding amphibians. The Journal of wildlife management:615-631.
- —. 2002. Critical elements for biologically based recovery plans of aquatic-breeding
 amphibians. Conservation biology 16:619-629.

- Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. Rodrigues, D. L. Fischman, and R. W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783-1786.
- Taylor, B. E., D. E. Scott, and J. W. Gibbons. 2006. Catastrophic reproductive failure, terrestrial survival, and persistence of the marbled salamander. Conservation Biology 20:792-801.
- Tischendorf, L., and L. Fahrig. 2001. On the use of connectivity measures in spatial ecology. A reply. Oikos 95:152-155.
- Trenham, P. C., and H. B. Shaffer. 2005. Amphibian upland habitat use and its consequences for population viability. Ecological Applications 15:1158-1168.
- USFWS. 2007. Chiricahua leopard frog (Rana chiricahuensis) recovery plan. Albuquerque, NM, Technical report, U.S. Fish and Wildlife Service.
- Walls, S. C., W. J. Barichivich, and M. E. Brown. 2013. Drought, deluge and declines: the impact of precipitation extremes on amphibians in a changing climate. Biology 2:399-418.
- Welch, N. E., and J. A. MacMahon. 2005. Identifying habitat variables important to the rare Columbia spotted frog in Utah (USA): an information-theoretic approach. Conservation Biology 19:473-481.

Table 4.1. Posterior mean, median, standard deviation, and 95% credible intervals for metapopulation models assuming no influence of environmental variation on dynamics (Static) and PDSI (Drought).

		Static					Drought						
Parameter	Description	Mean	SD	2.5	Median	97.5	Mean	SD	2.5	Median	97.5		
sigma	Scale parameter of colonization function	3.54	0.80	2.30	3.42	5.36	3.43	0.82	2.10	3.33	5.32		
gamma1	Baseline colonization at intermittent ponds	0.02	0.01	0.01	0.02	0.05	0.02	0.01	0.01	0.02	0.05		
gamma2	Baseline colonization at semi- permanent ponds	0.22	0.08	0.09	0.22	0.40	0.26	0.08	0.11	0.25	0.44		
gamma3	Baseline colonization at permanent ponds	0.15	0.12	0.03	0.12	0.52	0.18	0.18	0.03	0.12	0.75		
epsilon1	Extinction probability at intermittent ponds	0.85	0.11	0.58	0.87	0.99	1.00	1.00	0.51	1.00	1.00		
epsilon2	Extinction probability at semi- permanent ponds	0.79	0.15	0.46	0.82	0.99	1.00	1.00	0.66	1.00	1.00		
epsilon3	Extinction probability at permanent ponds	0.13	0.11	0.02	0.10	0.40	0.04	0.98	0.00	0.04	1.00		
epsilon4	Effect of drought on pond level extinction rate	NA	NA	NA	NA	NA	0.26	0.98	0.00	0.44	0.97		
beta0	Intercept of detection model	0.89	0.57	0.83	0.89	0.93	0.88	0.57	0.82	0.88	0.93		
beta1	Effect of temperature on detection	0.57	0.59	0.42	0.56	0.75	0.56	0.59	0.41	0.54	0.74		
beta2	Effect of wind on detection	0.46	0.58	0.32	0.46	0.61	0.45	0.58	0.31	0.45	0.60		
z2003	Number of occupied ponds in 2003	3	0	3	3	3	3	0	3	3	3		
z2004	Number of occupied ponds in 2004	4.42	1.34	2	4	7	4.44	1.33	2	4	7		
z2005	Number of occupied ponds in 2005	5.59	1.79	3	5	10	5.54	1.74	3	5	9		
z2006	Number of occupied ponds in 2006	6.71	2.03	3	6	11	6.63	1.94	3	6	11		

z2007	Number of occupied ponds in 2007	7.90	1.97	5	8	13	7.94	1.94	5	8	13
z2008	Number of occupied ponds in 2008	9.61	2.20	6	9	15	9.36	2.02	6	9	14
z2009	Number of occupied ponds in 2009	9.48	2.54	6	9	15	9.19	2.40	6	9	15
z2010	Number of occupied ponds in 2010	10.11	2.73	6	10	16	9.51	2.45	6	9	15
z2011	Number of occupied ponds in 2011	12.79	2.86	8	12	19	12.32	2.61	8	12	18
z2012	Number of occupied ponds in 2012	10.98	3.06	6	11	18	10.21	2.71	6	10	16
z2013	Number of occupied ponds in 2013	13.89	3.23	9	13	21	13.00	2.86	8	13	20
z2014	Number of occupied ponds in 2014	17.63	3.43	12	17	26	17.03	3.11	12	17	24
z2015	Number of occupied ponds in 2015	23.24	3.85	18	23	33	22.76	3.66	17	22	32
z2016	Number of occupied ponds in 2016	20.33	4.57	14	20	31	19.74	4.17	14	19	30
z2017	Number of occupied ponds in 2017	19.46	5.41	12	18	33	18.63	4.93	11	18	31



Figure 4.1. Hydroperiod of ponds (human-made stock tanks) available for Chiricahua leopard frogs within the Buenos Aires National Wildlife Refuge (black polygon) and surrounding State Trust land in Arizona, USA. Dark gray symbols are ponds where frogs were reintroduced in 2003. Light gray symbols are ponds that are surveyed annually (presence-absence data 2007-2011, count data 2012-present). Symbols with black dots in them denote ponds where frogs have been found in at least one year from 2007-2015.



Figure 4.2. Mean (triangle = Static, circle = Drought) and 95% credible intervals (black lines = Static, blue lines = Drought) for the percent occupied ponds in each year on the Buenos Aires National Wildlife refuge, Arizona, USA. Projections (2018-2043) are based on Static or Drought models, assuming no management action and no ponds failed.



Figure 4.3. Mean proportion of occupied ponds over a 25 year time horizon for each model (Static, Stochastic, Drought) with varying levels of management (0, 1, 3, 6 ponds restored). The blow out line corresponds to a scenario where no ponds were restored, but permanent ponds were allowed to fail and remained unavailable throughout the projections.


Figure 4.4. Median (solid lines) and 95% credible intervals (dashed lines) for extinction risk over a 25 year time horizon for the Static and Drought models with varying levels of management (0, 1, 3, 6 ponds restored). The blow out line corresponds to a scenario where no ponds were restored, but permanent ponds were allowed to fail and remained unavailable throughout the projections.



Figure 4.5. Standardized Palmer Drought Severity Index (PDSI) over time (2003-2017). PDSI from 2015-2017 was predicted using a linear model of PDSI varying as a function of time.

CHAPTER 5

CONCLUSIONS

As landscapes become increasingly fragmented, the distributions of individuals will likely become more patchy, thereby increasing the relevance of metapopulation theory to conservation efforts (Hanski 1999). Spatio-temporal metapopulation dynamics are dependent on the demographic processes occurring within suitable patches and dispersal of individuals between patches (Hanski 1999; Hanski 2001). Hierarchical statistical models are powerful tools for bringing theory to bear when quantifying the patch and landscape level factors affecting metapopulation dynamics and for making probabilistic forecasts of metapopulation viability in the face of uncertainty.

Research in spatially-explicit metapopulation ecology has provided a wealth of theory for exploring how variation in patch quality and landscape structure influence metapopulation dynamics. However, spatially-explicit statistical metapopulation models have treated the landscape in between suitable patches as homogeneous (Risk et al. 2011; Sutherland et al. 2012; Chandler et al. 2015; Heard et al. 2015). This simplifying assumption of a homogenous landscape has prevented a synthetic understanding of the role of landscape structure in spatiotemporal metapopulation dynamics. Another gap in our understanding of metapopulation dynamics comes from the focus on modeling occurrence rather than abundance and density (Hanski 1999). Statistical models that can be used to estimate patch density, allow for testing hypotheses regarding the influence of demographic processes on extinction and colonization that underlie metapopulation dynamics. In addition to describing current and past spatio-temporal trends in metapopulation dynamics, metapopulation models can be used to make probabilistic predictions of viability in the face of future uncertainty (e.g., climate, management). For models of species' population viability to be useful, such models should be able to predict the consequences of management prescriptions (Sauer et al. 2013), while propagating the uncertainty in the sampling process, parameter estimation and trends in future environmental scenarios.

Through the development and enhancement of spatially-explicit metapopulation models, my results have increased the potential for using ecological theory in applied contexts (Chapters 2 and 3). The models developed and applied in each chapter are based on first principles of ecology and can be used to formalize hypotheses regarding the dynamics of real metapopulations. In Chapter 2, I was able to directly estimate landscape resistance in a metapopulation framework and quantify the influence of the landscape matrix on the colonization process. In the Chiricahua leopard frog system, landscape resistance increased with increasing elevation and distance to the nearest streambed. Colonization rate was also influenced by patch quality, with semi-permanent and permanent ponds contributing substantially more to the colonization of neighboring ponds relative to intermittent ponds. In Chapter 3, I developed a general statistical framework based on spatially-realistic metapopulation theory for estimating metapopulation abundance, using multiple data sets. This modeling framework is sufficiently flexible to estimate the influence of patch characteristics and density on local dynamics, emigration and immigration rates. Pond-specific population growth was influenced by pond hydroperiod and pond-specific density, such that semi-permanent patches with low densities of adult frogs experienced the highest annual population growth. Contrary to other metapopulation studies, emigration probability was not influenced by patch quality.

In addition to improving our ability to test tenets of ecological theory, the models developed herein can be used to predict future metapopulation extinction risk while propagating uncertainty in the sampling process, parameter estimation and future environmental conditions (Chapter 4). If environmental conditions remain static and invasive species that also rely on permanent ponds continue to be monitored and removed, metapopulation extinction risk was low (7%) over a 25-yr time horizon. However, if drought conditions continue to worsen and catastrophic tank failure occurs, metapopulation extinction risk may continue to increase (40% by 2043) regardless of functional connectivity and continued removal of invasive species. In this case, pond maintenance and restoration may be necessary to reduce extinction risk and improve long-term metapopulation viability.

Although I was able to develop a spatially-explicit, abundance-based metapopulation model, I only considered the influence of patch characteristics on the dispersal process. Future work should test hypotheses about whether emigration or immigration is influenced by local density. The focus of my dissertation was the federally-threatened Chiricahua leopard frog, however, there are several co-occurring amphibian species that temporally use aquatic habitat during the summer monsoons. Future work will focus on fitting spatially-explicit models to data collected on these other species to investigate whether this episodic influx of individuals has an impact on the metapopulation dynamics of the Chiricahua leopard frog. In this way we can gain a better understanding of how the community dynamics function within the BANWR.

Spatially-realistic metapopulation theory provides hypotheses and predictions for the potential influence of patch quality and patch dispersion on extinction and colonization rates that influence metapopulation dynamics over space and time (Hanski 2001). Until now what has been largely missing are statistical models that allow for the explicit estimation of how landscape

resistance influences colonization rates and spatially-explicit models estimating the effects of demographic processes on metapopulation dynamics. By developing modeling frameworks for addressing these concerns, I have attempted to enhance the applicability of existing spatiallyexplicit metapopulation theory, and to learn about the patch and landscape-scale factors affecting Chiricahua leopard frog metapopulation dynamics. The ultimate goal being an ability to use statistical models and data collected through traditional monitoring programs to provide probabilistic predictions of viability.

Literature Cited

Chandler, R. B., E. Muths, B. H. Sigafus, C. R. Schwalbe, C. J. Jarchow, and B. R. Hossack.
2015. Spatial occupancy models for predicting metapopulation dynamics and viability following reintroduction. Journal of Applied Ecology 52:1325-1333.

Hanski, I. 1999, Metapopulation ecology, v. 312, Oxford University Press Oxford.

- —. 2001. Spatially realistic theory of metapopulation ecology. Naturwissenschaften 88:372-381.
- Heard, G. W., C. D. Thomas, J. A. Hodgson, M. P. Scroggie, D. S. Ramsey, and N. Clemann.2015. Refugia and connectivity sustain amphibian metapopulations afflicted by disease.Ecol Lett 18:853-863.
- Risk, B. B., P. De Valpine, and S. R. Beissinger. 2011. A robust-design formulation of the incidence function model of metapopulation dynamics applied to two species of rails. Ecology 92:462-474.
- Sauer, J. R., P. J. Blank, E. F. Zipkin, J. E. Fallon, and F. W. Fallon. 2013. Using multi-species occupancy models in structured decision making on managed lands. The Journal of Wildlife Management 77:117-127.
- Sutherland, C., D. A. Elston, and X. Lambin. 2012. Multi-scale processes in metapopulations: contributions of stage structure, rescue effect, and correlated extinctions. Ecology 93:2465-2473.

APPENDIX A

STOCK TANK IMAGE



APPENDIX A. STOCK TANK IMAGE. Example of an earthen, man-made stock tank originally intended for use by cattle. Ranching is no longer permitted on the Buenos Aires National Wildlife Refuge. Stock tanks constitute the majority of available breeding sites for amphibians in the Altar Valley of Arizona.

APPENDIX B

PRIOR DISTRIBUTIONS

APPENDIX B. PRIOR DISTRIBUTIONS. Prior distributions for parameters estimated in the

spatially-explicit occupancy model.

Parameter	Symbol	Prior
Linear effect of elevation or distance to streambed on	0	
landscape resistance	u_1	Norm(0, 10)
Scale parameter of colonization function	σ	Gamma(0.001, 0.001)
Baseline colonization probability at intermittent		
patches	$ ho_1$	Uniform(- ∞,∞)
Baseline colonization probability at semi-permanent		
patches	$ ho_2$	Uniform($-\infty,\infty$)
Baseline colonization probability at permanent		
patches	$ ho_3$	Uniform(- ∞ , ∞)
Extinction probability at intermittent patches	\mathcal{E}_1	Beta(1, 1)
Extinction probability at semi-permanent patches	\mathcal{E}_2	Beta(1, 1)
Extinction probability at permanent patches	\mathcal{E}_3	Beta(1, 1)
Intercept of logit-linear detection model	β_0	Norm(0, 10)
Effect of temperature on logit(p)	β_1	Norm(0, 10)
Effect of wind on logit(p)	β_2	Norm(0, 10)

APPENDIX C

R SCRIPT FOR MCMC ALGORITHM

library(compiler)

```
## MCMC algorithm
dynroccH <- function(y,</pre>
                                  # nSampled x nVisits x nYear
array of detection/non-detection data
                                   # nSites x 2 matrix of site
                    x,
coordinates. Note that nSampled will usually be <nSites
                                   # resistance covariate
                    r.cov1,
                    r.cov2=NULL,  # resistance covariate
                    e.cov,
                                  # extinctio covariate
                                  # detection covariate
                    p.cov1,
                                  # detection covariate
                    p.cov2,
                    nIter=10,
                                  # MCMC iterations
                                   # Tuning order:
                    tune,
sigma,gamma0.i,gamma0.s,gamma0.p,eps.i,eps.s,eps.p,
beta0, beta1, beta2, alpha[1], alpha[2] (12 in total)
                    estAlpha=TRUE, # Estimate the resistance
coefficient?
                    inits=NULL, # until you run algorithm,
inits are based on what is given.
                    zProp=c("ind","vec"), # Update z matrix by
either proposing z(i,k) or z(,k), respectively
                    zProbs=NULL, # matrix of proposal probs
use if zProp="vec"
                    monitor.z=FALSE, # store each iteration of
the z matrix?
                    report=0, # Only report progress if >0
                    plot.z=FALSE, # Plot the latent presence-
absence state (if report>0)
                               # This will reject a proposal of
                    tol=0)
z(i,k)=1 if mu(i,k-1) < tol
{
  zProp <- match.arg(zProp)</pre>
  ## Dimensions
 nSites <- nrow(x) #Number of possible sites instead of only
the sites sampled
 nReps <- ncol(y)</pre>
 nYears <- dim(y)[3]
  ## Using this to avoid likelihood calculations for sites not
sampled
```

```
nSampled <- nrow(y)</pre>
  dataYears <- apply(!is.na(y), 3, any)</pre>
  anyDetections <- matrix(FALSE, nSites, nYears)</pre>
  anyDetections[1:nSampled,] <- apply(y, c(1,3), sum,</pre>
na.rm=TRUE) > 0
  #Failed is a chr string with names of sites no longer sampled
because they were destroyed
  known0 <- matrix(FALSE, nSites, nYears)</pre>
  rownames(known0) <- rownames(x)</pre>
  known0[failed, 8:nYears] <- TRUE</pre>
  notFailed <- 1 - known0</pre>
  if(any(anyDetections & known0))
       stop("detection data doesn't match blowout data")
  y.wide <- matrix(y, nSampled)</pre>
  isInter <- e.cov=="Intermittent"</pre>
  isSemi <- e.cov=="Semi-permanent"</pre>
  isPerm <- e.cov=="Permanent"</pre>
  epsilon <- rep(NA, nSites)</pre>
  gamma0 <- rep(NA, nSites)</pre>
    rc2 <- is.null(r.cov2)</pre>
    if(rc2) {
      r.cov2 <- r.cov1
       }
  ## initial values
  gamma <- muz <- matrix(NA, nSites, nYears-1)</pre>
  if(is.null(inits)) {
      epsilon.p<-epsilon.s<-epsilon.i<-runif(1)</pre>
      sigma <- runif(1,3,4)
      gamma0.i <- runif(1, 0.01, 0.3)
      gamma0.s <- runif(1, 0.01, 0.3)
      gamma0.p <- runif(1, 0.01, 0.3)
      gamma0[isInter] <- gamma0.i</pre>
      gamma0[isSemi] <- gamma0.s</pre>
      gamma0[isPerm] <- gamma0.p</pre>
      beta0<-runif(1, 0.1, 0.6)
      epsilon[isInter] <- epsilon.i</pre>
      epsilon[isSemi] <- epsilon.s</pre>
      epsilon[isPerm] <- epsilon.p</pre>
      beta0 <- rnorm(1)</pre>
```

```
beta1 <- rnorm(1)
beta2 <- rnorm(1)
alpha <- c(0, 0)
p <- plogis(beta0 + beta1*p.cov1 + beta2*p.cov2)
z <- matrix(0, nSites, nYears)
#Which sites were the reintroduction sites
reintroSites <- which(rownames(coords) %in% c("Carpenter
Tank", "Rock Tank", "HQ Breeding Site"))
```

z[reintroSites,1] <- 1</pre>

NOTE: For some organisms and systems the maximum dispersal distance within a single time step (e.g., annual) may be known and it could be considered very unlikely that colonists would arrive from patches exceeding this distance. To speed up computation, a neighborhood matrix for each patch could be supplied to eliminate consideration of colonization from neighboring patches that exceed a reasonable distance from the focal patch.

```
## create resistance surface
      cost <- exp(alpha[1]*r.cov1 + alpha[2]*r.cov2)</pre>
      ## calculate conductances among neighbors
      tr1 <- transition(cost, transitionFunction=function(x)</pre>
1/mean(x), directions=16)
      #adjust diag.conductances
      trlCorrC <- geoCorrection(trl, type="c",</pre>
multpl=FALSE, scl=FALSE)
      ## calculate least cost distance between all pairs of
sites.
      if(!estAlpha)
           alpha <- c(0,0) ## Force alpha to be 0 if you aren't
estimating it. Results in appox Euclidean dist
      #calculate the ecological distance matrix
      D <- costDistance(tr1CorrC,x,x)/1000</pre>
      G \leq \operatorname{gamma0*exp}(-D^2/(2*\operatorname{sigma^2}))
      for(k in 2:nYears) {
           PrNotColonizedByNeighbor <- 1 - gamma0*exp(-</pre>
D^2/(2*sigma^2)) * t(z[,rep(k-1, nSites)])
           PrNotColonizedAtAll <- apply(PrNotColonizedByNeighbor,</pre>
1, prod)
           gamma[,k-1] <- 1 - PrNotColonizedAtAll</pre>
           muz[,k-1] <- z[,k-1]*(1-epsilon*(1-qamma[,k-1])) + (1-</pre>
z[,k-1])*gamma[,k-1] #Rescue effect
```

```
muz[,k-1] <- muz[,k-1]*notFailed[,k] #Exclude 3 sites</pre>
no longer sampled
           z[,k] <- rbinom(nSites, 1, muz[,1])</pre>
           z[known0[,k],k] <- 0</pre>
           z[which(anyDetections[,k]),k] <- 1</pre>
       }
  } else {
      gamma0.i <- inits$samples["gamma0.i"]</pre>
      gamma0.s <- inits$samples["gamma0.s"]</pre>
      gamma0.p <- inits$samples["gamma0.p"]</pre>
      gamma0[isInter] <- gamma0.i</pre>
      gamma0[isSemi] <- gamma0.s</pre>
      gamma0[isPerm] <- gamma0.p</pre>
       sigma <- inits$samples["sigma"]</pre>
      epsilon.i <- inits$samples["epsilon.i"]</pre>
      epsilon.s <- inits$samples["epsilon.s"]</pre>
      epsilon.p <- inits$samples["epsilon.p"]</pre>
      epsilon <- rep(NA, nSites)</pre>
      epsilon[isInter] <- epsilon.i</pre>
      epsilon[isSemi] <- epsilon.s</pre>
      epsilon[isPerm] <- epsilon.p</pre>
      alpha<-c(inits$samples["alpha1"],inits$samples["alpha2"])</pre>
      D <- inits$D
      beta0 <- inits$samples["beta0"]</pre>
      beta1 <- inits$samples["beta1"]</pre>
      beta2 <- inits$samples["beta2"]</pre>
      p <- plogis(beta0 + beta1*p.cov1 + beta2*p.cov2)</pre>
      z <- inits$z
       .Random.seed <- inits$seed ## use same random seed as
before
  }
  ll.z <- matrix(0, nSites, nYears)</pre>
  ll.y <- array(0, c(nSampled, nReps, nYears))</pre>
  for(k in 2:nYears) {
       PrNotColonizedByNeighbor <- 1 - gamma0*exp(-D^2/(2*sigma^2))</pre>
)) *t(z[,rep(k-1, nSites)])
      PrNotColonizedAtAll <- apply(PrNotColonizedByNeighbor, 1,</pre>
prod)
      gamma[,k-1] <- 1 - PrNotColonizedAtAll</pre>
      muz[,k-1] <- z[,k-1]*(1-epsilon*(1-gamma[,k-1])) + (1-</pre>
z[,k-1])*gamma[,k-1] #PH rescue effect
      muz[,k-1] <- muz[,k-1]*notFailed[,k]</pre>
      ll.z[,k-1] <- dbinom(z[,k], 1, muz[,k-1], log=TRUE)</pre>
      if (k > 4) { ## Ignore first 4 years without data
```

```
## Now p has the same dimensions of y. No need to do
p[,,k-4]
           ## p is now an array. Note k-4 b/c p only has 6 years.
Should make dims of p and y consistent
           ll.y[,,k] <- dbinom(y[,,k], 1, z[1:nSampled,k]*p[,,k],</pre>
log=TRUE)
      }
  ļ
  ll.z.cand <- ll.z</pre>
  ll.z.sum <- sum(ll.z)</pre>
  ll.y.cand <- ll.y</pre>
  ll.y.sum <- sum(ll.y, na.rm=TRUE)</pre>
  gamma.cand <- gamma</pre>
  muz.cand <- muz</pre>
    nz1 <- z ## Used to compute expected occupancy at each site
    zkup <- rep(0, nYears-1)</pre>
  ## posterior samples
  nPar <- 13+nYears
  samples <- array(NA, c(nIter, nPar))</pre>
  zK <- matrix(NA, nSites, nIter)</pre>
  colnames(samples) <- c("sigma", "gamma0.i", "gamma0.s",</pre>
"gamma0.p",
                           "epsilon.i", "epsilon.s", "epsilon.p",
                           "beta0", "beta1", "beta2", "alpha1",
"alpha2",
                           paste("zk", 1:nYears, sep=""),
"deviance")
  reportit <- report>0
    nzup <- rep(0, nYears-1)</pre>
  zA <- NULL
  if (monitor.z)
      zA <- array(NA integer , c(nSites, nYears, nIter))</pre>
  if(reportit) {
      cat("iter 1\n")
      cat("
             theta =",
round(c(sigma,gamma0.i,gamma0.s,gamma0.p,epsilon.i,epsilon.s,eps
ilon.p,beta0,beta1,beta2,alpha), 5), "\n")
                z[k] =", round(colSums(z), 2), "\n")
      cat("
      cat("
                ll.z =", round(sum(ll.z), 2), "\n")
                deviance =", round(-2*11.y.sum, 2), "\n")
      cat("
      cat("
                time =", format(Sys.time()), "\n")
```

```
if(plot.z) {
          library(lattice)
          zd <- data.frame(z=as.integer(z),</pre>
year=factor(rep(2003:2017, each=nSites)),
                            x=as.numeric(x[,1])/1000,
y=as.numeric(x[,2])/1000)
          print(xyplot(y ~ x | year, zd, groups=z, aspect="iso",
pch=c(1,16), as.table=TRUE))
      }
  }
  ## Sample from posteriors
  for(s in 1:nIter) {
    ll.z.sum <- sum(ll.z) ## This is important!</pre>
    if(reportit) {
    if (s %in% c(2:100) || s %% report == 0) {
      cat("iter", s, "\n")
              theta =", round(samples[s-1,1:12], 5), "n")
      cat("
               z[k] =", zk, "∖n")
      cat("
      cat("
               accepted", round(zkup/(nSites)*100, 1), "percent
of z[k] proposals \n")
      cat("
               sum(ll.z) =", ll.z.sum, "\n")
      cat("
               deviance =", round(samples[s-1, "deviance"], 2),
"\n")
      cat(" time =", format(Sys.time()), "\n")
      if(plot.z) {
          library(lattice)
          zd$z <- as.integer(z)</pre>
          print(xyplot(y ~ x | year, zd, groups=z, aspect="iso",
pch=c(1,16), as.table=TRUE))
      }
    }
    }
    if(estAlpha) {
      library(qdistance)
    #Metropolis update for alpha
    alpha1.cand <- rnorm(1, alpha[1], tune[11])</pre>
    #create resistance surface
    cost <- exp(alpha1.cand*r.cov1 + alpha[2]*r.cov2)</pre>
    ## calculate conductances among neighbors
    tr1 <- transition(cost, transitionFunction=function(x)</pre>
1/mean(x), directions=16)
```

```
trlCorrC <- geoCorrection(trl, type="c",</pre>
multpl=FALSE,scl=FALSE) #adjust diag.conductances
    ## calculate least cost distance between all pairs of sites.
    D.cand <- costDistance(tr1CorrC,x,x)/1000 #calculate the
ecological distance matrix
    G.cand <- gamma0*exp(-D.cand^2/(2*sigma^2))
    for(k in 2:nYears) {
      zkt <- matrix(z[,k-1], nSites, nSites, byrow=TRUE)</pre>
      gamma.cand[,k-1] <- 1 - exp(rowSums(log(1-G.cand*zkt)))</pre>
      muz.cand[,k-1] <- (z[,k-1]*(1-epsilon*(1-gamma.cand[,k-</pre>
1])) + (1-z[,k-1])*gamma.cand[,k-1])*notFailed[,k]
      ll.z.cand[,k-1] <- dbinom(z[,k], 1, muz.cand[,k-1],</pre>
log=TRUE)
    }
    prior.alpha.cand <- dnorm(alpha1.cand, 0, 10, log=TRUE)</pre>
    prior.alpha <- dnorm(alpha[1], 0, 10, log=TRUE)</pre>
    ll.z.sum.cand <- sum(ll.z.cand)</pre>
    if(runif(1) < exp((ll.z.sum.cand + prior.alpha.cand) -
                          (ll.z.sum + prior.alpha))) {
      alpha[1] <- alpha1.cand</pre>
      D <- D.cand
      G <- G.cand
      gamma <- gamma.cand</pre>
      muz <- muz.cand</pre>
      ll.z <- ll.z.cand</pre>
      ll.z.sum <- ll.z.sum.cand</pre>
      }
    if(!rc2) {
    #Metropolis update for alpha[2]
    alpha2.cand <- rnorm(1, alpha[2], tune[12])</pre>
    #create resistance surface
    cost <- exp(alpha[1]*r.cov1 + alpha2.cand*r.cov2)</pre>
    ## calculate conductances among neighbors
    tr1 <- transition(cost, transitionFunction=function(x)</pre>
1/mean(x), directions=16)
    trlCorrC <- geoCorrection(trl, type="c",</pre>
multpl=FALSE,scl=FALSE) #adjust diag.conductances
    ## calculate least cost distance between all pairs of sites.
    D.cand <- costDistance(tr1CorrC,x,x)/1000 #calculate the
ecological distance matrix
    G.cand <- gamma0*exp(-D.cand^2/(2*sigma^2))</pre>
```

```
for(k in 2:nYears) {
      zkt <- matrix(z[,k-1], nSites, nSites, byrow=TRUE)</pre>
      gamma.cand[,k-1] <- 1 - exp(rowSums(log(1-G.cand*zkt)))</pre>
      muz.cand[,k-1] <- (z[,k-1]*(1-epsilon*(1-gamma.cand[,k-</pre>
1])) + (1-z[,k-1])*gamma.cand[,k-1])*notFailed[,k]
      ll.z.cand[,k-1] <- dbinom(z[,k], 1, muz.cand[,k-1],</pre>
log=TRUE)
    }
    prior.alpha.cand <- dnorm(alpha2.cand, 0, 10, log=TRUE)
    prior.alpha <- dnorm(alpha[2], 0, 10, log=TRUE)</pre>
    ll.z.sum.cand <- sum(ll.z.cand)</pre>
    if(runif(1) < exp((ll.z.sum.cand + prior.alpha.cand) -</pre>
                           (ll.z.sum + prior.alpha))) {
      alpha[2] <- alpha2.cand</pre>
      D < - D.cand
      G <- G.cand
      gamma <- gamma.cand
      muz <- muz.cand</pre>
      ll.z <- ll.z.cand
      ll.z.sum <- ll.z.sum.cand</pre>
      }
    }
}
    ## Metropolis update for sigma
    sigma.cand <- rnorm(1, sigma, tune[1])</pre>
    if(sigma.cand > 0) {
         G.cand <- gamma0*exp(-D^2/(2*sigma.cand^2))
      for(k in 2:nYears) {
         zkt <- matrix(z[,k-1], nSites, nSites, byrow=TRUE)</pre>
         gamma.cand[,k-1] <- 1 - exp(rowSums(log(1-G.cand*zkt)))</pre>
        muz.cand[,k-1] <- (z[,k-1]*(1-epsilon*(1-gamma.cand[,k-</pre>
1])) + (1-z[,k-1])*gamma.cand[,k-1])*notFailed[,k]
        ll.z.cand[,k-1] <- dbinom(z[,k], 1, muz.cand[,k-1],</pre>
log=TRUE)
      }
      prior.sigma.cand <- dgamma(sigma.cand, 0.001, 0.001)</pre>
      prior.sigma <- dgamma(sigma, 0.001, 0.001)</pre>
      ll.z.sum.cand <- sum(ll.z.cand)</pre>
      if(runif(1) < exp((ll.z.sum.cand + prior.sigma.cand) -
                           (ll.z.sum + prior.sigma))) {
           sigma <- sigma.cand</pre>
           gamma <- gamma.cand</pre>
           ll.z <- ll.z.cand</pre>
           ll.z.sum <- ll.z.sum.cand</pre>
```

```
114
```

```
muz <- muz.cand</pre>
           G <- G.cand
      }
    }
    #Metropolis update for gamma0 at intermittent sites (part of
the gammaDist calculation)
      prior.gamma0.cand <- prior.gamma0 <- 0</pre>
    gamma0.i.cand <- rnorm(1, gamma0.i, tune[2])</pre>
    if(gamma0.i.cand > 0 & gamma0.i.cand < 1) {
        gamma0.cand <- gamma0</pre>
        gamma0.cand[isInter] <- gamma0.i.cand</pre>
        G.cand <- gamma0.cand*exp(-D^2/(2*sigma^2)
                                                       ))
      for(k in 2:nYears) { #nYears
         zkt <- matrix(z[,k-1], nSites, nSites, byrow=TRUE)</pre>
        gamma.cand[,k-1] <- 1 - exp(rowSums(log(1-G.cand*zkt)))</pre>
        muz.cand[,k-1] <- (z[,k-1]*(1-epsilon*(1-gamma.cand[,k-</pre>
1])) + (1-z[,k-1])*gamma.cand[,k-1])*notFailed[,k]
        ll.z.cand[,k-1] <- dbinom(z[,k], 1, muz.cand[,k-1],</pre>
log=TRUE)
    }
      ll.z.sum.cand <- sum(ll.z.cand)</pre>
      if(runif(1) < exp((ll.z.sum.cand + prior.gamma0.cand) -
                          (ll.z.sum + prior.gamma0))) {
        gamma0.i <- gamma0.i.cand
        gamma0 <- gamma0.cand</pre>
        gamma <- gamma.cand
        muz <- muz.cand</pre>
        ll.z <- ll.z.cand</pre>
        ll.z.sum <- ll.z.sum.cand</pre>
        G <- G.cand
    }
  }
    #Metropolis update for gamma0 at semi-permanent sites (part
of the gammaDist calculation)
    gamma0.s.cand <- rnorm(1, gamma0.s, tune[3])</pre>
    if (gamma0.s.cand > 0 & gamma0.s.cand < 1) {
        gamma0.cand <- gamma0</pre>
        gamma0.cand[isSemi] <- gamma0.s.cand</pre>
        G.cand <- gamma0.cand*exp(-D^2/(2*sigma^2))
      for(k in 2:nYears) { #nYears
         zkt <- matrix(z[,k-1], nSites, nSites, byrow=TRUE)</pre>
        qamma.cand[,k-1] <- 1 - exp(rowSums(log(1-G.cand*zkt)))</pre>
```

```
muz.cand[,k-1] <-(z[,k-1]*(1-epsilon*(1-gamma.cand[,k-</pre>
1])) + (1-z[,k-1])*gamma.cand[,k-1])*notFailed[,k]
         ll.z.cand[,k-1] <- dbinom(z[,k], 1, muz.cand[,k-1],</pre>
log=TRUE)
    }
      ll.z.sum.cand <- sum(ll.z.cand)</pre>
      if(runif(1) < exp((ll.z.sum.cand + prior.gamma0.cand) -
                           (ll.z.sum + prior.gamma0))) {
         gamma0.s <- gamma0.s.cand</pre>
         gamma0 <- gamma0.cand</pre>
        gamma <- gamma.cand
        muz <- muz.cand</pre>
         ll.z <- ll.z.cand</pre>
         ll.z.sum <- ll.z.sum.cand</pre>
        G <- G.cand
    }
  }
    #Metropolis update for gamma0 at permanent sites (part of
the gammaDist calculation)
    gamma0.p.cand <- rnorm(1, gamma0.p, tune[4])</pre>
    if(gamma0.p.cand > 0 & gamma0.p.cand < 1) {
         gamma0.cand <- gamma0</pre>
         gamma0.cand[isPerm] <- gamma0.p.cand</pre>
         G.cand <- gamma0.cand*exp(-D^2/(2*sigma^2)
                                                        ))
      for(k in 2:nYears) { #nYears
         zkt <- matrix(z[,k-1], nSites, nSites, byrow=TRUE)</pre>
         gamma.cand[,k-1] <- 1 - exp(rowSums(log(1-G.cand*zkt)))</pre>
        muz.cand[,k-1] <-(z[,k-1]*(1-epsilon*(1-gamma.cand[,k-</pre>
1])) + (1-z[,k-1])*gamma.cand[,k-1])*notFailed[,k]
         ll.z.cand[,k-1] <- dbinom(z[,k], 1, muz.cand[,k-1],
log=TRUE)
    }
      ll.z.sum.cand <- sum(ll.z.cand)</pre>
      if(runif(1) < exp((ll.z.sum.cand + prior.gamma0.cand) -</pre>
                           (ll.z.sum + prior.gamma0))) {
         gamma0.p <- gamma0.p.cand</pre>
         gamma0 <- gamma0.cand</pre>
        gamma <- gamma.cand
        muz <- muz.cand</pre>
         ll.z <- ll.z.cand
        ll.z.sum <- ll.z.sum.cand</pre>
        G <- G.cand
    }
  }
```

```
## Metropolis update for epsilon (intermittent sites)
    epsilon.i.cand <- rnorm(1, epsilon.i, tune[5])</pre>
    if(epsilon.i.cand > 0 & epsilon.i.cand < 1) {</pre>
        for(k in 2:nYears) {
             muz.cand[isInter,k-1] <- z[isInter,k-1]*(1-</pre>
epsilon.i.cand*(1-gamma[isInter,k-1])) + (1-z[isInter,k-
1])*gamma[isInter,k-1]
             muz.cand[isInter,k-1] <- muz.cand[isInter,k-</pre>
1] *notFailed[isInter,k]
             ll.z.cand[isInter,k-1] <- dbinom(z[isInter,k], 1,</pre>
muz.cand[isInter,k-1], log=TRUE)
        prior.epsilon.i.cand <- dbeta(epsilon.i.cand, 1, 1,</pre>
log=TRUE)
        prior.epsilon.i <- dbeta(epsilon.i, 1, 1, log=TRUE)</pre>
        if(runif(1) < exp((sum(ll.z.cand[isInter,]) +</pre>
prior.epsilon.i.cand) -
                            (sum(ll.z[isInter,]) +
prior.epsilon.i))) {
             epsilon.i <- epsilon.i.cand
             epsilon[isInter] <- epsilon.i.cand</pre>
             muz[isInter,] <- muz.cand[isInter,]</pre>
             ll.z[isInter,] <- ll.z.cand[isInter,]</pre>
        }
    }
    ## Metropolis update for epsilon (semi-permanent sites)
    epsilon.s.cand <- rnorm(1, epsilon.s, tune[6])</pre>
    if(epsilon.s.cand > 0 & epsilon.s.cand < 1) {</pre>
        for(k in 2:nYears) {
             muz.cand[isSemi,k-1] <- z[isSemi,k-1]*(1-</pre>
epsilon.s.cand*(1-gamma[isSemi,k-1])) + (1-z[isSemi,k-
1])*gamma[isSemi,k-1]
             muz.cand[isSemi,k-1] <- muz.cand[isSemi,k-</pre>
1]*notFailed[isSemi,k]
             ll.z.cand[isSemi,k-1] <- dbinom(z[isSemi,k], 1,</pre>
muz.cand[isSemi,k-1], log=TRUE)
        prior.epsilon.s.cand <- dbeta(epsilon.s.cand, 1, 1,</pre>
log=TRUE)
        prior.epsilon.s <- dbeta(epsilon.s, 1, 1, log=TRUE)
        if(runif(1) < exp((sum(ll.z.cand[isSemi,]) +</pre>
prior.epsilon.s.cand) -
                            (sum(ll.z[isSemi,]) +
prior.epsilon.s))) {
```

```
epsilon.s <- epsilon.s.cand
             epsilon[isSemi] <- epsilon.s.cand</pre>
             muz[isSemi,] <- muz.cand[isSemi,]</pre>
             ll.z[isSemi,] <- ll.z.cand[isSemi,]</pre>
         }
    }
    ## Metropolis update for epsilon (permanent sites)
    epsilon.p.cand <- rnorm(1, epsilon.p, tune[7])</pre>
    if(epsilon.p.cand > 0 & epsilon.p.cand < 1) {</pre>
         for(k in 2:nYears) {
             muz.cand[isPerm,k-1] <- z[isPerm,k-1]*(1-</pre>
epsilon.p.cand*(1-gamma[isPerm,k-1])) + (1-z[isPerm,k-
1])*gamma[isPerm,k-1]
             muz.cand[isPerm,k-1] <- muz.cand[isPerm,k-</pre>
1]*notFailed[isPerm,k]
             ll.z.cand[isPerm,k-1] <- dbinom(z[isPerm,k], 1,</pre>
muz.cand[isPerm,k-1], log=TRUE)
        prior.epsilon.p.cand <- dbeta(epsilon.p.cand, 1, 1,</pre>
log=TRUE)
        prior.epsilon.p <- dbeta(epsilon.p, 1, 1, log=TRUE)</pre>
         if(runif(1) < exp((sum(ll.z.cand[isPerm,]) +</pre>
prior.epsilon.p.cand) -
                             (sum(ll.z[isPerm,]) +
prior.epsilon.p))) {
             epsilon.p <- epsilon.p.cand</pre>
             epsilon[isPerm] <- epsilon.p.cand</pre>
             muz[isPerm,] <- muz.cand[isPerm,]</pre>
             ll.z[isPerm,] <- ll.z.cand[isPerm,]</pre>
         }
    }
    ## update z
    ## We can update each z(i,t) individually, and it results in
better mixing than updating a vector of z's
    zkup <- rep(0, nYears-1)</pre>
   for(k in 2:nYears) {
       anyDet <- anyDetections[,k]==1</pre>
       zknown <- anyDet | !notFailed[,k]</pre>
       prop.back <- prop.cand <- 0</pre>
       for(i in 1:nSites) {
                                   118
```

```
if(zknown[i])
                next
            ## Reject highly unlikely proposals (before proposing
them)
            ## This speed trick shouldn't affect anything but
            ## can double check by changing toleranc (tol)
            if(z[i,k]<1 & muz[i,k-1]<tol)
                next
            zk.wide <- matrix(z[,k], nSites, nReps)</pre>
            zk.cand < - z[,k]
            zk.cand[i] < -1-z[i,k]
            zk.cand.wide <- matrix(zk.cand, nSites, nReps)</pre>
            11.y.tmp <- 0
            ll.y.cand.tmp <- 0</pre>
            if((k > 4) \& (i \le nSampled)) \{ \#\# Ignore first 4 \}
years without data
                ll.y.cand.tmp <- dbinom(y[i,,k], 1,</pre>
zk.cand[i]*p[i,,k], log=TRUE)
                ll.y.tmp <- sum(ll.y[i,,k], na.rm=TRUE)</pre>
            }
            ## RC: Prior must be calculated for time k and k+1
b/c change in z affects both
            ll.z.cand[i,k-1] <- dbinom(zk.cand[i], 1, muz[i,k-1],</pre>
log=TRUE)
            11.z2 <- 11.z2.cand <- 0
            if(k < nYears) {</pre>
                zkt.cand <- matrix(zk.cand, nSites, nSites,</pre>
byrow=TRUE)
                gamma.cand[,k] <- 1 - exp(rowSums(log(1-</pre>
G*zkt.cand)))
                muz.cand[,k] <- (zk.cand*(1-epsilon*(1-</pre>
gamma.cand[,k])) + (1-zk.cand)*gamma.cand[,k])*notFailed[,k+1]
                ll.z.cand[,k] <- dbinom(z[,k+1], 1, muz.cand[,k],</pre>
log=TRUE)
                ll.z2 <- sum(ll.z[,k])</pre>
                ll.z2.cand <- sum(ll.z.cand[,k])</pre>
            }
            if(runif(1) < exp((sum(ll.y.cand.tmp, na.rm=TRUE) +</pre>
ll.z.cand[i,k-1] +
                                 ll.z2.cand + prop.back) -
                                (ll.y.tmp + ll.z[i, k-1] +
                                 11.z2 + prop.cand))) {
                z[,k] <- zk.cand</pre>
                ll.z[i,k-1] <- ll.z.cand[i,k-1]</pre>
                if(k < nYears) {</pre>
```

```
gamma[,k] <- gamma.cand[,k]</pre>
                     muz[,k] <- muz.cand[,k]</pre>
                     ll.z[,k] <- ll.z.cand[,k]</pre>
                 }
                if ((i <= nSampled) & (k>4)) {
                     ll.y[i,,k] <- ll.y.cand.tmp</pre>
                 }
                 zkup[k-1] <- zkup[k-1] + 1
            }
       }
   }
    nz1 <- nz1+z
    #Update for beta0
    beta0.cand<-rnorm(1, beta0, tune[8])</pre>
    p.cand <- plogis(beta0.cand + beta1*p.cov1 + beta2*p.cov2)</pre>
    z.wide <- z[,rep(1:nYears, each=nReps)]</pre>
    z.a <- array(z.wide, c(nSites, nReps, nYears))</pre>
    ll.y[,,dataYears] <- dbinom(y[,,dataYears], 1,</pre>
z.a[1:nSampled,,dataYears]*p[,,dataYears], log=TRUE)
    ll.y.cand[,,dataYears] <- dbinom(y[,,dataYears], 1,</pre>
z.a[1:nSampled,,dataYears]*p.cand[,,dataYears], log=TRUE)
    prior.beta0.cand <- dnorm(beta0.cand, 0, 10, log=TRUE)</pre>
    prior.beta0 <- dnorm(beta0, 0, 10, log=TRUE)</pre>
    ll.y.sum <- sum(ll.y, na.rm=TRUE)</pre>
    ll.y.sum.cand <- sum(ll.y.cand, na.rm=TRUE)</pre>
    if(runif(1) < exp((ll.y.sum.cand + prior.beta0.cand) -</pre>
                         (ll.y.sum + prior.beta0))) {
        beta0 <- beta0.cand</pre>
        p < - p.cand
        ll.y <- ll.y.cand</pre>
        ll.y.sum <- ll.y.sum.cand</pre>
    }
    #Update for beta1
    betal.cand<-rnorm(1, betal, tune[9])</pre>
    p.cand <- plogis(beta0 + beta1.cand*p.cov1 + beta2*p.cov2)</pre>
    z.wide <- z[,rep(1:nYears, each=nReps)]</pre>
    z.a <- array(z.wide, c(nSites, nReps, nYears))</pre>
    ll.y.cand[,,dataYears] <- dbinom(y[,,dataYears], 1,</pre>
z.a[1:nSampled,,dataYears]*p.cand[,,dataYears], log=TRUE)
    prior.betal.cand <- dnorm(betal.cand, 0, 10, log=TRUE)
```

```
prior.beta1 <- dnorm(beta1, 0, 10, log=TRUE)</pre>
    ll.y.sum.cand <- sum(ll.y.cand, na.rm=TRUE)</pre>
    if(runif(1) < exp((ll.y.sum.cand + prior.beta0.cand) -
                        (ll.y.sum + prior.beta0))) {
        beta1 <- beta1.cand</pre>
        p <- p.cand
        ll.y <- ll.y.cand
        ll.y.sum <- ll.y.sum.cand</pre>
    }
    #Update for beta2
    beta2.cand<-rnorm(1, beta2, tune[10])</pre>
    p.cand <- plogis(beta0 + beta1*p.cov1 + beta2.cand*p.cov2)</pre>
    z.wide <- z[,rep(1:nYears, each=nReps)]</pre>
    z.a <- array(z.wide, c(nSites, nReps, nYears))</pre>
    ll.y.cand[,,dataYears] <- dbinom(y[,,dataYears], 1,</pre>
z.a[1:nSampled,,dataYears]*p.cand[,,dataYears], log=TRUE)
    prior.beta2.cand <- dnorm(beta2.cand, 0, 10, log=TRUE)</pre>
    prior.beta2 <- dnorm(beta2, 0, 10, log=TRUE)</pre>
    ll.y.sum.cand <- sum(ll.y.cand, na.rm=TRUE)</pre>
    if(runif(1) < exp((ll.y.sum.cand + prior.beta0.cand) -
                        (ll.y.sum + prior.beta0))) {
        beta2 <- beta2.cand</pre>
        p < - p.cand
        ll.y <- ll.y.cand
        ll.y.sum <- ll.y.sum.cand</pre>
    }
    zk <- colSums(z)</pre>
    samples[s,] <- c(sigma, gamma0.i, gamma0.s, gamma0.p,</pre>
                       epsilon.i, epsilon.s, epsilon.p,
                       beta0, beta1, beta2, alpha, zk=zk,
deviance=-2*11.y.sum)
    zK[,s] <- z[,nYears]</pre>
    if(monitor.z)
        zA[,,s] <- z
  }
  final.state <- list(z=z, D=D, samples=samples[s,])</pre>
  library(coda)
  return(list(samples=samples, final.state=final.state,
               zK=zK, zA=zA, Ez=nz1/nIter,
```

seed=.Random.seed))

dynroccHC <- cmpfun(dynroccH)</pre>

}

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APPENDIX D

JOINT POSTERIOR DISTRIBUTIONS FOR MCMC SAMPLER

APPENDIX D. JOINT POSTERIOR DISTRIBUTIONS FOR MCMC SAMPLER. Description of joint posterior distributions and full conditional distributions used in the MCMC algorithm. The full joint posterior distribution of the parameters, conditional on the data, is proportional to the product of likelihood and prior probability distributions:

$$p(\varepsilon, \boldsymbol{\alpha}, \boldsymbol{\rho}, \sigma, \boldsymbol{z}, \boldsymbol{p} | \boldsymbol{y}) \propto p(\boldsymbol{y} | \boldsymbol{z}, \boldsymbol{p}) p(\boldsymbol{z}_t | \boldsymbol{z}_{t-1} \varepsilon, \boldsymbol{\alpha}, \boldsymbol{\rho}, \boldsymbol{\sigma}) p(\varepsilon) p(\boldsymbol{\alpha}) p(\boldsymbol{\rho}) p(\sigma) p(\boldsymbol{p})$$
Eq. S1

Where p() indicates a probability distribution, and bold font indicates a vector or array. Indexing has been omitted from dynamic parameters, latent variables and data for clarity. Here, **z** indicates the latent occupancy state and **y** is the presence-absence data.

The joint density of the data conditional on the latent occupancy state is:

$$p(\mathbf{y}|\mathbf{z}, \mathbf{p}) = \prod_{\{i=1\}}^{M} \prod_{\{j=1\}}^{J} \prod_{\{k=1\}}^{K} Bern(z_{\{ik\}} \times p_{\{ijk\}})$$
Eq. S2

We used a Gibbs sampler to draw values from the joint posterior. Gibbs sampling involves sampling each parameter (or blocks of parameters) from its full conditional distribution, which is the distribution of parameter conditional on the data and all other parameters in the model. For example, the full conditional distribution of ε_1 is $p(\varepsilon_1 | \mathbf{y}, \mathbf{z}, \boldsymbol{\alpha}, \boldsymbol{\rho}, \sigma, \mathbf{p})$, but because several of the probability densities do not include ε_1 , we can simplify it to:

$$p(\varepsilon_1|\mathbf{z},) \propto p(\mathbf{z}_t|\mathbf{z}_{t-1}, \varepsilon, \alpha, \rho, \sigma)p(\varepsilon_1)$$
 Eq. S3

Because \mathbf{z} does not change when ε changes, we do not need $p(\mathbf{y}|\mathbf{z})$, so it can be omitted from the left-hand side of the equation. Additionally, $p(\varepsilon_1)$ can be omitted from the right-hand side of Equation 2 because \mathbf{z} does not appear in $p(\varepsilon_1)$. Below is the full conditional, after omitting unnecessary terms:

$$p(\mathbf{z}|\mathbf{y},\varepsilon_1) \propto p(\mathbf{y}|\mathbf{z})p(\mathbf{z}_t|\mathbf{z}_{t-1},\varepsilon,\alpha,\rho,\sigma)$$
 Eq. S4

All other full condition distributions are computed in the same fashion. We used the Metropolis-Hastings algorithm to sample. The joint posterior distribution for the extinction rate of semipermanent ε_2 and permanent ponds ε_3 along with the scale parameter of the colonization function σ , baseline colonization probability for intermittent ρ_1 , semi-permanent ρ_2 and permanent ponds ρ_3 , the resistance parameter α_1 , the intercept for the probability of detection β_0 , effect of wind on detection β_2 and effect of temperature β_1 on detection have the same notation, with the exception of the epsilon parameter. As described in APPENDIX B, our prior distribution, (e.g., $p(\varepsilon_1)$), is as follows: $\alpha_1 \sim Unif(-10,10)$, $\sigma \sim Gamma(1,0.1)$, $\rho_1 = 0$, $\rho_2 =$ 0, $\rho_3 = 0$, $\varepsilon_1 \sim Beta(1,1)$, $\varepsilon_2 \sim Beta(1,1)$, $\varepsilon_3 \sim Beta(1,1)$, $\beta_0 \sim Normal(0,10)$, $\beta_1 \sim$ *Normal*(0,10), $\beta_2 \sim Normal(0,10)$.

For the latent variable \mathbf{z} , the full conditional distribution is somewhat more complicated as \mathbf{z} in the current year at a given patch is dependent on the previous year patch occupancy and subsequent year patch occupancy.

The full conditional for $z_{i,k}$ is as follows:

$$p(z_{i,k}|y_{i,k}, z_{i,k-1}, z_{i,k+1}) \propto p(y_{i,k}|z_{i,k}) p(z_{i,k}|z_{i,k-1}, z_{k+1})$$
Eq. S5

The prior for $z_{i,k}$ takes the following form:

$$z_{i,k} = \prod_{i=1}^{M} \prod_{k=1}^{K} Bern(\psi_{i,k-1})$$
 Eq. S6

Where $\psi_{i,k-1}$ is dependent on dynamic colonization and extinction rate parameters and is computed using Equation 1 from the manuscript:

$$\psi_{i,k} = \gamma_{i,k-1} (1 - z_{i,k-1}) + (1 - \varepsilon_{i,k-1} (1 - \gamma_{i,k-1}))(z_{i,k-1})$$
Eq. S7

The joint likelihood for our data takes on the following form:

$$p(\mathbf{y}|\mathbf{z}) = \prod_{i=1}^{M} \prod_{k=1}^{K} Bern(y_{i,j}|z_i)$$
Eq. S8

Where M is the number of patches in the metapopulation (M=273), and K is the number of years (K=15) of our study. Bold indicates an array.

APPENDIX E

CONVERGENCE DIAGNOSTICS

APPENDIX E. CONVERGENCE DIAGNOSTICS. Trace plots and posterior density for elevation model.



Iteration number



APPENDIX F

PARAMETER ESTIMATES
APPENDIX F. PARAMETER ESTIMATES. Estimates of the posterior mean, standard deviation and 95% credible intervals for detection and occupancy parameters for our spatially explicit model of the influence of A) no landscape structure (i.e., colonization probability based on Euclidean distance among patches), B) distance to nearest streambed, and C) both elevation and distance to nearest streambed on landscape resistance and metapopulation dynamics.

A. No landscape structure

Parameter	Description	Mean	SD	2.5	97.5
sigma	Scale parameter of colonization function	3.51	0.8	2.32	5.2
gamma1	Baseline colonization probability at intermittent patches	0.02	0	0.01	0.05
gamma2	Baseline colonization probability at semi-permanent patches	0.23	0.1	0.1	0.39
gamma3	Baseline colonization probability at permanent patches	0.16	0.1	0.03	0.51
eps1	Extinction probability at intermittent patches	0.85	0.1	0.58	0.99
eps2	Extinction probability at semi- permanent patches	0.79	0.2	0.46	0.99
eps3	Extinction probability at permanent patches Intercept of logit-linear detection	0.13	0.1	0.02	0.41
beta0	model	2.07	0.3	1.57	2.63
beta1	Effect of temperature on logit(p)	0.3	0.4	-0.31	1.1
beta2	Effect of wind on logit(p)	-0.15	0.3	-0.77	0.46
z2003	Number of occupied patches in 2003	3	0	3	3
z2004	Number of occupied patches in 2004	4.41	1.3	2	7
z2005	Number of occupied patches in 2005	5.56	1.8	3	9
z2006	Number of occupied patches in 2006	6.66	2	3	11
z2007	Number of occupied patches in 2007	7.85	1.9	5	12
z2008	Number of occupied patches in 2008	9.55	2.2	6	15
z2009	Number of occupied patches in 2009	9.42	2.5	6	15
z2010	Number of occupied patches in 2010	10.03	2.7	6	16

z2011	Number of occupied patches in 2011	12.71	2.8	8	19
z2012	Number of occupied patches in 2012	10.89	3	6	18
z2013	Number of occupied patches in 2013	13.78	3.2	9	21
z2014	Number of occupied patches in 2014	17.51	3.4	12	25
z2015	Number of occupied patches in 2015	23.11	3.8	18	32
z2016	Number of occupied patches in 2016	20.17	4.5	14	31
z2017	Number of occupied patches in 2017	19.28	5.4	12	32
Deviance	Deviance	142.58	9.81	131.37	165.27

B. Distance to nearest streambed

Parameter	Description	Mean	SD	2.5	97.5
sigma	Scale parameter of colonization function	2.42	0.6	1.53	3.88
gamma1	Baseline colonization probability at intermittent patches	0.03	0.02	0.01	0.09
gamma2	Baseline colonization probability at semi-permanent patches	0.31	0.1	0.14	0.53
gamma3	Baseline colonization probability at permanent patches	0.18	0.13	0.04	0.56
eps1	Extinction probability at intermittent patches	0.85	0.11	0.57	0.99
eps2	Extinction probability at semi- permanent patches	0.82	0.14	0.49	0.99
eps3	Extinction probability at permanent patches	0.12	0.1	0.02	0.39
beta0	model	2.07	0.27	1.57	2.63
beta1	Effect of temperature on logit(p)	0.3	0.36	-0.32	1.08
beta2	Effect of wind on logit(p)	-0.14	0.32	-0.77	0.47
	Linear effect of elevation on landscape				
alpha1	resistance	0.79	0.32	0.11	1.36
z2003	Number of occupied patches in 2003	3	0	3	3
z2004	Number of occupied patches in 2004	4.41	1.23	2	7
z2005	Number of occupied patches in 2005	5.42	1.62	3	9
z2006	Number of occupied patches in 2006	6.34	1.79	3	10
z2007	Number of occupied patches in 2007	7.4	1.67	5	11
z2008	Number of occupied patches in 2008	9.07	1.89	6	14
z2009	Number of occupied patches in 2009	8.77	2.24	6	14

z2010	Number of occupied patches in 2010	9.43	2.48	6	15
z2011	Number of occupied patches in 2011	12.42	2.74	8	19
z2012	Number of occupied patches in 2012	10.94	3.09	6	18
z2013	Number of occupied patches in 2013	14.67	3.45	9	23
z2014	Number of occupied patches in 2014	19.36	3.95	13	29
z2015	Number of occupied patches in 2015	25.77	4.68	19	37
z2016	Number of occupied patches in 2016	23.96	5.76	15	37
z2017	Number of occupied patches in 2017	23.99	6.96	14.00	40.00
Deviance	Deviance	142.23	9.58	131.39	164.87

C. Elevation and Distance to Nearest Streambed

Parameter	Description	Mean	SD	2.5	07.5
	Scale parameter of colonization	witali	50	2.3	71.5
sigmo	function	2 12	0.68	1 1	27
sigilla	Deceling colonization probability at	2.13	0.08	1.1	5.7
commo 1	baseline colonization probability at	0.02	0.02	0.01	0.00
gamma1	Deceling colonization probability at	0.05	0.02	0.01	0.08
	Baseline colonization probability at	0.20	0.1	0.11	0.40
gamma2	semi-permanent patches	0.28	0.1	0.11	0.49
2	Baseline colonization probability at	0.04	0.17	0.05	07
gamma3	permanent patches	0.24	0.17	0.05	0.7
	Extinction probability at intermittent	0.05	0.10	0.54	0.00
epsl	patches	0.85	0.12	0.56	0.99
	Extinction probability at semi-	0.01		o 1 -	0.00
eps2	permanent patches	0.81	0.14	0.47	0.99
_	Extinction probability at permanent				
eps3	patches	0.15	0.13	0.02	0.52
	Intercept of logit-linear detection				
beta0	model	2.07	0.27	1.57	2.64
beta1	Effect of temperature on logit(p)	0.3	0.36	-0.32	1.09
beta2	Effect of wind on logit(p)	-0.15	0.32	-0.78	0.47
	Linear effect of elevation on				
alpha1	landscape resistance	0.81	0.48	-0.05	1.8
	Linear effect of distance to streambed				
alpha2	on landscape resistance	0.47	0.46	-0.47	1.27
z2003	Number of occupied patches in 2003	3	0	3	3
z2004	Number of occupied patches in 2004	4.24	1.22	2	7
z2005	Number of occupied patches in 2005	5.2	1.62	3	9
z2006	Number of occupied patches in 2006	6.16	1.82	3	10
z2007	Number of occupied patches in 2007	7.37	1.75	5	12
z2008	Number of occupied patches in 2008	9.15	2.02	6	14
z2009	Number of occupied patches in 2009	8.78	2.31	5	14
z2010	Number of occupied patches in 2010	9.35	2.45	6	15
	100		-	-	-

z2011	Number of occupied patches in 2011	12.09	2.56	8	18
z2012	Number of occupied patches in 2012	10.29	2.73	6	16
z2013	Number of occupied patches in 2013	13.37	2.92	9	20
z2014	Number of occupied patches in 2014	17.32	3.23	12	25
z2015	Number of occupied patches in 2015	22.79	3.63	17	31
z2016	Number of occupied patches in 2016	20.2	4.39	14.00	31.00
z2017	Number of occupied patches in 2017	19.51	5.33	12	32
Deviance	Deviance	142.37	9.70	131.38	165.28

APPENDIX G

COMPARISON OF RASTER RESOLUTIONS

APPENDIX G. COMPARISON OF RASTER RESOLUTIONS. Estimates of the median and 95% credible intervals for resistance coefficients for our spatially explicit model of the influence of elevation (black squares) and distance to nearest streambed (open triangles) on landscape resistance and metapopulation dynamics.



APPENDIX H

JAGS MODEL CODE FOR ABUNDANCE MODELS

APPENDIX H. JAGS MODEL CODE FOR ABUNDANCE MODELS. JAGS model code for

each of our model of Chiricahua leopard frog metapopulation dynamics.

```
model{
  #Ecological process - Abundance
  #Site productivity
  alpha1 ~ dnorm(0,0.1) #Inter site coefficient for productivity
  alpha2 ~ dnorm(0,0.1) # Perm site coefficient for productivity
  alpha3 ~ dnorm(0,0.1) # Semi-permanent site coefficient for
productivity
  alpha4 \sim dunif(-20, 0) #Pond area coefficient for productivity
  #Abundance in first year after reintroduction.
  N[15,1] ~ dpois(3) #Carpenter
  N[33,1] \sim dpois(3) \#Rock
  N[274,1] ~ dpois(3) #HQ Breeding Site
  #Dispersal parameters
  rho0[1] ~ dunif(0,1) # Pr(not dispersing from Inter site)
  rho0[2] ~ dunif(0,1) # Pr(not dispersing from Semi site)
  rho0[3] ~ dunif(0,1) # Pr(not dispersing from Perm site)
  #combination of sigma (shape of dispersal kernel) and gamma0.
Should be small, positive
  rho1 ~ dgamma(0.001, 0.001)
  #Data model
  pOA ~ dnorm(0, 0.1) #observer 1 detection rate intercept
  tempA ~ dnorm(0, 0.1) \# both observer detection rate temp
  windA ~ dnorm(0, 0.1) \# both observer detection rate wind
#Transition probs
for(i in 1:nSites) { #site loop
  #Probability of not leaving a patch, based on hydroperiod
  #These are the non-migrants from a given patch
  pi[i,i] <- rho0[hydro[i]] #diagonals</pre>
 pi0[i,i] <- 0 #set diagonals of the transition matrix to 0,
b/c they will not be defined in the indexing below
  for(m in 1:(i-1)) {
  #This indexing will fill the bottom half of a square matrix
```

```
#Unnormalized probability of moving from site i to site m,
depends on distance among sites
  #And hydroperiod of neighboring site
  pi0[i,m] <- exp(-rho1*d[i,m]) #bottom half of matrix
  #Normalized probability of moving from site i to m
  pi[i,m] <- (1-pi[i,i])*pi0[i,m] / nc[i] #Rows of pi must sum</pre>
to 1. A frog either stays or leaves a focal patch.
 }
  for(m in (i+1):nSites) {
    #This indexing will fill the top half of a square matrix
    pi0[i,m] <- exp(-rho1*d[i,m]) #top half of matrix</pre>
    pi[i,m] <- (1-pi[i,i])*pi0[i,m] / nc[i]</pre>
  }
  #Probability of going from i to any site in the network
 nc[i] <- sum(pi0[i,1:nSites])</pre>
 }
    #N in year 1
    Ntotal[1] <- sum(N[,1])
    for(t in 2:nYears) { #year loop
      for(i in 1:nSites) {
       #recruitment
       lambda[i, t-1]<-exp(alpha1*Inter[i] + alpha2*Perm[i] +</pre>
alpha3*Semi[i] + alpha4*N[i,t-1]/area[i])
        #expected number of individuals at site i
        EN[i,t] <- pi[,i] %*% (N[,t-1]*lambda[,t-1])</pre>
        # N[i,t] is Poisson since the sum of multinomial
outcomes is
        # Poisson, if multinomial size is also Poisson. Here
multinomial
        # size is Pois(N[i,t-1]*lambda), but we're using
expected value
        #instead of realized.
          N[i,t] ~ dpois(EN[i,t]) #number of individuals at site
i
        }
        #N in subsequent years
        Ntotal[t] <- sum(N[,t])</pre>
```

```
#Occupancy data. Year of reintroduction 2003 (so adults could be
seen 2004 onward). 2007-2012.
for (i in 1:nSampled) {#surveyed sites only
  for (k in 1:nReps) { #3 replicate surveys
    for (t in 4:9) { #years 2007 to 2012
    y[i,k,t] \sim dbern(p[i,k,t])
    p[i,k,t]<-1-(1-r[i,k,t])^N[i,t]
    logit(r[i,k,t])<-p0A + windA*wind[i,k,t]+tempA*temp[i,k,t]</pre>
    } #close year loop
    }#close rep loop
  for(k in 1:2) {
    for (t in 10:nYears) { #year 10-14, 2013-2017
    logit(r1[i,k,t])<- p0A + tempA*temp[i,k,t] +</pre>
windA*wind[i,k,t]
    y1[i,k,t] \sim dbin(r1[i,k,t], N[i,t])
    logit(r2[i,k,t])<- p0A + tempA*temp[i,k,t] +</pre>
windA*wind[i,k,t]
    y2[i,k,t] ~dbin(r2[i,k,t], N[i,t]-y1[i,k,t])
    } #close year loop
  } #close rep loop
} #close site loop
}
```

}

APPENDIX I

CONVERGENCE DIAGNOSTICS FOR ABUNDANCE MODEL

APPENDIX I. CONVERGENCE DIAGNOSTICS FOR ABUNDANCE MODEL. Trace plots and posterior density for coefficients from the model of Chiricahua leopard frog metapopulation dynamics.





APPENDIX J

R SCRIPT FOR MCMC ALGORITHM USED IN PVA

library(compiler)

MCMC algorithm

```
dynroccH <- function(y,
                                 # nSampled x nVisits x nYear
array of detection/non-detection data
                                   # nSites x 2 matrix of site
                    x,
coordinates. Note that nSampled will usually be <nSites
                    r.cov1, # resistance covariate
                    r.cov2=NULL, # resistance covariate
                                  # extinction covariate
                    e.cov,
                    e.cov2,
                                 # extinction covariate
                                  # detection covariate
                    p.cov1,
                    p.cov2,
                                 # detection covariate
                    nIter=10,
                                 # MCMC iterations
                                  # Tuning order:
                    tune,
sigma,gamma0.i,gamma0.s,gamma0.p,eps.i,eps.s,eps.p,
beta0,beta1,beta2,alpha[1],alpha[2] (12 in total)
                    estAlpha=TRUE, # Estimate the resistance
coefficient?
                    inits=NULL, # until you run algorithm,
inits are based on what is given.
                    zProp=c("ind", "vec"), # Update z matrix by
either proposing z(i,k) or z(,k), respectively
                    zProbs=NULL, # matrix of proposal probs
use if zProp="vec"
                   monitor.z=FALSE, # store each iteration of
the z matrix?
                              # Only report progress if >0
                    report=0,
                   plot.z=FALSE, # Plot the latent presence-
absence state (if report>0)
                               # This will reject a proposal of
                    tol=0)
z(i,k)=1 if mu(i,k-1)<tol
{
  zProp <- match.arg(zProp)</pre>
 ## Dimensions
 nSites <- nrow(x)
 nReps <- ncol(y)</pre>
 nYears <- dim(y)[3]
  ## Using this to avoid likelihood calculations for sites not
sampled
 nSampled <- nrow(y)</pre>
```

```
dataYears <- apply(!is.na(y), 3, any)</pre>
  anyDetections <- matrix(FALSE, nSites, nYears)</pre>
  anyDetections[1:nSampled,] <- apply(y, c(1,3), sum,</pre>
na.rm=TRUE) > 0
  known0 <- matrix(FALSE, nSites, nYears)</pre>
  rownames(known0) <- rownames(x)</pre>
  known0[failed, 8:nYears] <- TRUE #failed is a chr string with</pre>
names of sites no longer sampled.
  notFailed <- 1 - known0</pre>
  if (any (any Detections & known0))
       stop("detection data doesn't match blowout data")
  y.wide <- matrix(y, nSampled)</pre>
  #For colonization, use this handy trick
  isInter <- e.cov=="Intermittent"</pre>
  isSemi <- e.cov=="Semi-permanent"</pre>
  isPerm <- e.cov=="Permanent"</pre>
  #For extinction risk, need to have a logit linear model
because drought varies over time not space
  water<-model.matrix(~ e.cov-1)</pre>
  colnames(water)<-c("Inter", "Perm", "Semi")</pre>
  rownames (water) <-rownames (x)</pre>
  #set up dummy variables
  Inter<-water[,1]</pre>
  Perm<-water[,2]</pre>
  Semi<-water[,3]</pre>
  #PDSI for extinction risk that varies over time with drought
  pdsi<-e.cov2
  gamma0 <- rep(NA, nSites)</pre>
    rc2 <- is.null(r.cov2)</pre>
  if(rc2) {
      r.cov2 <- r.cov1
  }
  ## initial values
```

```
gamma <- muz <- epsilon<- matrix(NA, nSites, nYears-1)</pre>
    if(is.null(inits)) {
      epsilon.p<-epsilon.s<-epsilon.i<-epsilon.c<-runif(1)</pre>
      sigma <- runif(1,3,4)
      gamma0.i <- runif(1, 0.01, 0.3)</pre>
      gamma0.s <- runif(1, 0.01, 0.3)</pre>
      gamma0.p <- runif(1, 0.01, 0.3)
      gamma0[isInter] <- gamma0.i</pre>
      gamma0[isSemi] <- gamma0.s</pre>
      gamma0[isPerm] <- gamma0.p</pre>
      beta0<-runif(1, 0.1, 0.6)
      beta0 <- rnorm(1)</pre>
      beta1 <- rnorm(1)</pre>
      beta2 <- rnorm(1)</pre>
      alpha < - c(0, 0)
      p <- plogis(beta0 + beta1*p.cov1 + beta2*p.cov2) ## inits</pre>
for p
      z <- matrix(0, nSites, nYears)</pre>
      reintroSites <- which(rownames(coords) %in%</pre>
                                 c("Carpenter Tank", "Rock Tank",
"HQ Breeding Site")) # reintroduction sites
      z[reintroSites,1] <- 1</pre>
      cost <- exp(alpha[1]*r.cov1 + alpha[2]*r.cov2)</pre>
      ## calculate conductances among neighbors
      tr1 <- transition(cost, transitionFunction=function(x)</pre>
1/\text{mean}(x), directions=16) ##8)
      trlCorrC <- geoCorrection(trl, type="c",</pre>
multpl=FALSE,scl=FALSE) #adjust diag.conductances
      ## calculate least cost distance between all pairs of
sites.
      if(!estAlpha)
           alpha <- c(0,0) ## Force alpha to be 0 if you aren't
estimating it. Results in appox Euclidean dist
      D <- costDistance(tr1CorrC,x,x)/1000 #calculate the</pre>
ecological distance matrix
      G \leq \operatorname{gamma0*exp}(-D^2/(2*\operatorname{sigma^2}))
      for(k in 2:nYears) { #nYears
           epsilon[,k-1]<-plogis(epsilon.i*Inter + epsilon.s*Semi</pre>
+ epsilon.p*Perm + epsilon.c*e.cov2[k-1])
           PrNotColonizedByNeighbor <- 1 - gamma0*exp(-
D^2/(2*sigma^2)) * t(z[,rep(k-1, nSites)])
```

```
PrNotColonizedAtAll <- apply(PrNotColonizedByNeighbor,
1, prod)
           gamma[,k-1] <- 1 - PrNotColonizedAtAll</pre>
           muz[,k-1] <- z[,k-1]*(1-epsilon[,k-1]*(1-gamma[,k-1]))</pre>
+ (1-z[,k-1])*gamma[,k-1] # rescue effect
           muz[,k-1] <- muz[,k-1]*notFailed[,k] # Exclude 3 sites</pre>
no longer sampled
           z[,k] <- rbinom(nSites, 1, muz[,1]) ##Only works with</pre>
muz[,1]
           z[known0[,k],k] <- 0
           z[which(anyDetections[,k]),k] <- 1 #detections in y, z</pre>
must be 1
      }#close years
  } else {
      gamma0.i <- inits$samples["gamma0.i"]</pre>
      gamma0.s <- inits$samples["gamma0.s"]</pre>
      gamma0.p <- inits$samples["gamma0.p"]</pre>
      gamma0[isInter] <- gamma0.i</pre>
      gamma0[isSemi] <- gamma0.s</pre>
      gamma0[isPerm] <- gamma0.p</pre>
      sigma <- inits$samples["sigma"]</pre>
      epsilon.i <- inits$samples["epsilon.i"]</pre>
      epsilon.s <- inits$samples["epsilon.s"]</pre>
      epsilon.p <- inits$samples["epsilon.p"]</pre>
      epsilon.c <- inits$samples["epsilon.c"]</pre>
      alpha<-c(inits$samples["alpha1"],inits$samples["alpha2"])</pre>
      D <- inits$D
      beta0 <- inits$samples["beta0"]</pre>
      beta1 <- inits$samples["beta1"]</pre>
      beta2 <- inits$samples["beta2"]</pre>
      p <- plogis(beta0 + beta1*p.cov1 + beta2*p.cov2)</pre>
      z <- inits$z
       .Random.seed <- inits$seed ## use same random seed as
before
  }
  ## Added starting values for gamma, conditional on inits for z
  ## browser()
  ll.z <- matrix(0, nSites, nYears)</pre>
  ll.y <- array(0, c(nSampled, nReps, nYears))</pre>
  for(k in 2:nYears) {
      epsilon[,k-1]<-plogis(epsilon.i*Inter + epsilon.s*Semi +</pre>
epsilon.p*Perm + epsilon.c*e.cov2[k-1])
      PrNotColonizedByNeighbor <- 1 - gamma0*exp(-D^2/(2*sigma^2)
))*t(z[,rep(k-1, nSites)])
```

```
PrNotColonizedAtAll <- apply(PrNotColonizedByNeighbor, 1,
prod)
      gamma[,k-1] <- 1 - PrNotColonizedAtAll</pre>
      muz[,k-1] <- z[,k-1]*(1-epsilon[,k-1]*(1-gamma[,k-1])) +</pre>
(1-z[,k-1])*gamma[,k-1]
      muz[,k-1] <- muz[,k-1]*notFailed[,k]</pre>
      ll.z[,k-1] <- dbinom(z[,k], 1, muz[,k-1], log=TRUE)</pre>
      if (k > 4) { ## Ignore first 4 years without data
           ## Now p has the same dimensions of y. No need to do
p[,,k-4]
           ## p is now an array. Note k-4 b/c p only has 6 years.
Should make dims of p and y consistent
           ll.y[,,k] <- dbinom(y[,,k], 1, z[1:nSampled,k]*p[,,k],</pre>
log=TRUE)
      }
  }
  ll.z.cand <- ll.z</pre>
  ll.z.sum <- sum(ll.z)</pre>
  ll.y.cand <- ll.y</pre>
  ll.y.sum <- sum(ll.y, na.rm=TRUE)</pre>
  epsilon.cand <- epsilon</pre>
  gamma.cand <- gamma
  muz.cand <- muz</pre>
  nz1 <- z ## Used to compute expected occupancy at each site
  zkup <- rep(0, nYears-1)</pre>
  ## posterior samples
  nPar <- 14+nYears
  samples <- array(NA, c(nIter, nPar))</pre>
  zK <- matrix(NA, nSites, nIter)</pre>
  colnames(samples) <- c("sigma", "gamma0.i", "gamma0.s",</pre>
"gamma0.p",
                           "epsilon.i", "epsilon.s", "epsilon.p",
"epsilon.c",
                           "beta0", "beta1", "beta2", "alpha1",
"alpha2",
                           paste("zk", 1:nYears, sep=""),
"deviance")
  reportit <- report>0
    nzup <- rep(0, nYears-1)</pre>
  zA <- NULL
  if(monitor.z)
      zA <- array(NA integer , c(nSites, nYears, nIter))</pre>
                                  149
```

```
if(reportit) {
      cat("iter 1\n")
      cat("
              theta =",
round(c(sigma,gamma0.i,gamma0.s,gamma0.p,epsilon.i,epsilon.s,eps
ilon.p,epsilon.c,beta0,beta1,beta2,alpha), 5), "\n")
               z[k] =", round(colSums(z), 2), "\n")
      cat("
               ll.z =", round(sum(ll.z), 2), "\n")
      cat("
               deviance =", round(-2*11.y.sum, 2), "\n")
      cat("
      cat("
              time =", format(Sys.time()), "\n")
      if(plot.z) {
##
            browser()
          library(lattice)
          zd <- data.frame(z=as.integer(z),</pre>
year=factor(rep(2003:2017, each=nSites)),
                           x=as.numeric(x[,1])/1000,
y=as.numeric(x[,2])/1000)
          print(xyplot(y ~ x | year, zd, groups=z, aspect="iso",
pch=c(1,16), as.table=TRUE))
      }
  }
  ## Sample from posteriors
  for(s in 1:nIter) {
    ll.z.sum <- sum(ll.z) ## This is important!</pre>
    if(reportit) {
    if(s %in% c(2:100) || s %% report == 0) {
      cat("iter", s, "\n")
      cat("
              theta =", round(samples[s-1,1:13], 5), "\n")
               z[k] =", zk, "\n")
      cat("
      cat("
               accepted", round(zkup/(nSites)*100, 1), "percent
of z[k] proposals n")
      cat("
               sum(ll.z) =", ll.z.sum, "\n")
               deviance =", round(samples[s-1,"deviance"], 2),
      cat("
"\n")
             time =", format(Sys.time()), "\n")
      cat("
      if(plot.z) {
          library(lattice)
          zd$z <- as.integer(z)</pre>
          print(xyplot(y ~ x | year, zd, groups=z, aspect="iso",
pch=c(1,16), as.table=TRUE))
      }
    }
    }
```

```
if(estAlpha) {
    #Metropolis update for alpha
    alpha1.cand <- rnorm(1, alpha[1], tune[11])</pre>
    cost <- exp(alpha1.cand*r.cov1 + alpha[2]*r.cov2) #create</pre>
resistance surface
    ## calculate conductances among neighbors
    tr1 <- transition(cost, transitionFunction=function(x)</pre>
1/\text{mean}(x), directions=16) ##8)
    trlCorrC <- geoCorrection(trl, type="c",</pre>
multpl=FALSE,scl=FALSE) #adjust diag.conductances
    ## calculate least cost distance between all pairs of sites.
    D.cand <- costDistance(tr1CorrC,x,x)/1000 #calculate the
ecological distance matrix
    G.cand <- gamma0*exp(-D.cand^2/(2*sigma^2))</pre>
    for(k in 2:nYears) {
      zkt <- matrix(z[,k-1], nSites, nSites, byrow=TRUE)</pre>
      gamma.cand[,k-1] <- 1 - exp(rowSums(log(1-G.cand*zkt)))</pre>
      muz.cand[,k-1] <- (z[,k-1]*(1-epsilon[,k-1]*(1-</pre>
gamma.cand[,k-1])) + (1-z[,k-1])*gamma.cand[,k-1])*notFailed[,k]
      ll.z.cand[,k-1] <- dbinom(z[,k], 1, muz.cand[,k-1],</pre>
log=TRUE)
      }
      prior.alpha.cand <- dnorm(alpha1.cand, 0, 10, log=TRUE)
      prior.alpha <- dnorm(alpha[1], 0, 10, log=TRUE)</pre>
      ll.z.sum.cand <- sum(ll.z.cand)</pre>
      if(runif(1) < exp((ll.z.sum.cand + prior.alpha.cand) -</pre>
                          (ll.z.sum + prior.alpha))) {
      alpha[1] <- alpha1.cand</pre>
      D < - D.cand
      G <- G.cand
      gamma <- gamma.cand
      muz <- muz.cand</pre>
      ll.z <- ll.z.cand</pre>
      ll.z.sum <- ll.z.sum.cand</pre>
      }
    if(!rc2) {
    #Metropolis update for alpha[2]
    alpha2.cand <- rnorm(1, alpha[2], tune[12])</pre>
```

```
cost <- exp(alpha[1]*r.cov1 + alpha2.cand*r.cov2) #create</pre>
resistance surface
    ## calculate conductances among neighbors
    tr1 <- transition(cost, transitionFunction=function(x)</pre>
1/\text{mean}(x), directions=16) ##8)
    trlCorrC <- geoCorrection(trl, type="c",</pre>
multpl=FALSE,scl=FALSE) #adjust diag.conductances
    ## calculate least cost distance between all pairs of sites.
    D.cand <- costDistance(tr1CorrC,x,x)/1000 #calculate the
ecological distance matrix
    G.cand <- gamma0*exp(-D.cand^2/(2*sigma^2))</pre>
    for(k in 2:nYears) {
      zkt <- matrix(z[,k-1], nSites, nSites, byrow=TRUE)</pre>
      gamma.cand[,k-1] <- 1 - exp(rowSums(log(1-G.cand*zkt)))</pre>
      muz.cand[,k-1] <- (z[,k-1]*(1-epsilon[,k-1]*(1-</pre>
gamma.cand[,k-1])) + (1-z[,k-1])*gamma.cand[,k-1])*notFailed[,k]
      ll.z.cand[,k-1] <- dbinom(z[,k], 1, muz.cand[,k-1],</pre>
log=TRUE)
      }
      prior.alpha.cand <- dnorm(alpha2.cand, 0, 10, log=TRUE)</pre>
      prior.alpha <- dnorm(alpha[2], 0, 10, log=TRUE)</pre>
      ll.z.sum.cand <- sum(ll.z.cand)</pre>
      if(runif(1) < exp((ll.z.sum.cand + prior.alpha.cand) -
                          (ll.z.sum + prior.alpha))) {
      alpha[2] <- alpha2.cand</pre>
      D < - D.cand
      G <- G.cand
      gamma <- gamma.cand</pre>
      muz <- muz.cand</pre>
      ll.z <- ll.z.cand
      ll.z.sum <- ll.z.sum.cand</pre>
      }
    }
  }
    ## Metropolis update for sigma
    sigma.cand <- rnorm(1, sigma, tune[1])</pre>
    if(sigma.cand > 0) {
        G.cand <- gamma0*exp(-D^2/(2*sigma.cand^2)
                                                       ))
      for(k in 2:nYears) {
        zkt <- matrix(z[,k-1], nSites, nSites, byrow=TRUE)</pre>
                                  152
```

```
gamma.cand[,k-1] <- 1 - exp(rowSums(log(1-G.cand*zkt)))</pre>
        muz.cand[,k-1] <- (z[,k-1]*(1-epsilon[,k-1]*(1-</pre>
gamma.cand[,k-1])) + (1-z[,k-1])*gamma.cand[,k-1])*notFailed[,k]
         ll.z.cand[,k-1] <- dbinom(z[,k], 1, muz.cand[,k-1],</pre>
log=TRUE)
      prior.sigma.cand <- dgamma(sigma.cand, 0.001, 0.001)</pre>
      prior.sigma <- dgamma(sigma, 0.001, 0.001)</pre>
      ll.z.sum.cand <- sum(ll.z.cand)</pre>
      if(runif(1) < exp((ll.z.sum.cand + prior.sigma.cand) -
                           (ll.z.sum + prior.sigma))) {
           sigma <- sigma.cand</pre>
           gamma <- gamma.cand
           ll.z <- ll.z.cand</pre>
           ll.z.sum <- ll.z.sum.cand</pre>
           muz <- muz.cand</pre>
           G <- G.cand
      }
    }
    #Metropolis update for gamma0 (part of the gammaDist
calculation)
      prior.gamma0.cand <- prior.gamma0 <- 0</pre>
    gamma0.i.cand <- rnorm(1, gamma0.i, tune[2])</pre>
    if (gamma0.i.cand > 0 & gamma0.i.cand < 1) {
         gamma0.cand <- gamma0</pre>
         gamma0.cand[isInter] <- gamma0.i.cand</pre>
         G.cand <- gamma0.cand*exp(-D^2/(2*sigma^2))
      for(k in 2:nYears) { #nYears
         zkt <- matrix(z[,k-1], nSites, nSites, byrow=TRUE)</pre>
         gamma.cand[,k-1] <- 1 - exp(rowSums(log(1-G.cand*zkt)))</pre>
        muz.cand[,k-1] <- (z[,k-1]*(1-epsilon[,k-1]*(1-</pre>
gamma.cand[,k-1]) + (1-z[,k-1])*gamma.cand[,k-1])*notFailed[,k]
         ll.z.cand[,k-1] <- dbinom(z[,k], 1, muz.cand[,k-1],</pre>
log=TRUE) # [isocc]
    }
      ll.z.sum.cand <- sum(ll.z.cand)</pre>
      if(runif(1) < exp((ll.z.sum.cand + prior.gamma0.cand) -
                           (ll.z.sum + prior.gamma0))) {
         gamma0.i <- gamma0.i.cand</pre>
         gamma0 <- gamma0.cand</pre>
        gamma <- gamma.cand
        muz <- muz.cand</pre>
         ll.z <- ll.z.cand</pre>
         ll.z.sum <- ll.z.sum.cand</pre>
        G <- G.cand
```

```
}
```

```
#Metropolis update for gamma0 (part of the gammaDist
calculation)
    gamma0.s.cand <- rnorm(1, gamma0.s, tune[3])</pre>
    if(gamma0.s.cand > 0 & gamma0.s.cand < 1) {
         gamma0.cand <- gamma0</pre>
        gamma0.cand[isSemi] <- gamma0.s.cand</pre>
        G.cand <- gamma0.cand*exp(-D^2/(2*sigma^2)
                                                       ))
      for(k in 2:nYears) { #nYears
         zkt <- matrix(z[,k-1], nSites, nSites, byrow=TRUE)</pre>
        gamma.cand[,k-1] <- 1 - exp(rowSums(log(1-G.cand*zkt)))</pre>
        muz.cand[,k-1] <- (z[,k-1]*(1-epsilon[,k-1]*(1-</pre>
gamma.cand[,k-1])) + (1-z[,k-1])*gamma.cand[,k-1])*notFailed[,k]
         ll.z.cand[,k-1] <- dbinom(z[,k], 1, muz.cand[,k-1],</pre>
log=TRUE) # [isocc]
    }
      ll.z.sum.cand <- sum(ll.z.cand)</pre>
      if(runif(1) < exp((ll.z.sum.cand + prior.gamma0.cand) -
                           (ll.z.sum + prior.gamma0))) {
        gamma0.s <- gamma0.s.cand</pre>
        gamma0 <- gamma0.cand</pre>
        gamma <- gamma.cand
        muz <- muz.cand</pre>
        ll.z <- ll.z.cand</pre>
        ll.z.sum <- ll.z.sum.cand</pre>
        G <- G.cand
    }
  }
    #Metropolis update for gamma0 (part of the gammaDist
calculation)
    gamma0.p.cand <- rnorm(1, gamma0.p, tune[4])</pre>
    if (gamma0.p.cand > 0 & gamma0.p.cand < 1) {
        gamma0.cand <- gamma0</pre>
        gamma0.cand[isPerm] <- gamma0.p.cand</pre>
        G.cand <- gamma0.cand*exp(-D^2/(2*sigma^2)
                                                        ))
      for(k in 2:nYears) { #nYears
         zkt <- matrix(z[,k-1], nSites, nSites, byrow=TRUE)</pre>
        gamma.cand[,k-1] <- 1 - exp(rowSums(log(1-G.cand*zkt)))</pre>
        muz.cand[,k-1] <- (z[,k-1]*(1-epsilon[,k-1]*(1-</pre>
gamma.cand[,k-1])) + (1-z[,k-1])*gamma.cand[,k-1])*notFailed[,k]
```

```
ll.z.cand[,k-1] <- dbinom(z[,k], 1, muz.cand[,k-1],</pre>
log=TRUE) # [isocc]
    }
      ll.z.sum.cand <- sum(ll.z.cand)</pre>
      if(runif(1) < exp((ll.z.sum.cand + prior.gamma0.cand) -
                           (ll.z.sum + prior.gamma0))) {
        gamma0.p <- gamma0.p.cand</pre>
        gamma0 <- gamma0.cand</pre>
        gamma <- gamma.cand
        muz <- muz.cand</pre>
        ll.z <- ll.z.cand
        ll.z.sum <- ll.z.sum.cand</pre>
        G <- G.cand
    }
  }
    ## Metropolis update for epsilon (intermittent sites)
    epsilon.i.cand <- rnorm(1, epsilon.i, tune[5])</pre>
    for(k in 2:nYears) {
      ##calculate epsilon.cand
      epsilon.cand[,k-1]<-plogis(epsilon.i.cand*Inter +</pre>
epsilon.s*Semi + epsilon.p*Perm + epsilon.c*pdsi[k-1])
      ##calculate muz
      muz.cand[,k-1] <- z[,k-1]*(1-epsilon.cand[,k-1]*(1-</pre>
gamma[,k-1]) + (1-z[,k-1])*gamma[,k-1]
      muz.cand[,k-1] <- muz.cand[,k-1]*notFailed[,k]</pre>
      ll.z.cand[,k-1] <- dbinom(z[,k], 1, muz.cand[,k-1],</pre>
log=TRUE)
    }
      ## Priors
      prior.epsilon.i.cand <- dnorm(epsilon.i.cand, 0, 10,</pre>
log=TRUE)
      prior.epsilon.i <- dnorm(epsilon.i, 0, 10, log=TRUE)</pre>
      ll.z.sum.cand <- sum(ll.z.cand)</pre>
      if(runif(1) < exp((ll.z.sum.cand + prior.epsilon.i.cand) -
                           (ll.z.sum + prior.epsilon.i))) {
        epsilon.i <- epsilon.i.cand</pre>
        epsilon<- epsilon.cand
        muz <- muz.cand</pre>
        ll.z<-ll.z.cand
        ll.z.sum <- ll.z.sum.cand</pre>
      }
```

```
## Metropolis update for epsilon (semi-perm sites)
      epsilon.s.cand <- rnorm(1, epsilon.s, tune[6])</pre>
      for(k in 2:nYears) {
        ##calculate epsilon.cand
        epsilon.cand[,k-1]<-plogis(epsilon.i*Inter +</pre>
epsilon.s.cand*Semi + epsilon.p*Perm + epsilon.c*pdsi[k-1])
        ##calculate muz
        muz.cand[,k-1] <- z[,k-1]*(1-epsilon.cand[,k-1]*(1-</pre>
gamma[,k-1])) + (1-z[,k-1])*gamma[,k-1]
        muz.cand[,k-1] <- muz.cand[,k-1]*notFailed[,k]</pre>
        ll.z.cand[,k-1] <- dbinom(z[,k], 1, muz.cand[,k-1],</pre>
log=TRUE)
      ## Priors
      prior.epsilon.s.cand <- dnorm(epsilon.s.cand, 0, 10,</pre>
log=TRUE)
      prior.epsilon.s <- dnorm(epsilon.s, 0, 10, log=TRUE)</pre>
      ll.z.sum.cand <- sum(ll.z.cand)</pre>
      if(runif(1) < exp((ll.z.sum.cand + prior.epsilon.s.cand) -
                          (ll.z.sum + prior.epsilon.s))) {
        epsilon.s <- epsilon.s.cand</pre>
        epsilon<- epsilon.cand</pre>
        muz <- muz.cand</pre>
        ll.z<-ll.z.cand
        ll.z.sum <- ll.z.sum.cand</pre>
      }
      ## Metropolis update for epsilon (perm sites)
      epsilon.p.cand <- rnorm(1, epsilon.p, tune[7])</pre>
      for(k in 2:nYears) {
        ##calculate epsilon.cand
        epsilon.cand[,k-1]<-plogis(epsilon.i*Inter +</pre>
epsilon.s*Semi + epsilon.p.cand*Perm + epsilon.c*pdsi[k-1])
        ##calculate muz
        muz.cand[,k-1] <- z[,k-1]*(1-epsilon.cand[,k-1]*(1-</pre>
gamma[,k-1])) + (1-z[,k-1])*gamma[,k-1]
        muz.cand[,k-1] <- muz.cand[,k-1]*notFailed[,k]</pre>
        ll.z.cand[,k-1] <- dbinom(z[,k], 1, muz.cand[,k-1],</pre>
log=TRUE)
      }
```

```
## Priors
      prior.epsilon.p.cand <- dnorm(epsilon.p.cand, 0, 10,</pre>
log=TRUE)
      prior.epsilon.p <- dnorm(epsilon.p, 0, 10, log=TRUE)</pre>
      ll.z.sum.cand <- sum(ll.z.cand)</pre>
      if(runif(1) < exp((ll.z.sum.cand + prior.epsilon.p.cand) -
                           (ll.z.sum + prior.epsilon.p))) {
        epsilon.p <- epsilon.p.cand</pre>
        epsilon<- epsilon.cand</pre>
        muz <- muz.cand</pre>
        ll.z<-ll.z.cand
        ll.z.sum <- ll.z.sum.cand</pre>
      }
      ## Metropolis update for epsilon (perm sites)
      epsilon.c.cand <- rnorm(1, epsilon.c, tune[8])</pre>
      for(k in 2:nYears) {
         ##calculate epsilon.cand
        epsilon.cand[,k-1]<-plogis(epsilon.i*Inter +</pre>
epsilon.s*Semi + epsilon.p*Perm + epsilon.c.cand*pdsi[k-1])
        ##calculate muz
        muz.cand[,k-1] <- z[,k-1]*(1-epsilon.cand[,k-1]*(1-
gamma[,k-1])) + (1-z[,k-1])*gamma[,k-1]
        muz.cand[,k-1] <- muz.cand[,k-1]*notFailed[,k]</pre>
        ll.z.cand[,k-1] <- dbinom(z[,k], 1, muz.cand[,k-1],</pre>
log=TRUE)
      }
      ## Priors
      prior.epsilon.c.cand <- dnorm(epsilon.c.cand, 0, 10,</pre>
log=TRUE)
      prior.epsilon.c <- dnorm(epsilon.c, 0, 10, log=TRUE)</pre>
      ll.z.sum.cand <- sum(ll.z.cand)</pre>
      if(runif(1) < exp((ll.z.sum.cand + prior.epsilon.c.cand) -
                           (ll.z.sum + prior.epsilon.p))) {
        epsilon.c <- epsilon.c.cand</pre>
        epsilon<- epsilon.cand</pre>
        muz <- muz.cand</pre>
        ll.z<-ll.z.cand
        ll.z.sum <- ll.z.sum.cand</pre>
                                  157
```

```
## update z
    ## We can update each z(i,t) individually, and it results in
better mixing
    zkup <- rep(0, nYears-1)</pre>
   for(k in 2:nYears) {
       anyDet <- anyDetections[,k]==1</pre>
       zknown <- anyDet | !notFailed[,k]</pre>
       prop.back <- prop.cand <- 0</pre>
       for(i in 1:nSites) {
            if(zknown[i])
                next
            ## Reject highly unlikely proposals (before proposing
them)
            ## This speed trick shouldn't affect anything but
            ## can double check by changing toleranc (tol)
            if(z[i,k]<1 & muz[i,k-1]<tol)
                next
            zk.wide <- matrix(z[,k], nSites, nReps)</pre>
            zk.cand < - z[,k]
            zk.cand[i] < -1-z[i,k]
            zk.cand.wide <- matrix(zk.cand, nSites, nReps)</pre>
            ll.y.tmp <- 0
            ll.y.cand.tmp <- 0</pre>
            if((k > 4) & (i <= nSampled)) { ## Ignore first 4
years without data
                ll.y.cand.tmp <- dbinom(y[i,,k], 1,</pre>
zk.cand[i]*p[i,,k], log=TRUE)
                ll.y.tmp <- sum(ll.y[i,,k], na.rm=TRUE)</pre>
            }
            ## Prior must be calculated for time k and k+1 b/c
change in z affects both
            ll.z.cand[i,k-1] <- dbinom(zk.cand[i], 1, muz[i,k-1],</pre>
log=TRUE)
            ll.z2 <- ll.z2.cand <- 0
            if(k < nYears) {</pre>
                zkt.cand <- matrix(zk.cand, nSites, nSites,</pre>
byrow=TRUE)
                gamma.cand[,k] <- 1 - exp(rowSums(log(1-</pre>
G*zkt.cand)))
                muz.cand[,k] <- (zk.cand*(1-epsilon[,k]*(1-</pre>
gamma.cand[,k])) + (1-zk.cand)*gamma.cand[,k])*notFailed[,k+1]
```

}

```
ll.z.cand[,k] <- dbinom(z[,k+1], 1, muz.cand[,k],</pre>
log=TRUE)
                11.z2 < - sum(11.z[,k])
                ll.z2.cand <- sum(ll.z.cand[,k])</pre>
            }
            if(runif(1) < exp((sum(ll.y.cand.tmp, na.rm=TRUE) +</pre>
ll.z.cand[i,k-1] +
                                 ll.z2.cand + prop.back) -
                                 (ll.y.tmp + ll.z[i,k-1] +
                                 11.z2 + prop.cand))) {
                 z[,k] < - zk.cand
                ll.z[i,k-1] <- ll.z.cand[i,k-1]</pre>
                 if(k < nYears) {</pre>
                     gamma[,k] <- gamma.cand[,k]</pre>
                     muz[,k] <- muz.cand[,k]</pre>
                     ll.z[,k] <- ll.z.cand[,k]</pre>
                 }
                if((i <= nSampled) & (k>4)) {
                     ll.y[i,,k] <- ll.y.cand.tmp</pre>
                 zkup[k-1] <- zkup[k-1] + 1
            }
       }
   }
    nz1 <- nz1+z
    #Update for beta0
    beta0.cand<-rnorm(1, beta0, tune[9])</pre>
    p.cand <- plogis(beta0.cand + beta1*p.cov1 + beta2*p.cov2)</pre>
    z.wide <- z[,rep(1:nYears, each=nReps)]</pre>
    z.a <- array(z.wide, c(nSites, nReps, nYears))</pre>
    ll.y[,,dataYears] <- dbinom(y[,,dataYears], 1,</pre>
z.a[1:nSampled,,dataYears]*p[,,dataYears], log=TRUE)
    ll.y.cand[,,dataYears] <- dbinom(y[,,dataYears], 1,</pre>
z.a[1:nSampled,,dataYears]*p.cand[,,dataYears], log=TRUE)
    prior.beta0.cand <- dnorm(beta0.cand, 0, 10, log=TRUE)
    prior.beta0 <- dnorm(beta0, 0, 10, log=TRUE)</pre>
    ll.y.sum <- sum(ll.y, na.rm=TRUE)</pre>
    ll.y.sum.cand <- sum(ll.y.cand, na.rm=TRUE)</pre>
    if(runif(1) < exp((ll.y.sum.cand + prior.beta0.cand) -
                         (ll.y.sum + prior.beta0))) {
        beta0 <- beta0.cand</pre>
```

```
p <- p.cand
        ll.y <- ll.y.cand</pre>
        ll.y.sum <- ll.y.sum.cand</pre>
    }
    #Update for beta1
    betal.cand<-rnorm(1, betal, tune[10])</pre>
    p.cand <- plogis(beta0 + beta1.cand*p.cov1 + beta2*p.cov2)</pre>
    z.wide <- z[,rep(1:nYears, each=nReps)]</pre>
    z.a <- array(z.wide, c(nSites, nReps, nYears))</pre>
    ll.y.cand[,,dataYears] <- dbinom(y[,,dataYears], 1,</pre>
z.a[1:nSampled,,dataYears]*p.cand[,,dataYears], log=TRUE)
    prior.beta1.cand <- dnorm(beta1.cand, 0, 10, log=TRUE)
    prior.beta1 <- dnorm(beta1, 0, 10, log=TRUE)</pre>
    ll.y.sum.cand <- sum(ll.y.cand, na.rm=TRUE)</pre>
    if(runif(1) < exp((ll.y.sum.cand + prior.beta0.cand) -
                         (ll.y.sum + prior.beta0))) {
        beta1 <- beta1.cand</pre>
        p <- p.cand</pre>
        ll.y <- ll.y.cand</pre>
        ll.y.sum <- ll.y.sum.cand</pre>
    }
    #Update for beta2
    beta2.cand<-rnorm(1, beta2, tune[11])</pre>
    p.cand <- plogis(beta0 + beta1*p.cov1 + beta2.cand*p.cov2)</pre>
    z.wide <- z[,rep(1:nYears, each=nReps)]</pre>
    z.a <- array(z.wide, c(nSites, nReps, nYears))</pre>
    ll.y.cand[,,dataYears] <- dbinom(y[,,dataYears], 1,</pre>
z.a[1:nSampled,,dataYears]*p.cand[,,dataYears], log=TRUE)
    prior.beta2.cand <- dnorm(beta2.cand, 0, 10, log=TRUE)</pre>
    prior.beta2 <- dnorm(beta2, 0, 10, log=TRUE)</pre>
    ll.y.sum.cand <- sum(ll.y.cand, na.rm=TRUE)</pre>
    if(runif(1) < exp((ll.y.sum.cand + prior.beta0.cand) -
                         (ll.y.sum + prior.beta0))) {
        beta2 <- beta2.cand</pre>
        p <- p.cand
        ll.y <- ll.y.cand</pre>
        ll.y.sum <- ll.y.sum.cand</pre>
    }
```

}

```
dynroccHC <- cmpfun(dynroccH)</pre>
```

#This software has been approved for release by the U.S. Geological Survey (USGS). Although the software has been subjected to rigorous review, the USGS reserves the right to update the software as needed pursuant to further analysis and review. No warranty, expressed or implied, is made by the USGS or the U.S. Government as to the functionality of the software and related material nor shall the fact of release constitute any such warranty. Furthermore, the software is released on condition that neither the USGS nor the U.S. Government shall be held liable for any damages resulting from its authorized or unauthorized use.

APPENDIX K

CONVERGENCE DIAGNOSTICS FOR PVA

APPENDIX K. CONVERGENCE DIAGNOSTICS FOR PVA. Trace plots and posterior density for A) model without PDSI and B) model with PDSI.

A)



Iteration number





Iteration number

