

MOVEMENT AND SURVIVAL OF AN ENDANGERED AMPHIBIAN: THE
FACULTATIVE USE OF A MODIFIED ARID LANDSCAPE BY THE SONORAN TIGER
SALAMANDER

by

Colin W. Brocka

Copyright © Colin W. Brocka 2020

A Thesis Submitted to the Faculty of the

SCHOOL OF NATURAL RESOURCES AND THE ENVIRONMENT

In Partial Fulfillment of the Requirements

For the Degree of

MASTER OF SCIENCE

WILDLIFE CONSERVATION AND MANAGEMENT

In the Graduate College

THE UNIVERSITY OF ARIZONA

2020

THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

As members of the Master's Committee, we certify that we have read the thesis prepared by: Colin Brocka
titled:

and recommend that it be accepted as fulfilling the thesis requirement for the Master's Degree.



John L Koprowski

Date: Jul 6, 2020



Michael Bogan

Date: Jul 6, 2020



Thomas Jones

Date: Jul 6, 2020

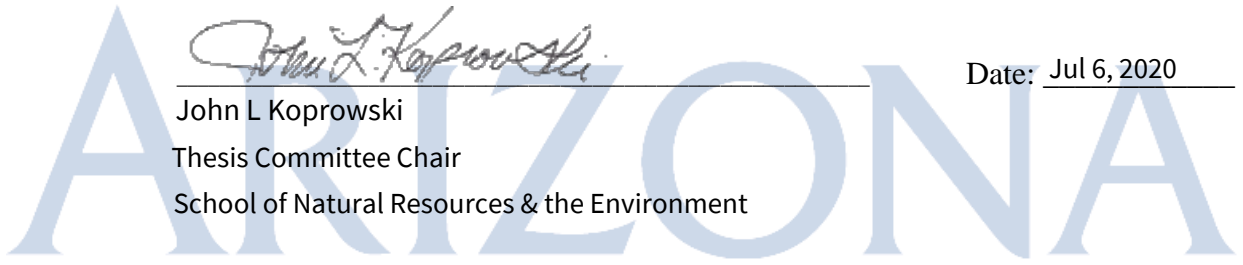
Final approval and acceptance of this thesis is contingent upon the candidate's submission of the final copies of the thesis to the Graduate College.

I hereby certify that I have read this thesis prepared under my direction and recommend that it be accepted as fulfilling the Master's requirement.



John L Koprowski
Thesis Committee Chair
School of Natural Resources & the Environment

Date: Jul 6, 2020



ACKNOWLEDGMENTS

I have been incredibly fortunate to meet and work with an outstanding group of people during this project. Without their endless support, guidance, and patience it would not have been possible. I was very lucky to work with this community of amazing people, spend my countless days of field work in one of the most beautiful places I have ever been, and discover the incredible Sonoran Desert.

I would like to thank my advisor John Koprowski for this amazing opportunity, and for his guidance and work throughout the project. Big thanks to my committee members Tom Jones and Michael Bogan for their help and support. Thanks to Maria Vittoria Mazzamuto and Melissa Merrick for their assistance in writing, software, and data analysis. Thanks to Vicki Greer for endless administrative help with permits, vehicles, and more. Thanks to Paul Bartelt for his guidance on radio-transmitter implantation. Thanks to Bibiana Law and her lab for autoclave access. For field assistance, thanks to Dustin Curley, Nicole Bokanoski, Alexis Blair, Anne-Laure Blanche, Melissa Merrick, Vicki Greer, Brian Blais, Kelsi Thacker, Kellie Sheehan, Meagan Bethel, Annie Dixon, David Ziegler, Brandon Mayer, Kaycie Waters, Neil Dutt, Shambhu Paudel, Akanksha Sharma, and Sandy Slovikosky. I am very grateful for the valuable assistance, support, and feedback of all Koprowski Conservation Research Lab members.

Thanks to Cat Crawford and the US Fish and Wildlife Service, John Kraft and Coronado National Forest, and Karuna Patil (Arizona University Animal Care) for their work in making this project possible. Thanks to the University of Arizona Institutional Animal Care and Use Committee for their assistance (Protocol 16-147). Thank you to the Arizona Game and Fish Department (Heritage Fund) and T&E Inc. for funding this project.

Thanks to my family and friends who supported me during my time as a graduate student, especially Kaycie Waters, Cas, Mike, and Thackery Kanne.

TABLE OF CONTENTS

LIST OF TABLES	5
LIST OF FIGURES	6
ABSTRACT.....	7
INTRODUCTION	8
PRESENT STUDY.....	12
References.....	13
APPENDIX A: MOVEMENT AND SURVIVAL OF AN ENDANGERED AMPHIBIAN: THE FACULTATIVE USE OF A MODIFIED ARID LANDSCAPE BY THE SONORAN TIGER SALAMANDER.....	19
ABSTRACT	20
INTRODUCTION.....	21
METHODS.....	25
RESULTS.....	29
DISCUSSION	34
Acknowledgments.....	39
References	40
APPENDIX B. SUPPORTING TABLES AND FIGURES	57

LIST OF TABLES

Table 1. Sonoran tiger salamanders (*Ambystoma mavortium stebbinsi*) captured in 2018 and 2019 in the San Rafael Valley, Arizona. “Terr” column = Terrestrial metamorphosed adults captured and implanted; “Branch” column = mature branchiate morphs captured; “Juv” column = juvenile and larval individuals captured.....51

Table 2. Sonoran tiger salamander (*Ambystoma mavortium stebbinsi*) used habitat type compared to expected based on availability within an MCP home range including all STS locations found in 2017 and 2018 in the San Rafael Valley, Arizona. Bonferroni confidence interval lower and upper bounds show that none of the three habitat types were occupied more or less than would be expected by chance.....52

LIST OF FIGURES

Fig. 1. Maximum movement distance from stock tank for radio-transmitter implanted Sonoran tiger salamanders (*Ambystoma mavortium stebbinsi*) in the San Rafael Valley, Arizona (n=77). One depredated individual outlier had a maximum movement distance of 1,334 m but was removed due to possible transport by a predator. The maximum migration distance recorded for a living salamander was 974 m from tank edge.....53

Fig. 2. Survival curves for radio-transmitter implanted Sonoran tiger salamanders (*Ambystoma mavortium stebbinsi*) in the San Rafael Valley, Arizona after leaving stock tank. Survival curve A includes all individuals that moved into terrestrial habitat excluding subterranean mortalities (n=50). Survival curve B shows survival by season of dispersal. Median survival (where survival probability = 0.5) was 3 days. Spring dispersers left the stock tank in April or May (n=16). Summer dispersers left the stock tank in June or July (n=34).....54

Fig. 3. Depredation and desiccation events for radio-transmitter implanted Sonoran tiger salamanders (*Ambystoma mavortium stebbinsi*) in the San Rafael Valley, Arizona according to the documented movement number when they occurred. Movement 1 is initial movement out of tank, movement 2 is second movement event, and so forth. All individuals that survived past their fourth movement event, survived until the end the tracking period. The average time between movement events was 7.6 days (\pm 6.6), and the longest time between movement events recorded was 39 days.....55

Fig. 4. Causes of mortality following dispersal for radio-transmitter implanted Sonoran tiger salamanders (*Ambystoma mavortium stebbinsi*) in the San Rafael Valley, Arizona (n = 58). Spring (April + May) dispersers are shown in dark gray and summer dispersers (June + July) are depicted in light gray.....56

ABSTRACT

Connectivity is essential for the maintenance of genetic diversity and stability of wildlife populations. However, aquatic habitats are becoming more isolated, particularly in semiarid regions of the southwestern United States. An artificial aquatic mosaic of stock tanks often replaces natural surface water on the landscape. The federally endangered Sonoran tiger salamander (STS; *Ambystoma mavortium stebbinsi*) is endemic to the San Rafael Valley of southeastern Arizona and northern Sonora, Mexico, where the salamander depends on stock tanks as its primary breeding habitat. The dispersal of the terrestrial phase of STS life history is the only means of responding to aquatic threats and thus is critical for the maintenance of metapopulation dynamics. However, STS ecology outside of breeding tanks is virtually unknown, and previous studies based on *Ambystoma* terrestrial ecology have been restricted to woodland environments in the eastern United States. Predictions from mesic environments may not apply to STS and are of little use for management and conservation. To assess STS spatial ecology, survival, and habitat use, we used internal VHF radio transmitters to track 78 adult salamanders over a two-year study. We assessed home range size and movement metrics in relation to sex, site, and body condition using generalized linear models. STS dispersed up to 974 m from the tank edge. Average net movement distance from tank edge was 403.6 m (\pm 225.7 m), and average 95% kernel home range was 3,053.7 m² (\pm 4,511.1 m²). Maximum migration distances were higher than most *Ambystoma* species, but not sufficient on average to disperse to neighboring stock tanks. We found that mortality was higher than in prior *Ambystoma* studies. High mortality (81.03%) suggests that terrestrial dispersal is risky for STS and high mortality during terrestrial dispersal may contribute to isolated subpopulations and elevated levels of inbreeding. Management actions that improve and maintain artificial aquatic habitats on the

landscape may be needed to improve connectivity and population viability for pond-breeding amphibians in arid or semiarid regions.

INTRODUCTION

Connectivity is essential for the maintenance of genetic diversity and the stability of wildlife populations by facilitating interactions between subpopulations (Goodwin and Fahrig, 2002; Hanski, 1998). Habitat loss and fragmentation reduces connectivity and has been shown to reduce population viability across wildlife populations, including amphibians (Cushman, 2006). Amphibians are particularly vulnerable to habitat modification due to their limited dispersal ability, and their reliance on multiple vegetative communities for breeding or migration (deMaynadier and Hunter, 1999; Mims et al., 2015; Roe and Georges, 2007; Sinsch, 1990). Terrestrial habitat is particularly important because aquatic-breeding amphibians often spend the vast majority of their lives in the terrestrial environment (Madison and Farrand, 1998; Shoop, 1965). Limited dispersal success due to high mortality of dispersers can be a major cause of population declines in amphibians (Cushman, 2006; Taylor et al., 2006; Trenham and Shaffer, 2005). Movement and home range studies can be powerful tools to better understand amphibian population dynamics and viability in the face of climate change, habitat fragmentation, and other anthropogenic factors (Madison, 1997; Searcy et al., 2013; Semlitsch, 1981).

Human induced fragmentation of essential amphibian vegetation communities has been identified as a factor in the global decline of amphibians (Becker et al., 2007). In addition to the disconnect caused by human land use, climate change has led to the increased occurrence of extreme weather events such as drought that can change hydrologic regimes and reduce connectivity of amphibian habitats (Sodhi et al., 2008). Variation in climate and human

disturbance often form a mosaic of habitats available on the landscape (Semlitsch, 2000). This is especially true in the arid southwestern United States—a region with limited aquatic habitats—that is forecasted to experience increased drought severity in the future (Cook et al., 2015). In this region, drought and changing precipitation regimes have caused natural aquatic amphibian breeding habitats (i.e. cienegas, wetlands) to become highly isolated (Marshall et al., 2010) and led to the creation of man-made earthen impoundments (hereafter, stock tanks) in areas across the landscape to enable cattle grazing (Hendrickson and Minckley, 1984). These stock tanks are important for the biodiversity of arid or semiarid regions by providing additional aquatic habitat and stepping stones for connectivity (Brainwood and Burgin, 2009), despite often poor water quality (McIntyre et al., 2016; Schmutzer et al., 2008). These stock tanks serve as some of the only breeding habitat for many pond-breeding amphibians such as the endangered Sonoran tiger salamander (*Ambystoma mavortium stebbinsi*; STS).

Sonoran tiger salamanders, a subspecies of the barred tiger salamander (*Ambystoma mavortium*), are endemic to the San Rafael Valley and surrounding mountain foothills in southern Arizona and northern Sonora, Mexico. Previous work on mole salamanders (*Ambystoma* spp.) shows that metamorphosed adults spend much of the year in subterranean terrestrial habitat before returning to their natal breeding tank in the spring to breed (Gamble et al., 2007; Semlitsch, 1981; Trenham, 2001; Trenham et al., 2000; Whiteman et al., 1994). Like many amphibians, STS deposit their eggs on submerged structures and larvae develop in water (Arnold, 1976; Figiel and Semlitsch, 1995; Kern et al., 2013). Young either metamorphose into mature metamorphosed morphs (MMMs) or remain in aquatic habitats and mature into paedomorphic gilled adults (Collins et al., 1988; U.S. Fish and Wildlife Service, 2002). Protection of a portion of upland habitat surrounding aquatic breeding areas (buffer zones) can

guide conservation of amphibians, which can be informed by data on maximum movement distances of local species away from aquatic habitat (Schonewald-Cox, 1988; Semlitsch, 1998; Semlitsch and Bodie, 2003).

However, most studies on pond-breeding amphibian terrestrial ecology, and *Ambystoma* ecology in particular, have taken place in the eastern United States where most species are found in mesic woodlands with more consistent water present. Predictions from these eastern studies may not apply to western or grassland species (Searcy et al., 2013). Herpetologists have recommended that conservation would be improved by focusing on species and process specific recommendations instead of broad generalizations (Cushman, 2006; Semlitsch and Bodie, 1998). The STS can provide important insight, especially in the face of major threats such as its limited distribution, dependence on human-constructed stock tanks, elevated risk of die-offs due to disease or stock tank drying, and invasive species (Hossack et al., 2017; U.S. Fish and Wildlife Service, 2002). The STS was listed as federally endangered by the United States Fish and Wildlife Service in 1997 (U.S. Fish and Wildlife Service, 1997). The terrestrial phase of STS life history is the only means of responding to drying or disease events, and thus is critical for the maintenance of population persistence and connectivity. Genetic work suggests that STS subpopulations may suffer from high inbreeding rates and reduced gene flow (Jones et al., 1995, 1988; Storfer et al., 2014); however, the ecology and demography of terrestrial morphs is virtually unknown (U.S. Fish and Wildlife Service, 2002). The lack of knowledge of STS terrestrial morph ecology reveals a gap in conservation strategy. In the Sonoran Tiger Salamander Recovery Plan, the U.S Fish and Wildlife Service (USFWS) lists information on survivorship, spatial variation in dispersal, and habitat use of the terrestrial life history variant as among the critical data needs (U.S. Fish and Wildlife Service, 2002). Understanding the

landscape of risk, movement and habitat use of MMMs in an altered landscape is therefore necessary to develop effective landscape management actions to recover species.

PRESENT STUDY

This thesis includes a manuscript intended for publication in the peer reviewed journal *Biological Conservation*. All methods, results, and conclusions of the study are included as appendices to this thesis. The manuscript (Appendix A) is titled “Movement and survival of an endangered amphibian: The facultative use of a modified landscape by the Sonoran tiger salamander.” The paper documents and discusses the terrestrial ecology of an endangered and data-deficient amphibian endemic to a single valley in southeastern Arizona and northern Sonora, Mexico. We focus on how survival and movement distance from breeding habitat relate to the conservation and management of Sonoran tiger salamanders and other imperiled species that exist in modified landscapes.

References

- Arnold, S.J., 1976. Sexual behavior, sexual interference and sexual defense in the salamanders *Ambystoma maculatum*, *Ambystoma tigrinum* and *Plethodon jordani*. *Journal of Animal Psychology* 42, 247–300.
- Becker, C.G., Fonseca, C.R., Haddad, C.F.B., Batista, R.F., Prado, P.I., 2007. Habitat split and the global decline of amphibians. *Science* 318, 1775–1777.
- Brainwood, M., Burgin, S., 2009. Hotspots of biodiversity or homogeneous landscapes? Farm dams as biodiversity reserves in Australia. *Biodiversity and Conservation* 18, 3043–3052.
- Carr, L.W., Fahrig, L., 2001. Effect of road traffic on two amphibian species of differing vagility. *Conservation Biology* 15, 1071–1078.
- Collins, J.P., Jones, T.R., Berna, H.J., 1988. Conserving genetically distinctive populations: The case of the Huachuca tiger salamander (*Ambystoma tigrinum stebbinsi* Lowe). General technical report RM-Rocky Mountain Forest and Range Experiment Station, US Department of Agriculture, Forest Service (USA).
- Cook, B.I., Ault, T.R., Smerdon, J.E., 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. *Science Advances* 1, e1400082.
- Cushman, S.A., 2006. Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biological Conservation* 128, 231–240.
- Davies, S.J., Clusella-Trullas, S., Hui, C., McGeoch, M.A., 2013. Farm dams facilitate amphibian invasion: Extra-limital range expansion of the painted reed frog in South Africa. *Austral Ecology* 38, 851–863.
- deMaynadier, P.G., Hunter, M.L., 1999. Forest canopy closure and juvenile emigration by pool-breeding amphibians in Maine. *Journal of Wildlife Management* 63, 441–450.

- Figiel, C.R., Semlitsch, R.D., 1995. Experimental determination of oviposition site selection in the marbled salamander, *Ambystoma opacum*. *Journal of Herpetology* 29, 452–454.
- Gamble, L.R., McGarigal, K., Compton, B.W., 2007. Fidelity and dispersal in the pond-breeding amphibian, *Ambystoma opacum*: Implications for spatio-temporal population dynamics and conservation. *Biological Conservation* 139, 247–257.
- Goodwin, B.J., Fahrig, L., 2002. How does landscape structure influence landscape connectivity? *Oikos* 99, 552–570.
- Hanski, I., 1998. Metapopulation dynamics. *Nature* 396, 41–49.
- Harper, E.B., Rittenhouse, T. A. G., Semlitsch, R.D., 2008. Demographic consequences of terrestrial habitat loss for pool-breeding amphibians: Predicting extinction risks associated with inadequate size of buffer zones. *Conservation Biology* 22, 1205–1215.
- Hendrickson, D.A., Minckley, W.L., 1984. Ciénegas - Vanishing climax communities of the American Southwest. *Desert Plants* 6, 129–176.
- Hossack, B.R., Honeycutt, R.K., Sigafus, B.H., Muths, E., Crawford, C.L., Jones, T.R., Sorensen, J.A., Rorabaugh, J.C., Chambert, T., 2017. Informing recovery in a human-transformed landscape: Drought-mediated coexistence alters population trends of an imperiled salamander and invasive predators. *Biological Conservation* 209, 377–394.
- Jones, T.R., Collins, J.P., Kocher, T.D., Mitton, J.B., 1988. Systematic status and distribution of *Ambystoma tigrinum stebbinsi* Lowe (Amphibia: Caudata). *Copeia* 1988, 621–635.
- Jones, T.R., Routman, E.J., Begun, D.J., Collins, J.P., 1995. Ancestry of an isolated subspecies of salamander, *Ambystoma tigrinum stebbinsi* Lowe: The evolutionary significance of hybridization. *Molecular Phylogenetics and Evolution* 4, 194–202.

- Kern, M.M., Nassar, A.A., Guzy, J.C., Dorcas, M.E., 2013. Oviposition site selection by spotted salamanders (*Ambystoma maculatum*) in an isolated wetland. *Journal of Herpetology* 47, 445–449.
- Madison, D.M., 1997. The emigration of radio-implanted spotted salamanders, *Ambystoma maculatum*. *Journal of Herpetology* 31, 542–551.
- Madison, D.M., Farrand III, L., 1998. Habitat use during breeding and emigration in radio-implanted tiger salamanders, *Ambystoma tigrinum*. *Copeia* 1998, 402–410.
- Maret, T.J., Snyder, J.D., Collins, J.P., 2006. Altered drying regime controls distribution of endangered salamanders and introduced predators. *Biological Conservation* 127, 129–138.
- Marsh, D.M., Trenham, P.C., 2001. Metapopulation dynamics and amphibian conservation. *Conservation Biology* 15, 40–49.
- Marshall, R.M., Robles, M.D., Majka, D.R., Haney, J.A., 2010. Sustainable water management in the southwestern United States: Reality or rhetoric? *PLoS ONE* 5, e11687.
- McIntyre, N.E., Drake, J.C., Griffis-Kyle, K.L., 2016. A connectivity and wildlife management conflict in isolated desert waters. *Journal of Wildlife Management* 80, 655–666.
- Mims, M.C., Phillipsen, I.C., Lytle, D.A., Kirk, E.E.H., Olden, J.D., 2015. Ecological strategies predict associations between aquatic and genetic connectivity for dryland amphibians. *Ecology* 96, 1371–1382.
- O’Grady, J.J., Brook, B.W., Reed, D.H., Ballou, J.D., Tonkyn, D.W., Frankham, R., 2006. Realistic levels of inbreeding depression strongly affect extinction risk in wild populations. *Biological Conservation* 133, 42–51.

- Orloff, S.G., 2011. Movement patterns and migration distances in an upland population of California tiger salamander (*Ambystoma californiense*). *Herpetological Conservation and Biology* 6, 266–276.
- Reh, W., Seitz, A., 1990. The influence of land use on the genetic structure of populations of the common frog *Rana temporaria*. *Biological Conservation* 54, 239–249.
- Rittenhouse, T.A., Semlitsch, R.D., 2006. Grasslands as movement barriers for a forest-associated salamander: Migration behavior of adult and juvenile salamanders at a distinct habitat edge. *Biological Conservation* 131, 14–22.
- Roe, J.H., Georges, A., 2007. Heterogeneous wetland complexes, buffer zones, and travel corridors: Landscape management for freshwater reptiles. *Biological Conservation* 135, 67–76.
- Schmutzer, A.C., Gray, M.J., Burton, E.C., Miller, D.L., 2008. Impacts of cattle on amphibian larvae and the aquatic environment. *Freshwater Biology* 53, 2613–2625.
- Schonewald-Cox C.M., 1988. Boundaries in the protection of nature reserves. *Bioscience* 38, 480-486.
- Searcy, C.A., Gabbai-Saldate, E., Shaffer, H.B., 2013. Microhabitat use and migration distance of an endangered grassland amphibian. *Biological Conservation* 158, 80–87.
- Semlitsch, R.D., 2000. Principles for management of aquatic-breeding amphibians. *Journal of Wildlife Management* 64, 615–631.
- Semlitsch, R.D., 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. *Conservation Biology* 12, 1113–1119.
- Semlitsch, R.D., 1981. Terrestrial activity and summer home range of the mole salamander (*Ambystoma talpoideum*). *Canadian Journal of Zoology*. 59, 315–322.

- Semlitsch, R.D., Bodie, J.R., 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conservation Biology* 17, 1219–1228.
- Semlitsch, R.D., Bodie, J.R., 1998. Are small, isolated wetlands expendable? *Conservation Biology* 12, 1129–1133.
- Shoop, C.R., 1965. Orientation of *Ambystoma maculatum*: Movements to and from breeding ponds. *Science* 149, 558–559.
- Sinsch, U., 1990. Migration and orientation in anuran amphibians. *Ethology Ecology & Evolution* 2, 65–79.
- Sodhi, N.S., Bickford, D., Diesmos, A.C., Lee, T.M., Koh, L.P., Brook, B.W., Sekercioglu, C.H., Bradshaw, C.J.A., 2008. Measuring the meltdown: Drivers of global amphibian extinction and decline. *PLoS ONE* 3, e1636.
- Storfer, A., Mech, S.G., Reudink, M.W., Lew, K., 2014. Inbreeding and strong population subdivision in an endangered salamander. *Conservation Genetics* 15, 137–151.
- Taylor, B.E., Scott, D.E., Gibbons, J.W., 2006. Catastrophic reproductive failure, terrestrial survival, and persistence of the marbled salamander. *Conservation Biology* 20, 792–801.
- Trenham, P.C., 2001. Terrestrial habitat use by adult California tiger salamanders. *Journal of Herpetology* 35, 343–346.
- Trenham, P.C., Bradley Shaffer, H., Koenig, W.D., Stromberg, M.R., Ross, S.T., 2000. Life history and demographic variation in the California tiger salamander (*Ambystoma californiense*). *Copeia* 2000, 365–377.
- Trenham, P.C., Shaffer, H.B., 2005. Amphibian upland habitat use and its consequences for population viability. *Ecological Applications* 15, 1158–1168.

U.S. Fish and Wildlife Service, 2002. Sonora tiger salamander recovery plan (*Ambystoma tigrinum stebbinsi*). U.S. Fish and Wildlife Service, Phoenix, AZ.

U.S. Fish and Wildlife Service, 1997. Endangered and threatened wildlife and plants; determination of endangered status for three wetland species found in southern Arizona and northern Sonora, Mexico. Federal Register 669–688.

Whiteman, H.H., Wissinger, S.A., Bohonak, A.J., 1994. Seasonal movement patterns in a subalpine population of the tiger salamander, *Ambystoma tigrinum nebulosum*. Canadian Journal of Zoology 72, 1780–1787.

APPENDIX A: MOVEMENT AND SURVIVAL OF AN ENDANGERED AMPHIBIAN: THE FACULTATIVE USE OF A MODIFIED ARID LANDSCAPE BY THE SONORAN TIGER SALAMANDER

Colin W. Brocka and John L. Koprowski

This article will be submitted to *Biological Conservation* for publication.

MOVEMENT AND SURVIVAL OF AN ENDANGERED AMPHIBIAN: THE FACULTATIVE USE OF A MODIFIED ARID LANDSCAPE BY THE SONORAN TIGER SALAMANDER

COLIN W. BROCKA* AND JOHN L. KOPROWSKI

School of Natural Resources and the Environment, University of Arizona, Environment and Natural Resources 2, 1064 East Lowell Street, Tucson, AZ 85721 *Corresponding author: *cbrocka@email.arizona.edu*

ABSTRACT

Connectivity is essential for the maintenance of genetic diversity and stability of wildlife populations. However, aquatic habitats are becoming more isolated, particularly in arid or semiarid regions of the southwestern United States. An artificial aquatic mosaic of stock tanks often replaces natural surface water on the landscape. The federally endangered Sonoran tiger salamander (STS; *Ambystoma mavortium stebbinsi*) is endemic to the San Rafael Valley of southeastern Arizona and northern Sonora, Mexico, where the salamander depends on stock tanks as its primary breeding habitat. The dispersal of the terrestrial phase of STS life history is the only means of responding to aquatic threats and thus is critical for the maintenance of metapopulation dynamics. However, STS ecology outside of stock tanks is virtually unknown, and previous studies based on *Ambystoma* terrestrial ecology have been restricted to woodland environments in the eastern United States. Predictions from mesic environments may not apply to STS and are of little use for management and conservation. To assess STS spatial ecology, survival, and habitat use, we used internal VHF radio transmitters to track 78 adult salamanders over a two-year study. We assessed home range size and movement metrics in relation to sex, site, and body condition using generalized linear models. STS dispersed up to 974 m from the tank edge. Average net movement distance from tank edge was 403.6 m (± 225.7 m), and average 95% kernel home range was 3,053.7 m² ($\pm 4,511.1$ m²). Maximum migration distances were higher than most *Ambystoma* species, but not sufficient on average to disperse to neighboring stock tanks. We found that mortality was higher than in prior *Ambystoma* studies (81.03%). High mortality suggests that terrestrial dispersal is risky for STS and high mortality during terrestrial dispersal may contribute to isolated subpopulations and elevated levels of inbreeding. Management actions that improve and maintain artificial aquatic habitats on the landscape may be needed to improve connectivity and population viability for pond-breeding amphibians in arid regions.

INTRODUCTION

Connectivity is essential for the maintenance of genetic diversity and the stability of wildlife populations by facilitating interactions between subpopulations (Goodwin and Fahrig, 2002; Hanski, 1998). Connectivity allows for gene flow among habitat patches as well as re-population of habitat patches if a local extinction event occurs (Becker et al., 2007; Marsh and Trenham, 2001; Semlitsch and Bodie, 1998). Insufficient connectivity can lead to isolated populations that are more vulnerable to demographic stochasticity or extreme environmental events (O'Grady et al., 2006; Semlitsch and Bodie, 1998). Habitat loss and fragmentation reduces connectivity and population viability across wildlife populations, including amphibians (Cushman, 2006). Amphibians are particularly vulnerable to habitat modification due to their limited dispersal ability when compared to other vertebrates (Sinsch, 1990), and exhibit an elevated risk of mortality when moving across roads or through modified terrain (Carr and Fahrig, 2001; deMaynadier and Hunter, 1999; Reh and Seitz, 1990; Rittenhouse and Semlitsch, 2006). Aquatic habitat connectivity is particularly important for gene flow in aquatic amphibians with complex life cycles that require movement between multiple vegetative communities for breeding or migration (deMaynadier and Hunter, 1999; Mims et al., 2015; Roe and Georges, 2007). Terrestrial habitat is particularly important because aquatic-breeding amphibians often spend the vast majority of their lives in the terrestrial environment (Madison and Farrand, 1998; Shoop, 1965). Limited dispersal success or juvenile recruitment due to high mortality of dispersers can be a major cause of population declines in amphibians (Cushman, 2006; Taylor et al., 2006; Trenham and Shaffer, 2005). Movement and home range studies can be powerful tools to better understand amphibian population dynamics and viability in the face of climate change,

habitat fragmentation, and other anthropogenic factors (Madison, 1997; Searcy et al., 2013; Semlitsch, 1981).

Human induced fragmentation of terrestrial habitats that amphibians rely on for dispersal is a factor in the global decline of amphibians (Becker et al., 2007). In addition to the fragmentation caused by human land use, climate change has led to the increased occurrence of extreme weather events such as drought that can change hydrologic regimes and reduce connectivity of amphibian habitats (Sodhi et al., 2008). Variation in climate and human disturbance often form a mosaic of habitats available on the landscape (Semlitsch, 2000). This is especially true in the arid southwestern United States—a region with limited aquatic habitats—that is forecasted to experience increased drought severity in the future (Cook et al., 2015). In this region, drought and changing precipitation regimes have caused natural aquatic amphibian breeding habitats (i.e. cienegas, wetlands) to become highly isolated or disappear completely (Marshall et al., 2010) and led to the construction of earthen impoundments (hereafter, stock tanks) in areas across the landscape to capture and store drinking water for free-ranging livestock (Hendrickson and Minckley, 1984). Stock tanks are important for aquatic biodiversity of arid regions by providing additional aquatic habitat and stepping stones for connectivity (Brainwood and Burgin, 2009), despite often poor water quality (McIntyre et al., 2016; Schmutzer et al., 2008). However, the extended hydroperiod of some of these artificial ponds can facilitate the spread of invasive predators such as American bullfrogs (*Lithobates catesbeianus*) and fish (Davies et al., 2013; Hossack et al., 2017; Maret et al., 2006). These stock tanks serve as some of the only breeding habitat for many pond-breeding amphibians such as the endangered Sonoran tiger salamander (*Ambystoma mavortium stebbinsi*).

Sonoran tiger salamanders (hereafter, STS) are endemic to the San Rafael Valley and surrounding mountain foothills of southeastern Arizona and adjacent Sonora, Mexico, and were listed as Endangered by the United States Fish and Wildlife Service in 1997 (USFWS, 1997). Collins (1981) and Collins et al. (1988) described life history variation in STS and other subspecies of *A. mavortium* that occur in Arizona. In all subspecies, some larvae metamorphose at the end of their first season, becoming immature metamorphosed morphs, after which they grow outside of the aquatic habitat into a mature metamorphosed morph (MMM). Alternatively, they may remain in aquatic habitats and mature into paedomorphic gilled adults, or mature branchiate morphs (MBM). Mature metamorphosed morphs return to stock tank breeding sites in late winter/early spring, where they and MBMs deposit their eggs singly on submerged structures (Collins et al. 1988). Previous work on other mole salamanders (*Ambystoma* spp.) shows that metamorphosed adults spend much of the year in subterranean terrestrial habitat before returning to their natal breeding site to breed (Gamble et al., 2007; Semlitsch, 1981; Trenham, 2001; Trenham et al., 2000; Whiteman et al., 1994). Protection of a portion of upland habitat surrounding aquatic breeding areas (buffer zones) can enhance conservation of amphibians. Decisions about which upland areas to protect can be informed by data on maximum movement distances of local species away from aquatic habitat (Schonewald-Cox, 1988; Semlitsch, 1998; Semlitsch and Bodie, 2003). Semlitsch (1998) calculated a buffer zone based on movement data for six *Ambystoma* species in the eastern U.S. and recommended a minimum of 164.3 m would be necessary to encompass the terrestrial needs for 95% of individuals. Harper et al. (2008) presented additional data for one of those species (*Ambystoma maculatum*) and recommended a buffer zone between 100-165 m. Orloff (2011) and Trenham and Shaffer (2005) studied the movements of *Ambystoma californiense*, and recommended larger buffer zones (> 630 m).

Most studies on pond-breeding amphibian terrestrial ecology, and *Ambystoma* ecology in particular, have taken place in the eastern United States where species are found in mesic forests with more reliable breeding sites. Predictions from these previous studies may not apply to desert or grassland species (Searcy et al., 2013). Ecological studies of *A. californiense* are the only assessments of *Ambystoma* ecology in semiarid habitats of the western United States, where water availability is more dynamic and less predictable (Orloff, 2011; Searcy et al., 2013; Trenham and Shaffer, 2005). Conservation would be improved by focusing on species- and process-specific recommendations in relation to migration and dispersal instead of broad generalizations (Cushman, 2006; Semlitsch and Bodie, 1998). The STS can provide important insight, especially in the face of major threats such as its limited distribution, dependence on human-constructed stock tanks, invasive species, and elevated risk of die-offs due to disease or stock tank drying (Hossack et al., 2017; USFWS, 2002). The terrestrial phase of the STS life cycle is the only means of responding to drying or disease events, and thus is critical for population persistence and connectivity. However, the terrestrial ecology and demography of STS is virtually unknown (USFWS, 2002). Collins et al., (1988) found that only 17-40% of larvae metamorphosed which makes metamorphosed salamanders uncommon and difficult to study. Genetic work suggests that STS subpopulations may suffer from high inbreeding rates and reduced gene flow (Jones et al., 1988, 1995; Storfer et al., 2014); The lack of information on STS terrestrial ecology reveals a gap in conservation strategy. In the Sonoran Tiger Salamander Recovery Plan, the United States Fish and Wildlife Service (USFWS) lists information on survivorship, spatial variation in dispersal, and habitat use of the terrestrial life history variant as among the critical data needs (USFWS, 2002). Understanding the landscape of risk, movement

and habitat use of MMMs in the face of human land use and climate change is therefore necessary to develop effective landscape management actions to recover species.

METHODS

Study Area

The San Rafael Valley is an 86,000 ha grassland situated between the Patagonia and Huachuca mountains in southeastern Arizona and far northern Sonora, Mexico (Hadley and Sheridan, 1995). The vegetation community is dominated by Plains grassland transitioning into Madrean oak-juniper woodland in surrounding foothills (Brown, 1982). Perennial grasses such as gramas (*Bouteloua* spp.), plains lovegrass (*Eragrostis intermedia*), and bluestems (*Andropogon* spp.) dominate (Brown, 1982; Hadley and Sheridan, 1995). The exotic Lehmann's lovegrass (*Eragrostis lehmanniana*) has been present in southeastern Arizona since the 1970's (McClaran, 2003) and is common in parts of the San Rafael Valley (Brocka pers. obs.) Natural springs and wetlands in the San Rafael Valley have largely disappeared from the area and have been replaced by stock tanks (Collins et al., 1988; Hendrickson and Minckley, 1984). Stock tanks serve as a water source for livestock and are the primary STS breeding habitat (Collins et al., 1988; Jones et al., 1988, 1995). We focused our study at three perennial stock tanks located within the San Rafael Valley that have a known history of STS presence (Collins et al. 1988).

Stock Tank Surveys and Salamander Measurements

We captured mature metamorphosed morphs (MMMs) at three stock tanks (Dan Tank, Upper 13 Reservoir, and Huachuca Tank) March-August 2017 and March-July 2018. We caught salamanders by pulling a bottom-weighted 9.1 m x 1.5 m bag seine across a tank—a technique used previously for amphibian surveys in stock tanks (Routman, 1984; Hossack et al., 2017), and

seined each tank one to ten times per sampling effort. Number of seine hauls varied based on capture rate, ending when a maximum of six MMMs were captured or three consecutive hauls were empty. Individuals weighing > 38 g were transported to the Central Animal Facility at the University of Arizona for radio-transmitter implantation. We anesthetized each metamorphosed salamander with a 0.2% solution of MS-222 buffered to neutral pH, weighed them to the nearest 0.1 g with a digital scale (HL-200i; A&D Co.), identified sex, and used a ruler (± 0.5 mm) to estimate snout-vent length (SVL) and total length. We calculated salamander body condition via linear regression residuals of body mass on snout-vent length (Jakob et al., 1996; Lowe et al., 2006; Schulte-Hostedde et al., 2005). All equipment, clothing, and footwear was disinfected with quaternary ammonia (Quat-128; 0.02% dilution) between sites to prevent disease transmission among sites (Phillott et al., 2010).

Data collection

In order to assess movement and survival of MMMs, we implanted a VHF radio transmitter (3.5 g, PD-2HX; Holohil Inc.) and a Passive Integrated Transponder (PIT) tag (9mm; Biomark Inc.) in each metamorphosed salamander (transmitter was $< 10\%$ of total salamander mass). We conducted implantation surgeries in the Central Animal Facility, using standard implantation methods (Faccio, 2003). We used an autoclave to sterilize surgery instruments before use. We made a small incision into the left ventrolateral wall 10 mm anterior to the hind leg and inserted the sterilized PIT tag and epoxy covered transmitter into the abdominal cavity. We closed the incision using dissolvable suture and applied analgesic and antiseptic spray (Bactine, WellSpring) to the incision area. We held salamanders for 24 hours before release back into their capture site. All methods and handling were done in accordance with IACUC standards (IACUC Protocol 16-147).

To determine locations, we tracked implanted salamanders 2–4 times per week during the spring (March–May) and summer (June–August), and 1–2 times per week during the fall and winter (September–February) in 2017 and 2018. We determined locations by homing and recorded all locations on a handheld GPS unit (eTrex Legend Cx; Garmin; ± 5 m).

Home Range

We calculated home ranges using both the kernel density and minimum convex polygon methods on ArcGIS (ArcGIS, 2018) and Geospatial Modeling Environment software (Beyer, 2014). For salamanders with ≥ 20 locations, we used the fixed kernel density estimator (KDE) with maximum likelihood cross validation of the smoothing parameter (CVh) to estimate total home range (95% KDE) and core area (50% KDE). We used the minimum convex polygon (MCP) to calculate the home range of salamanders with < 19 locations.

We explored the relationships between the KDE home range (50% and 95%) and sex and body condition of salamanders using generalized linear models in R version 3.5.1 (R Core Team, 2013). We also included the tank of origin, time spent in tank after transmitter implant, and the number of tracking days after dispersal from the tank as covariates to assess possible differences between sites and time spent in terrestrial habitat, respectively. Final models were selected via stepwise deduction methods.

Movement

We used ArcGIS and Geospatial Modeling Environment software to calculate the sum of all distances between fixes during tracking (hereafter, total distance), and the maximum linear distance from stock tank edge (hereafter, maximum distance). We used generalized linear models in R (R Core Team, 2013) to assess relationships between movement metrics and salamander

characteristics as predictors. In particular, we assessed the effect of sex, body condition, sex*body condition, tank of origin, and number of days in tank before dispersal on the total distance and maximum distance moved. To account for a difference in the movement metrics relative to survey effort, we included in our models the number of total locations recorded and the number of days between egress from the stock tank and the end of the survey. We used ArcGIS to calculate average nearest neighbor distance for known stock tank locations, based on prior Arizona Game and Fish Department STS surveys, to determine the distance necessary for STS to reach a neighboring stock tank.

Survival

To assess the survival of implanted salamanders, we used logistic regression with binary response (survived or not) to explore the effect of sex, body condition, sex*body condition, tank of origin, and season of dispersal (April+May = Spring, June+July = Summer) on whether an individual survived during the tracking period. We used a generalized linear mixed model (GLMM, Bolker et al., 2009) with year of sampling as a random factor to account for interannual differences in environmental conditions.

We used Program R and the package ‘survival’ (Therneau, 2015; Therneau and Grambsch, 2000) to visualize overall and seasonal survival rates with a Kaplan-Meier survival curve (Kaplan and Meier, 1958; Pollock et al.;1989). Additionally, we used a Cox proportional hazards model (Cox, 1972) to explore the effect of sex, tank of origin, and season of dispersal on the hazard rate of individuals during the study period.

Habitat Use

We used a vegetation communities map from the United States Forest Service Southwestern Region to identify vegetative communities in the uplands surrounding our study sites (USDA Forest Service, 2009). Vegetative communities in the San Rafael Valley included mixed plains grassland, mixed semi-desert shrubland, and mixed oak-juniper woodland, and we used ArcGIS to determine how many STS locations of MMMs occurred in each habitat type. To investigate STS third-order habitat selection (Johnson, 1980), we calculated the proportion of each habitat type within the area available to the salamander. For the purpose of this analysis, we defined available habitat as the area within a minimum convex polygon home range (MCP) of all salamander locations at each study site. We used a chi square goodness-of-fit test to determine if a significant difference existed between the habitat occupied by salamanders, and what would be expected based on availability of habitat. Finally, we constructed simultaneous Bonferroni confidence intervals for the used habitat proportion to test whether any specific habitat types were used more or less than would be expected (Nue et. al, 1974; Byers et. al, 1984). All mean values are expressed as \pm the standard deviation (SD), unless stated otherwise.

RESULTS

Stock Tank Surveys and Salamander Measurements

During 45 stock tank surveys over 38 total survey days (Average 3.51 ± 2.27 seine pulls/survey = ~ 18.55 man-hours/survey day), we captured and implanted 78 salamanders, 38 in 2017 and 40 in 2018 (Table 1). We captured 172 MMMs, 2,949 MBMs, and 7,231 larval and juvenile salamanders (Table 1). We had a near even sex ratio for implanted individuals with 40 males and 38 females (1.05:1). We sampled Dan Tank 17 times, Huachuca Tank 7 times, and

Upper 13 Reservoir 18 times. Huachuca Tank became too sediment-filled to continue sampling mid-way through 2018. We collected 647 total radio-telemetry locations of terrestrial salamanders.

Male MMMs were smaller than females on average (mass $\bar{x} = 52.06 \pm 10.15$ g versus $\bar{x} = 63.63 \pm 14.21$ g; $t = -4.14$, $p < 0.001$). With both sexes combined, salamanders captured in 2018 ($53.19 \text{ g} \pm 12.13 \text{ g}$) had a lower body mass than those captured in 2017 ($62.45 \text{ g} \pm 13.45 \text{ g}$; $t = -3.08$, $p = 0.003$). Salamander SVL was similar between sexes (Male = $122.1 \text{ mm} \pm 5.4 \text{ mm}$; Female = $121.9 \text{ mm} \pm 6.9 \text{ mm}$).

Home Ranges

Salamanders with greater than 19 locations ($n = 11$; 6 male, 5 female) were included in kernel home range analysis. The number of fixes per individual ranged between 20 and 65 fixes ($\bar{x} = 39 \pm 13$). Mean terrestrial home range size for STS using 95% KDE was $3,054 \pm 4,301 \text{ m}^2$. The home range core area (50% KDE) was $505 \text{ m}^2 \pm 610 \text{ m}^2$. On average, females had a larger 95% KDE home range than males (F: $5,271 \text{ m}^2$, M: $1,206 \text{ m}^2$), though sex was not significant in the model ($p = 0.17$). Body condition, tank of origin, time in tank after transmitter implant, and the number of tracking days after dispersal did not have a significant effect on 95% or 50% KDE home range size (all $p > 0.05$). Mean MCP home range size for STS with less than 19 locations ($n=7$) was $7,028 \text{ m}^2 \pm 17,082 \text{ m}^2$.

Movement

No implanted STS dispersed to a different stock tank. Average nearest neighbor distance among stock tanks in the valley was $760 \pm 877 \text{ m}$. The nearest salamander-positive tanks (stock tanks with a history of STS presence) to each of our study sites: Dan Tank, Upper 13 Reservoir,

and Huachuca Tank were 1,628 m away, 1,056 m away, and 2,178 m away. On average, implanted salamanders remained in the tank for 21 days after radio-transmitter implantation (SD = 13.9 days; range 4 to 61 days) before moving out of the tank. From there, implanted salamanders spent on average 54 terrestrial days before mortality or radio-transmitter battery expiration (SD = 94.2 days; range 1 to 371 days). On average, terrestrial salamanders moved every 7-8 days (7.6 ± 6.6 days; min 1, max = 39 days). We analyzed total distance and maximum distance from tank edge for implanted STS with at least 20 locations (n=11). Average tracking time was 190 ± 92 (range 77–361) days. Mean total distance moved was $751.5 \text{ m} \pm 353.8 \text{ m}$. On average, females moved greater total distances than males, but sex was not a significant variable in the model (F: $847.8 \text{ m} \pm 409.1 \text{ m}$, M: $671.2 \text{ m} \pm 352.9 \text{ m}$, $p = 0.16$). Mean maximum migration distance moved was $403.6 \text{ m} \pm 215.2 \text{ m}$. On average, females moved greater maximum distance than males (F: $449.3 \text{ m} \pm 227.3 \text{ m}$, M: $365.6 \pm 238.2 \text{ m}$), but sex did not have significant predictive power in the model ($p = 0.17$). One salamander that was tracked for a short period (9 locations) before going missing, traveled as far as 974 m from tank edge (Fig. 1). One depredated salamander was found 1,334 m from tank edge but may have been transported by the predator. Excluding unknown underground refugia, STS were located most often within mammal burrows (96% of salamander locations). Salamanders were occasionally found using other refuge, such as leaf litter (2%), tree stumps (2%), or rock ledges (>1%) for short periods.

Survival

We analyzed terrestrial survival on a subset of 58 salamanders. Eleven were excluded because they never dispersed from the tank—three were confirmed mortalities and transmitter battery expired for 8 others. A University of Arizona veterinarian performed a necropsy on one of the confirmed tank mortalities and concluded that transmitter implantation was not the cause of

death. Nine individuals were excluded because they were lost during tracking and survival or fate could not be confirmed.

We recorded high mortality rates during our study. Of the 58 individuals in the analysis, only 11 salamanders survived (81.03% mortality) until radio-transmitter expiration ($\bar{x} = 190 \pm 91.9$ days; range 77 – 361 days). The most common cause of terrestrial mortality was predation ($n = 26$; 44.8%). Depredation was commonly identified by the discovery of a radio transmitter, with yellow-green residue, and occasionally indications of tooth or beak marks. Some radio-transmitters from depredated salamanders were partially crushed or broken, and one transmitter was recovered from an owl pellet. The second most common cause of terrestrial mortality was desiccation ($n = 13$; 22.4%). Salamanders were typically found desiccated or partially dried on the ground with no evidence of predation. Eight subterranean individuals were excluded from survival analysis because the exact date and cause of death could not be determined. Three desiccated salamanders, not included in our study, were observed near our study sites, revealing that desiccation may be common for STS in the San Rafael Valley.

Upon leaving the tank, risk of mortality was substantial (survival probability at day 0 = 0.52 ± 0.07 SE) with few surviving until transmitter failure (survival probability 0.22 ± 0.06 SE.). On average, terrestrial STS survived for 82.5 days ± 20.9 SE (median = 3 days) based on the Kaplan-Meier survival curve (Fig. 2). Individuals that dispersed to terrestrial habitat in summer survived longer ($\bar{x} = 73.9 \pm$ SE 19.1 days; median = 3 days) than individuals that dispersed in spring ($\bar{x} = 21.8$ days \pm SE 14.9; median = 0 days) (log-rank test, $p = 0.09$). Mortality was most common following the first documented movement out of tank, and all predation or desiccation events occurred between the first and fourth documented movement events (Fig. 3). Of the 39

salamanders that died, individuals spent an average of 4.6 (SD = 9.6; range 1–41) terrestrial days before mortality.

We found a significant relationship between dispersal season and survival. Summer-dispersing salamanders (June – July) survived until the end of the tracking period (battery expiration) 23.15 % of the time, compared to 6.25 % for salamanders that dispersed during the spring (April – May) ($\beta = 2.504$, $z = 1.960$, $p = 0.05$). Of the individuals that did not survive in the spring, 75% were depredated. Of the individuals that did not survive in the summer, 45% were depredated (Fig. 4).

Habitat Use

Three vegetation communities were available to STS within the MCP that encompassed all salamander locations at each study site: mixed plains grassland, mixed oak-juniper woodland, and mixed semi-desert shrubland (USDA Forest Service, 2009). Mixed plains grassland is dominated by perennial grasses, with less than 10% shrub or canopy cover. Mixed semi-desert shrubland is defined by the presence of woody shrubs less than 5 m tall (e.g., *Arctostaphylos* spp., *Mimosa* spp.) and consists of 10-100% shrub cover. Mixed oak-juniper woodland is comprised of trees greater than 5 m tall (e.g., *Quercus arizonica*, *Q. emoryi*, *Juniperus deppeana*), with canopy closure 10-100%. The percent of each habitat type available was 62.1%, 32.3%, and 5.6%, respectively. We found that STS used all three habitat types: 64.5% of locations within mixed plains grassland, 33.2% within mixed oak-juniper woodland, and 2.3% within semi-desert shrubland. STS habitat was statistically different from a random distribution ($\chi^2 = 8.67$; $p = 0.013$). However, all expected habitat proportions fell within the Bonferroni confidence interval for the used habitat proportion, showing that no habitat type was used significantly more or less than expected (Table 2).

DISCUSSION

Movements suggest low connectivity

On average STS moved 0.7-6.7 times farther from aquatic habitat than movement distances reported for other *Ambystoma* species. Reported distances include *A. jeffersonianum* ($\bar{x} = 252.0$ m, Williams, 1973), *A. maculatum* ($\bar{x} = 118$ m, Kleeberger and Werner, 1983; $\bar{x} = 192.0$ m, Madison, 1997), *A. opacum* (mode = 297 m, Gamble et al., 2007; $\bar{x} = 193.7$ m, Williams, 1973), *A. talpoideum* ($\bar{x} = 178.0$ m, Semlitsch, 1981), or *A. tigrinum* ($\bar{x} = 60.5$ m, Madison and Farrand, 1998; $\bar{x} = 110.7$ m, Steen et al., 2006). *Ambystoma* species home range studies are uncommon in the literature due in part to their fossorial nature and difficulty of study. STS home range is 131 times larger than the only other *Ambystoma* study of which we are aware, that of *A. talpoideum* (MCP 0.11–23.3 m²) (Semlitsch, 1981). These prior *Ambystoma* studies were conducted in the eastern United States where water and forest cover are more common. Reduced water availability in the semiarid grasslands of the San Rafael Valley may contribute to higher STS movement. Studies on *A. californiense* are the only other literature to assess movement of a grassland *Ambystoma* salamander in the western United States (Searcy et al., 2013; Trenham, 2001; Trenham and Shaffer, 2005). *A. californiense* moved a median distance of 556 m (Searcy et al., 2013), suggesting that it may be more ecologically similar to STS than eastern species.

Despite the ability for long distance dispersal, none of our telemetered STS dispersed to a different stock tank, and on average did not disperse as far as the average nearest distance for neighboring stock tanks in the valley. Despite their long movements compared to other *Ambystoma* species, these movements may not be sufficient to provide continuous connectivity between subpopulations in the San Rafael Valley. However, we were not able to measure juvenile dispersal as their small body mass rendered them unfit for radio-transmitter implantation. This may have

reduced dispersal distance estimates, as juvenile dispersal is known to be a primary life-stage for dispersal in other amphibians (Cushman, 2006; Titus et al., 2014; Trenham and Shaffer, 2005). In addition, high mortality of dispersing salamanders suggests that movements in the landscape are constrained by high risk of predation and substantial risk of desiccation. While connectivity constrained, it is likely that a very small number of successful long-distance dispersers account for colonization of stock tanks after local extinction events and provide sufficient gene flow to isolated subpopulations (Mills and Allendorf, 1996). Random events such as flash-floods can also provide gene flow among subpopulations over extended time periods.

Movements in a semiarid landscape are risky

STS exhibited a mortality rate 1.6-7.7 times higher than those reported for other *Ambystoma* species. Previous *Ambystoma* studies estimated 10.5% annual mortality in *A. maculatum* (Whitford and Vinegar, 1966), 25.8% in *A. talpoideum* (Raymond and Hardy, 1990), and 50% for *A. californiense* (Trenham et al., 2000). Die-offs of metamorphosed *Ambystoma* species have been observed as a result of heat stress or desiccation (Holland et al., 1990; Semlitsch, 1983). *Ambystoma* species are vulnerable to high rates of desiccation in unsuitable conditions, especially if sufficient refuge is not available (Rothermel and Luhring, 2005). Increased ambient aridity may also reduce anti-predator behavior in amphibians, thus increasing risk of predation (Rohr and Madison, 2003). High STS mortality that we documented suggests that conditions in the San Rafael Valley are risky for metamorphosed morphs. These risks are likely greater in the semiarid San Rafael Valley, compared to *Ambystoma* habitats in the eastern United States. Southern Arizona exhibits a bimodal rainfall pattern, with winter rains from December through February and heavy summer monsoon rains from late June to August that provide the majority of its annual rain total (Smith, 1956; Adams and Comrie, 1997). STS had a higher survival percentage

when dispersing in the summer monsoon, while desiccation and depredation were more likely in the spring. This is possibly due to the lack of vegetative cover in the spring before monsoon rains. Lack of vegetative cover may increase mortality risk due to improved predator line of sight or decreased moisture retention (Ferraro and Burgin, 1993; Rohr and Madison, 2003). Body condition before dispersal from the tank did not influence survival. This suggests that other factors such as predation pressure or harsh environmental conditions may have had a greater influence on survival (deMaynadier and Hunter, 1999; Keane et al., 2007). High mortality resulting from risky terrestrial dispersal may contribute to high inbreeding and isolated subpopulations, and explains the genetic data for STS (Storfer et al., 2014).

STS larvae either metamorphose or exhibit paedomorphosis. Paedomorphosis in STS may be facultative, where environmental conditions determine that some salamanders attain sexual maturity while retaining larval characteristics resulting from environmental conditions (Collins et al., 1988). These aquatic adults are called mature branchiate morphs. Paedomorphosis is common among salamander species, where the process is either obligate as in the hellbender (*Cryptobranchus alleganiensis*; Duellman and Trueb, 1994) or facultative as in the mole salamander (*Ambystoma talpoideum*; Semlitsch and Gibbons, 1985). Facultative paedomorphosis is selectively maintained by different environmentally variable fitness payoffs to each morphology (Routman, 1993; Whiteman, 1994; Whiteman et al., 1996; Wilbur and Collins, 1973). One such mechanism, the “Paedomorph Advantage,” suggests that paedomorphs have a fitness advantage by remaining in aquatic habitat, and avoiding extreme terrestrial conditions (Whiteman, 1994). However, despite this advantage, MMMs are retained and especially important in the population during years when aquatic habitat quality is poor (Whiteman, 1994). High terrestrial mortality risk resulting from desiccation or depredation in the San Rafael Valley, coupled with increased water

permanence of stock tanks, likely select against dispersing individuals. Nonetheless, these dispersing individuals are important for repopulating stock tanks in the case of a die-off due to disease, or tank drying during a particularly dry year, as well as for maintaining gene flow. However, metamorphosed salamanders may be more successful and provide valuable gene flow or dispersal during particularly wet years.

Management of landscapes for connectivity is key

Conservation strategies for pond-breeding amphibians must include terrestrial habitat to be successful (Dodd and Cade, 1998). Terrestrial habitat protection for amphibians should be based on site-specific understanding of amphibian movement patterns (Dodd and Cade, 1998; Regosin et al., 2005; Titus et al., 2014). Buffer zone suggestions based on eastern *Ambystoma* species such as 164.3 m (Semlitsch, 1998), >100 m (Regosin et al., 2005), or 192 m-339 m (Semlitsch and Bodie, 2003) are not sufficient to encompass the life history variation in STS. Trenham and Shaffer (2005), and (Orloff, 2011) recommended larger buffer zones (> 630 m) for *A. californiense*, a species that also occupies semiarid habitats very similar to those in the San Rafael Valley. Based on Semlitsch's (1998) use of the 95th percentile of movement distances to estimate buffer zone extent, we suggest a buffer zone of 800 m for the STS. Our results are consistent with those of Searcy et al. (2013) who recognized that management recommendations for eastern *Ambystoma* species cannot be applied to western species such as the California tiger salamander. An understanding of species-specific requirements is essential to conservation and management of *Ambystoma* species.

Dispersal distances that are insufficient to reach other breeding sites, coupled with high mortality likely limit connectivity among STS subpopulations. Therefore, gene flow among subpopulations is likely provided only by rare successful dispersers. Management to improve

connectivity and protect stock tank habitats is essential to the recovery of this endangered species and other species dependent on these artificial aquatic habitats. Creation of stepping stone aquatic habitats may help improve connectivity but will likely increase encroachment by invasive predators like American bullfrogs (Hossack et al., 2017; McIntyre et al., 2016; Semlitsch, 2002). Removal of invasive predators can be a labor-intensive process, but it can have a positive effect on native species (Hale et al., 2015; Snow and Witmer, 2010; Boone et al., 2008). Translocation of individuals could be used to help improve gene flow in the STS (Marsh and Trenham, 2001; Germano and Bishop, 2009; Weeks et al., 2011), however very low heterozygosity in the STS leaves little variability to spread (Jones et al., 1995, 1988; Storfer et al., 2014). Management of aquatic habitats and upland areas within altered landscapes, such as the San Rafael Valley, is essential for the conservation and maintenance of at-risk amphibian populations that depend on appropriate levels of connectivity, especially in the face of climate change. Partnership between landowners, natural resource managers, and other stakeholders has improved other amphibian conservation efforts (Rosen and Schwalbe, 1997). STS conservation and management in the San Rafael Valley consists of various natural resource management agencies, private landowners, governments, and other stakeholders that have been successful, and must continue to work together to implement conservation of this unique and imperiled amphibian.

ACKNOWLEDGMENTS

We thank Tom Jones and Michael Bogan for their guidance and support during this project. Thank you to Maria Vittoria Mazzamuto and Melissa Merrick for their assistance in writing, software, and data analysis. Thanks to Vicki Greer for endless administrative help with permits, vehicles, and more. Thanks to Paul Bartelt for his guidance on radio-transmitter implantation. Thanks to Bibiana Law and her lab for autoclave access. For field assistance, thanks to Dustin Curley, Nicole Bokanoski, Alexis Blair, Anne-Laure Blanche, Melissa Merrick, Vicki Greer, Brian Blais, Kelsi Thacker, Kellie Sheehan, Meagan Bethel, Annie Dixon, David Ziegler, Brandon Mayer, Kaycie Waters, Neil Dutt, Shambhu Paudel, Akanksha Sharma, and Sandy Slovikosky. We are grateful for the valuable assistance of all Koprowski Conservation Research Lab members.

Thanks to Cat Crawford and the US Fish and Wildlife Service, John Kraft and Coronado National Forest, and Karuna Patil (Arizona University Animal Care) for their work in making this project possible. Thanks to the University of Arizona Institutional Animal Care and Use Committee for their assistance (Protocol 16-147). Thank you to the Arizona Game and Fish Department (Heritage Fund) and T&E Inc. for funding this project.

REFERENCES

- Adams, D.K., Comrie, A.C., 1997. The north American monsoon. *Bulletin of the American Meteorological Society* 78, 2197-2214.
- ArcGIS, 2018. Environmental Systems Research Institute, Redlands, CA.
- Arnold, S.J., 1976. Sexual behavior, sexual interference and sexual defense in the salamanders *Ambystoma maculatum*, *Ambystoma tigrinum* and *Plethodon jordani*. *Journal of Animal Psychology* 42, 247–300.
- Becker, C.G., Fonseca, C.R., Haddad, C.F.B., Batista, R.F., Prado, P.I., 2007. Habitat split and the global decline of amphibians. *Science* 318, 1775–1777.
- Beyer, H.L., 2014. Geospatial modeling environment. [http://www. spatial ecology. com/gme](http://www.spatial ecology.com/gme).
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.S.S., 2009. Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24, 127–135.
- Boone, M.D., Semlitsch, R.D., Mosby, C., 2008. Suitability of golf course ponds for amphibian metamorphosis when bullfrogs are removed. *Conservation Biology* 22, 172–179.
- Brainwood, M., Burgin, S., 2009. Hotspots of biodiversity or homogeneous landscapes? Farm dams as biodiversity reserves in Australia. *Biodiversity and Conservation* 18, 3043–3052.
- Brown, D.E. (ed.), 1982. Biotic communities of the American Southwest - United States and Mexico. *Desert Plants* 4.
- Byers, C.R., Steinhorst, R.K., Krausman, P.R., 1984. Clarification of a technique for analysis of utilization-availability data. *The Journal of Wildlife Management* 48, 1050-1053.

- Carr, L.W., Fahrig, L., 2001. Effect of road traffic on two amphibian species of differing vagility. *Conservation Biology* 15, 1071–1078.
- Collins, J.P., Jones, T.R., Berna, H.J., 1988. Conserving genetically distinctive populations: The case of the Huachuca tiger salamander (*Ambystoma tigrinum stebbinsi* Lowe). 45-53 In Szaro, R.C., K.E. Severson, and D.R. Patton (eds.) *Proceedings of a Symposium on Management of Amphibians, Reptiles and Small Mammals in North America*. USDA Forest Service RM-GTR-166, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Cook, B.I., Ault, T.R., Smerdon, J.E., 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. *Science Advances* 1, e1400082.
- Cox, D.R., 1972. Regression models and life-tables. *Journal of the Royal Statistical Society: Series B (Methodological)* 34, 187–202.
- Cushman, S.A., 2006. Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biological Conservation* 128, 231–240.
- Davies, S.J., Clusella-Trullas, S., Hui, C., McGeoch, M.A., 2013. Farm dams facilitate amphibian invasion: Extra-limital range expansion of the painted reed frog in South Africa. *Austral Ecology* 38, 851–863.
- deMaynadier, P.G., Hunter, M.L., 1999. Forest canopy closure and juvenile emigration by pool-breeding amphibians in Maine. *Journal of Wildlife Management* 63, 441–450.
- Dodd, C.K., Cade, B.S., 1998. Movement patterns and the conservation of amphibians breeding in small, temporary wetlands. *Conservation Biology* 12, 331–339.
- Duellman, W.E., Trueb, L., 1994. *Biology of amphibians*. Johns Hopkins University Press.

- Faccio, S.D., 2003. Postbreeding emigration and habitat use by Jefferson and spotted salamanders in Vermont. *Journal of Herpetology* 37, 479–489.
- Ferraro, T.J., Burgin, S., 1993. Amphibian decline: A case study in western Sydney. In: Lunney D, Ayres D (eds) *Herpetology in Australia: A diverse discipline*, 197–204.
- Figiel, C.R., Semlitsch, R.D., 1995. Experimental determination of oviposition site selection in the marbled salamander, *Ambystoma opacum*. *Journal of Herpetology* 29, 452–454.
- Gamble, L.R., McGarigal, K., Compton, B.W., 2007. Fidelity and dispersal in the pond-breeding amphibian, *Ambystoma opacum*: Implications for spatio-temporal population dynamics and conservation. *Biological Conservation* 139, 247–257.
- Germano, J.M., Bishop, P.J., 2009. Suitability of amphibians and reptiles for translocation. *Conservation Biology* 23, 7-15.
- Goodwin, B.J., Fahrig, L., 2002. How does landscape structure influence landscape connectivity? *Oikos* 99, 552–570.
- Hadley, D., Sheridan, T.E., 1995. Land use history of the San Rafael Valley, Arizona (1540-1960). USDA Forest Service RM-GTR-269, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Hale, J.R., Mims, M.C., Bogan, M.T., Olden, J.D., 2015. Links between two interacting factors, novel habitats and non-native predators, and aquatic invertebrate communities in a dryland environment. *Hydrobiologia* 746, 313–326.
- Hanski, I., 1998. Metapopulation dynamics. *Nature* 396, 41–49.
- Harper, E.B., Rittenhouse, T.A., Semlitsch, R.D., 2008. Demographic consequences of terrestrial habitat loss for pool-breeding amphibians: Predicting extinction risks associated with inadequate size of buffer zones. *Conservation Biology* 22, 1205–1215.

- Hendrickson, D.A., Minckley, W.L., 1984. Ciénegas - Vanishing climax communities of the American Southwest. *Desert Plants* 6, 129–176.
- Holland, D.C., Hayes, M.P., McMillan, E., 1990. Late summer movement and mass mortality in the California tiger salamander (*Ambystoma californiense*). *The Southwestern Naturalist* 35, 217–220.
- Hossack, B.R., Honeycutt, R.K., Sigafus, B.H., Muths, E., Crawford, C.L., Jones, T.R., Sorensen, J.A., Rorabaugh, J.C., Chambert, T., 2017. Informing recovery in a human-transformed landscape: Drought-mediated coexistence alters population trends of an imperiled salamander and invasive predators. *Biological Conservation* 209, 377–394.
- Jakob, E.M., Marshall, S.D., Uetz, G.W., 1996. Estimating fitness: A comparison of body condition indices. *Oikos* 1996, 61–67.
- Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61, 65–71.
- Jones, T.R., Collins, J.P., Kocher, T.D., Mitton, J.B., 1988. Systematic status and distribution of *Ambystoma tigrinum stebbinsi* Lowe (Amphibia: Caudata). *Copeia* 1988, 621–635.
- Jones, T.R., Routman, E.J., Begun, D.J., Collins, J.P., 1995. Ancestry of an isolated subspecies of salamander, *Ambystoma tigrinum stebbinsi* Lowe: The evolutionary significance of hybridization. *Molecular Phylogenetics and Evolution* 4, 194–202.
- Kaplan, E.L., Meier, P., 1958. Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association* 53, 457–481.
- Keane, B., Bryant, L., Goyal, U., Williams, S., Kortering, S.L., Lucia, K.E., Richmond, A.R., Solomon, N.G., 2007. No effect of body condition at weaning on survival and reproduction in prairie voles. *Canadian Journal of Zoology* 85, 718–727.

- Kern, M.M., Nassar, A.A., Guzy, J.C., Dorcas, M.E., 2013. Oviposition site selection by spotted salamanders (*Ambystoma maculatum*) in an isolated wetland. *Journal of Herpetology* 47, 445–449.
- Kleeberger, S.R., Werner, J.K., 1983. Post-breeding migration and summer movement of *Ambystoma maculatum*. *Journal of Herpetology* 17, 176–177.
- Lowe, W.H., Likens, G.E., Cosentino, B.J., 2006. Self-organisation in streams: The relationship between movement behaviour and body condition in a headwater salamander. *Freshwater Biology* 51, 2052–2062.
- Madison, D.M., 1997. The emigration of radio-implanted spotted salamanders, *Ambystoma maculatum*. *Journal of Herpetology* 31, 542–551.
- Madison, D.M., Farrand III, L., 1998. Habitat use during breeding and emigration in radio-implanted tiger salamanders, *Ambystoma tigrinum*. *Copeia* 1998, 402–410.
- Marsh, D.M., Trenham, P.C., 2001. Metapopulation dynamics and amphibian conservation. *Conservation Biology* 15, 40–49.
- Marshall, R.M., Robles, M.D., Majka, D.R., Haney, J.A., 2010. Sustainable water management in the southwestern United States: Reality or rhetoric? *PLoS ONE* 5, e11687.
- McClaran, M.P., 2003. A century of vegetation change on the Santa Rita Experimental Range. 16-33. In M. P. McClaran, P.F. Ffolliott, and C. B. Edminster, (eds) *Santa Rita Experimental Range: 100 years (1903 to 2003) of accomplishments and contributions. Conference Proceedings. November, 2003. Tucson, Arizona. USDA, Forest Service. Rocky Mountain Research Station, Ogden, Utah, USA.*
- McIntyre, N.E., Drake, J.C., Griffis-Kyle, K.L., 2016. A connectivity and wildlife management conflict in isolated desert waters. *Journal of Wildlife Management* 80, 655–666.

- Meffe, G.K., D.A. Hendrickson, and J.N. Rinne. 1982. Description of a new topminnow population in Arizona, with observations on topminnow/mosquitofish co-occurrence. *The Southwestern Naturalist* 27, 226–228.
- Mills, L.S., Allendorf, F.W., 1996. The one-migrant-per-generation rule in conservation and management. *Conservation Biology* 10, 1509-1518.
- Mims, M.C., Phillipsen, I.C., Lytle, D.A., Kirk, E.E.H., Olden, J.D., 2015. Ecological strategies predict associations between aquatic and genetic connectivity for dryland amphibians. *Ecology* 96, 1371–1382.
- Neu, C.W., Byers, C.R., Peek, J.M., 1974. A technique for analysis of utilization-availability data. *The Journal of Wildlife Management* 38, 541-545.
- O’Grady, J.J., Brook, B.W., Reed, D.H., Ballou, J.D., Tonkyn, D.W., Frankham, R., 2006. Realistic levels of inbreeding depression strongly affect extinction risk in wild populations. *Biological Conservation* 133, 42–51.
- Orloff, S.G., 2011. Movement patterns and migration distances in an upland population of California tiger salamander (*Ambystoma californiense*). *Herpetological Conservation and Biology* 6, 266–276.
- Phillott, A.D., Speare, R., Hines, H.B., Skerratt, L.F., Meyer, E., McDonald, K.R., Cashins, S.D., Mendez, D., Berger, L., 2010. Minimising exposure of amphibians to pathogens during field studies. *Diseases of Aquatic Organisms* 92, 175–185.
- Pollock, K.H., Winterstein, S.R., Bunck, C.M., Curtis, P.D., 1989. Survival analysis in telemetry studies: The staggered entry design. *Journal of Wildlife Management* 1989, 7–15.
- R Core Team, 2013. R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria.

- Raymond, L.R., Hardy, L.M., 1990. Demography of a population of *Ambystoma talpoideum* (Caudata: Ambystomatidae) in northwestern Louisiana. *Herpetologica* 1990, 371–382.
- Regosin, J.V., Windmiller, B.S., Homan, R.N., Reed, J.M., 2005. Variation in terrestrial habitat use by four pool-breeding amphibian species. *Journal of Wildlife Management* 69, 1481–1493.
- Reh, W., Seitz, A., 1990. The influence of land use on the genetic structure of populations of the common frog *Rana temporaria*. *Biological Conservation* 54, 239–249.
- Rittenhouse, T.A., Semlitsch, R.D., 2006. Grasslands as movement barriers for a forest-associated salamander: Migration behavior of adult and juvenile salamanders at a distinct habitat edge. *Biological Conservation* 131, 14–22.
- Roe, J.H., Georges, A., 2007. Heterogeneous wetland complexes, buffer zones, and travel corridors: Landscape management for freshwater reptiles. *Biological Conservation* 135, 67–76.
- Rohr, J.R., Madison, D.M., 2003. Dryness increases predation risk in efts: Support for an amphibian decline hypothesis. *Oecologia* 135, 657–664.
- Rosen, P.C., Schwalbe, C.R., 1997. Using managed waters for conservation of threatened frogs, in: *Proceedings of Symposium on Environmental, Economic, and Legal Issues Related to Rangeland Water Developments*. pp. 180–202.
- Rothermel, B.B., Luhring, T.M., 2005. Burrow availability and desiccation risk of mole salamanders (*Ambystoma talpoideum*) in harvested versus unharvested forest stands. *Journal of Herpetology* 39, 619–626.
- Routman, E.J. 1984. A modified seining technique for single person sampling of deep or cold water. *Herpetological Review* 15, 72-73.

- Routman, E.J., 1993. Population structure and genetic diversity of metamorphic and paedomorphic populations of the tiger salamander, *Ambystoma tigrinum*. *Journal of Evolutionary Biology* 3, 329–357.
- Schmutzer, A.C., Gray, M.J., Burton, E.C., Miller, D.L., 2008. Impacts of cattle on amphibian larvae and the aquatic environment. *Freshwater Biology* 53, 2613–2625.
- Schonewald-Cox, C.M., 1988. Boundaries in the protection of nature reserves. *Bioscience* 38, 480–486.
- Schulte-Hostedde, A.I., Zinner, B., Millar, J.S., Hickling, G.J., 2005. Restitution of mass–size residuals: Validating body condition indices. *Ecology* 86, 155–163.
- Searcy, C.A., Gabbai-Saldate, E., Shaffer, H.B., 2013. Microhabitat use and migration distance of an endangered grassland amphibian. *Biological Conservation* 158, 80–87.
- Semlitsch, R.D., 1981. Terrestrial activity and summer home range of the mole salamander (*Ambystoma talpoideum*). *Canadian Journal of Zoology* 59, 315–322.
- Semlitsch, R.D., 1983. Burrowing ability and behavior of salamanders of the genus *Ambystoma*. *Canadian Journal of Zoology* 61, 616–620.
- Semlitsch, R.D., 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. *Conservation Biology* 12, 1113–1119.
- Semlitsch, R.D., 2000. Principles for management of aquatic-breeding amphibians. *Journal of Wildlife Management* 64, 615–631.
- Semlitsch, R.D., 2002. Critical elements for biologically based recovery plans of aquatic-breeding amphibians. *Conservation Biology* 16, 619–629.
- Semlitsch, R.D., Bodie, J.R., 1998. Are small, isolated wetlands expendable? *Conservation Biology* 12, 1129–1133.

- Semlitsch, R.D., Bodie, J.R., 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conservation Biology* 17, 1219–1228.
- Semlitsch, R.D., Gibbons, J.W., 1985. Phenotypic variation in metamorphosis and pedomorphosis in the salamander *Ambystoma talpoideum*. *Ecology* 66, 1123–1130.
- Semlitsch, R.D., O'Donnell, K.M., Thompson III, F.R., 2014. Abundance, biomass production, nutrient content, and the possible role of terrestrial salamanders in Missouri Ozark forest ecosystems. *Canadian Journal of Zoology* 92, 997–1004.
- Shoop, C.R., 1965. Orientation of *Ambystoma maculatum*: Movements to and from breeding ponds. *Science* 149, 558–559.
- Sinsch, U., 1990. Migration and orientation in anuran amphibians. *Ethology Ecology & Evolution* 2, 65–79.
- Smith, H.V., 1956. The climate of Arizona. University of Arizona, Tucson, AZ. Agricultural Experiment Station Bulletin 279.
- Snow, N. P., Witmer, G., 2010. American bullfrogs as invasive species: A review of the introduction, subsequent problems, management options, and future directions. In R. M. Timm & K. A. Fagerstone (eds), *Proceedings of the 24th Vertebrate Pest Conference*: 86–89.
- Sodhi, N.S., Bickford, D., Diesmos, A.C., Lee, T.M., Koh, L.P., Brook, B.W., Sekercioglu, C.H., Bradshaw, C.J.A., 2008. Measuring the meltdown: Drivers of global amphibian extinction and decline. *PLoS ONE* 3, e1636.
- Steen, D.A., Smith, L.L., Miller, G.J., Sterrett, S.C., 2006. Post-breeding terrestrial movements of *Ambystoma tigrinum* (eastern tiger salamanders). *Southeastern Naturalist* 5, 285–288.

- Storfer, A., Mech, S.G., Reudink, M.W., Lew, K., 2014. Inbreeding and strong population subdivision in an endangered salamander. *Conservation Genetics* 15, 137–151.
- Taylor, B.E., Scott, D.E., Gibbons, J.W., 2006. Catastrophic reproductive failure, terrestrial survival, and persistence of the marbled salamander. *Conservation Biology* 20, 792–801.
- Therneau, T., 2015. A package for survival analysis in s. version 2.38. URL: <https://CRAN.R-project.org/package=survival>.
- Therneau, T.M., Grambsch, P.M., 2000. Modeling survival data: Extending the Cox model. Springer, New York.
- Titus, V., Madison, D., Green, T., 2014. The importance of maintaining upland forest habitat surrounding salamander breeding ponds: Case study of the eastern tiger salamander in New York, USA. *Forests* 5, 3070–3086.
- Trenham, P.C., 2001. Terrestrial habitat use by adult California tiger salamanders. *Journal of Herpetology* 35, 343–346.
- Trenham, P.C., Shaffer, H.B., Koenig, W.D., Stromberg, M.R., Ross, S.T., 2000. Life history and demographic variation in the California tiger salamander (*Ambystoma californiense*). *Copeia* 2000, 365–377.
- Trenham, P.C., Shaffer, H.B., 2005. Amphibian upland habitat use and its consequences for population viability. *Ecological Applications* 15, 1158–1168.
- U.S. Fish and Wildlife Service, 2002. Sonora tiger salamander recovery plan (*Ambystoma tigrinum stebbinsi*). U.S. Fish and Wildlife Service, Phoenix, AZ.
- U.S. Fish and Wildlife Service, 1997. Endangered and threatened wildlife and plants; Determination of endangered status for three wetland species found in southern Arizona and northern Sonora, Mexico. *Federal Register* 62, 669–688.

- USDA Forest Service, 2009. Mid-scale existing vegetation dominance type map units of the Coronado National Forest. USDA Forest Service, R3, Albuquerque, NM.
- Weeks, A.R., Sgro, C.M., Young, A.G., Frankham, R., Mitchell, N.J., Miller, K.A., Byrne, M., Coates, D.J., Eldridge, M.D.B., Sunnucks, P., Breed, M.F., James, E.A., Hoffmann, A.A., 2011. Assessing the benefits and risks of translocations in changing environments: A genetic perspective. *Evolutionary Applications* 4, 709-725.
- Whiteman, H.H., 1994. Evolution of facultative paedomorphosis in salamanders. *The Quarterly Review of Biology* 69, 205–221.
- Whiteman, H.H., Wissinger, S.A., Bohonak, A.J., 1994. Seasonal movement patterns in a subalpine population of the tiger salamander, *Ambystoma tigrinum nebulosum*. *Canadian Journal of Zoology* 72, 1780–1787.
- Whiteman, H.H., Wissinger, S.A., Brown, W.S., 1996. Growth and foraging consequences of facultative paedomorphosis in the tiger salamander, *Ambystoma tigrinum nebulosum*. *Evolutionary Ecology* 10, 433–446.
- Whitford, W.G., Vinegar, A., 1966. Homing, survivorship, and overwintering of larvae in spotted salamanders, *Ambystoma maculatum*. *Copeia* 1966, 515–519.
- Wilbur, H.M., Collins, J.P., 1973. Ecological aspects of amphibian metamorphosis: Nonnormal distributions of competitive ability reflect selection for facultative metamorphosis. *Science* 182, 1305–1314.
- Williams, P.K., 1973. Seasonal movements and population dynamics of four sympatric mole salamanders, genus *Ambystoma* (PhD Thesis). Indiana University.

TABLES AND FIGURES

Table 1. Sonoran tiger salamanders (*Ambystoma mavortium stebbinsi*) captured in 2018 and 2019 in the San Rafael Valley, Arizona. “Meta” column = Metamorphosed adults captured and implanted; “Branch” column = mature branchiate morphs captured; “Juv” column = juvenile and larval individuals captured.

Site	Year						Total		
	2017			2018			Meta	Branch	Juv
	Meta	Branch	Juv	Meta	Branch	Juv	Meta	Branch	Juv
Dan Tank	9	1044	708	14	752	890	23	1796	1598
Huachaca Tank	11	83	1324	2	168	314	13	251	1638
Upper 13 Reservoir	18	165	2630	24	737	1365	42	902	3995
Total	38	1292	4662	40	1657	2569	78	2949	7231

Table 2. Sonoran tiger salamander (*Ambystoma mavortium stebbinsi*) used habitat type compared to expected based on availability within an MCP home range including all STS locations found in 2017 and 2018 in the San Rafael Valley, Arizona. Bonferroni confidence interval lower and upper bounds show that none of the three habitat types were occupied more or less than would be expected by chance.

Habitat Type	Used Proportion	Expected Proportion	Bonferroni Confidence Interval	
			Lower	Upper
Semi-desert Shrubland	0.023	0.056	0.006	0.082
Plains Grassland	0.645	0.621	0.590	0.677
Oak-Juniper Woodland	0.332	0.323	0.277	0.377

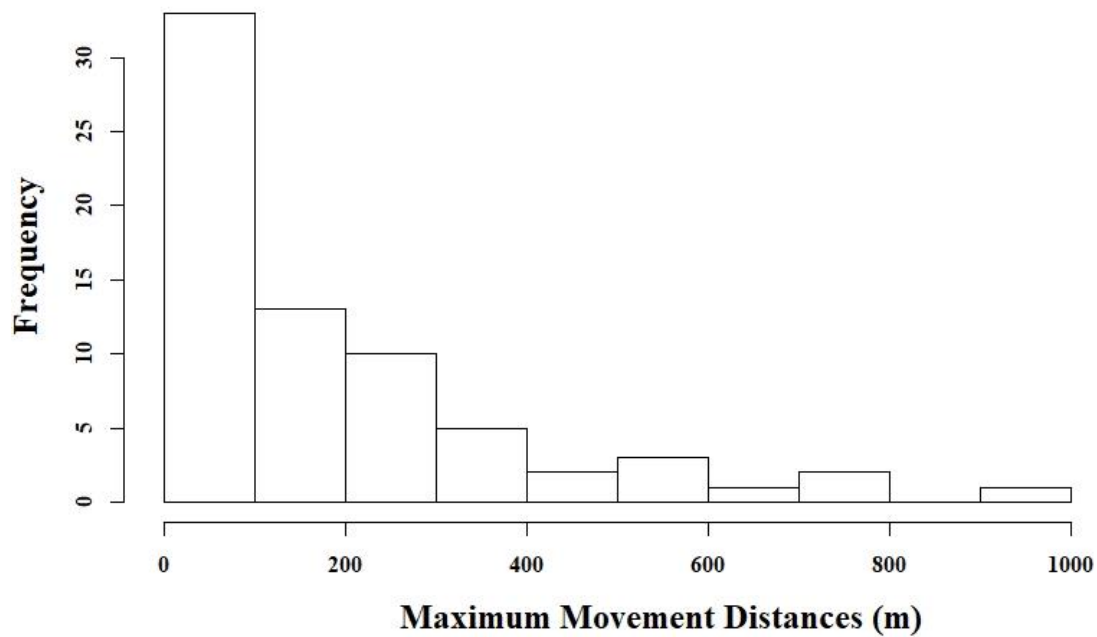


Fig. 1. Maximum movement distance from stock tank for radio-transmitter implanted Sonoran tiger salamanders (*Ambystoma mavortium stebbinsi*) in the San Rafael Valley, Arizona (n = 77). One depredated individual outlier had a maximum movement distance of 1,334 m but was removed from the analysis due to possible transport by a predator. The maximum movement distance recorded for a living salamander was 974 m from tank edge.

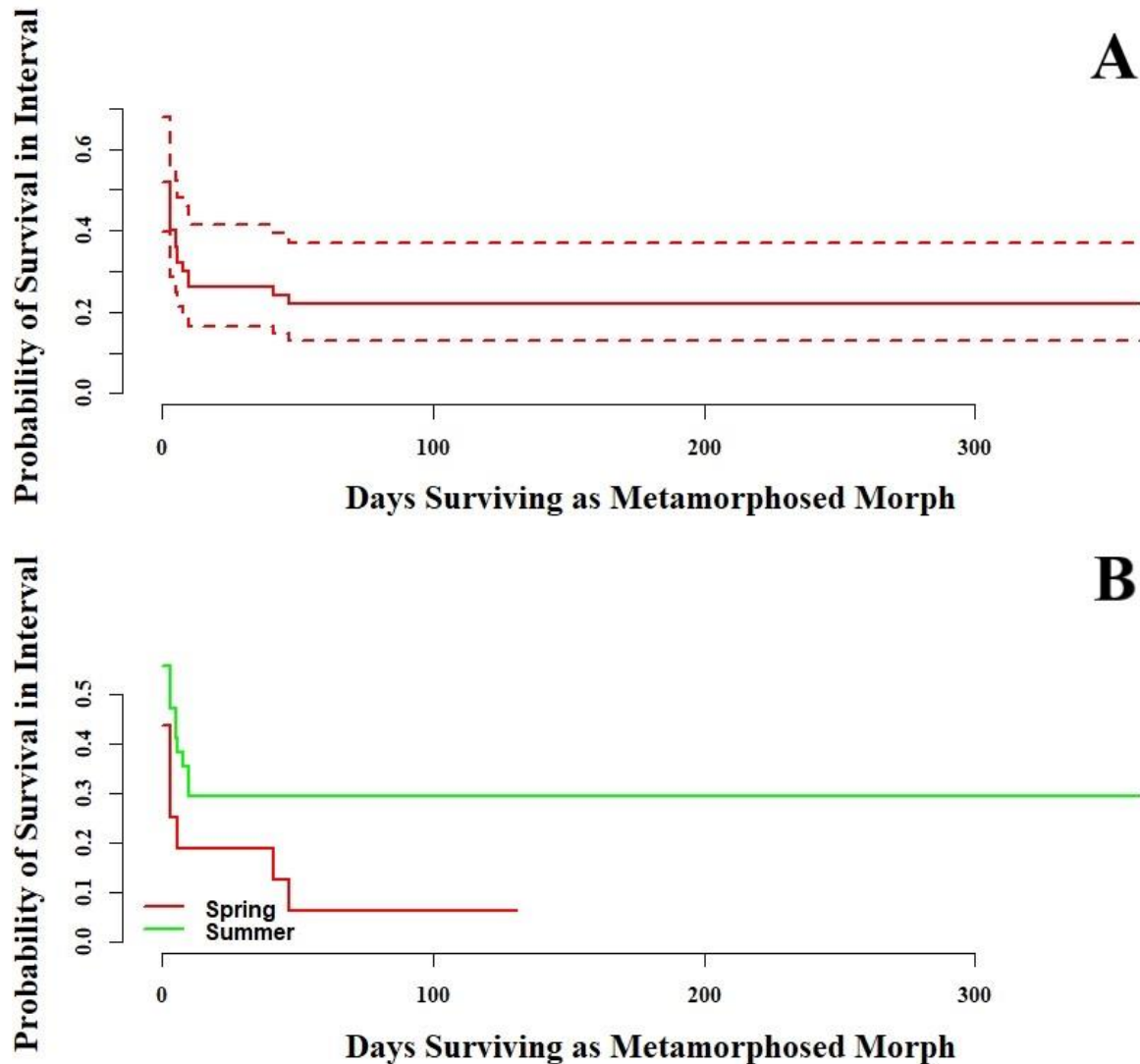


Fig. 2. Survival curves for radio-transmitter implanted Sonoran tiger salamanders (*Ambystoma mavortium stebbinsi*) in the San Rafael Valley, Arizona after leaving stock tank. Survival curve A includes all individuals that moved into terrestrial habitat excluding subterranean mortalities (n=50). Survival curve B shows survival by season of dispersal. Median survival (where survival probability = 0.5) was 3 days. Spring dispersers left the stock tank in April or May (n=16). Summer dispersers left the stock tank in June or July (n=34).

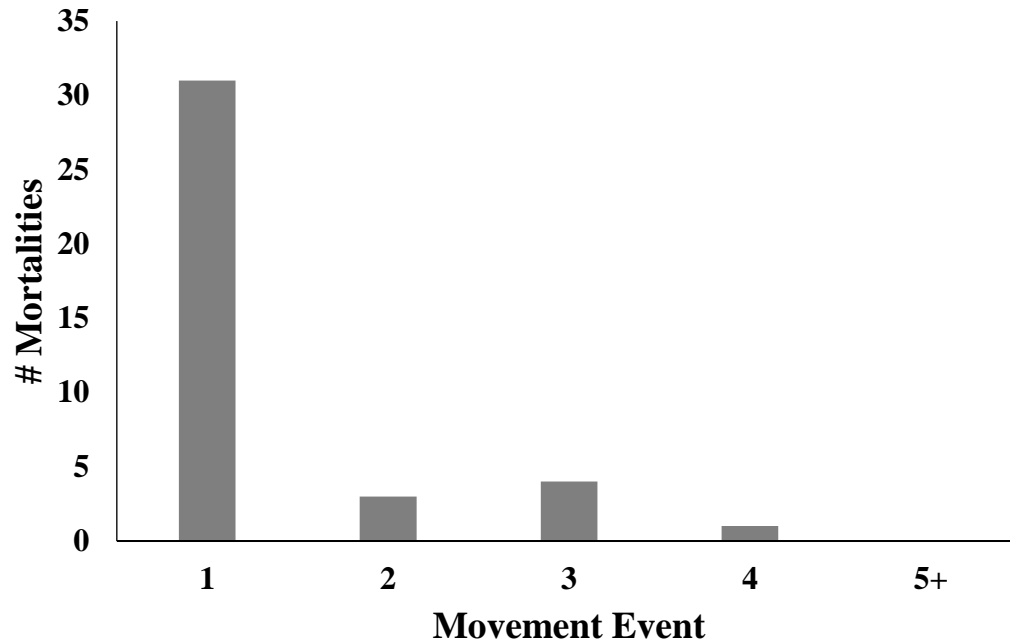


Fig. 3. Number of mortalities for radio-transmitter implanted Sonoran tiger salamanders (*Ambystoma mavortium stebbinsi*) in the San Rafael Valley, Arizona according to the documented movement number when they occurred. Movement 1 is initial movement out of tank, movement 2 is second movement event, and so forth. All individuals that survived past their fourth movement event, survived until the end the tracking period. The average time between movement events was 7.6 days (± 6.6), and the longest time between movement events recorded was 39 days.

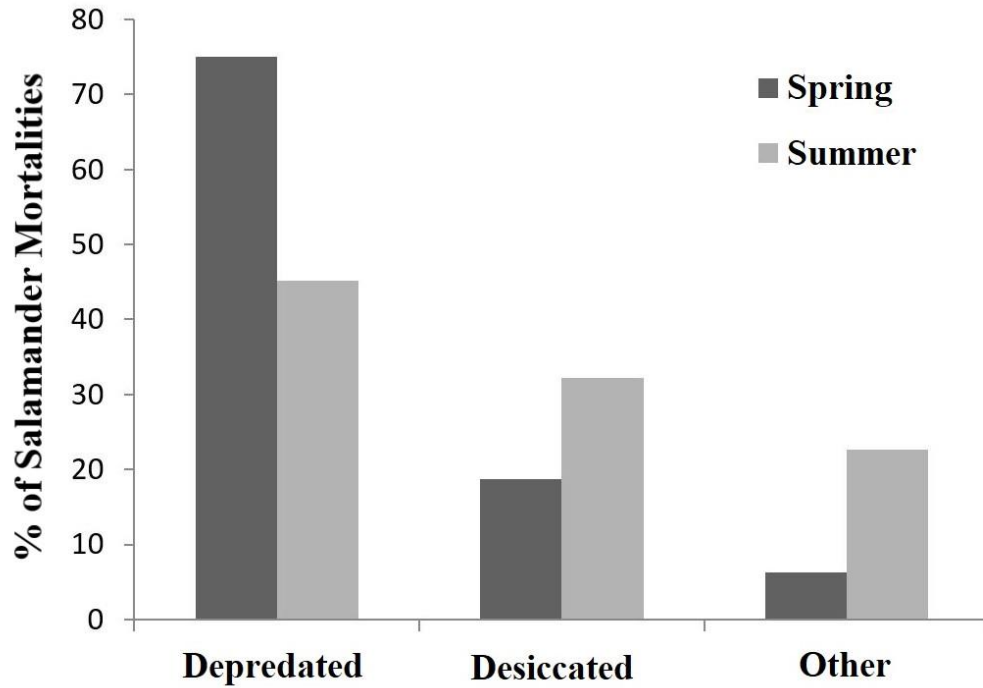


Fig. 4. Causes of mortality following dispersal for radio-transmitter implanted Sonoran tiger salamanders (*Ambystoma mavortium stebbinsi*) in the San Rafael Valley, Arizona (n = 58).

Spring season (April + May) dispersers are shown in dark gray and summer dispersers (June + July) are depicted in light gray.

APPENDIX B. SUPPORTING TABLES AND FIGURES

Appendix BI. Sonoran tiger salamanders (*Ambystoma mavortium stebbinsi*) in the San Rafael Valley, Arizona with greater than 19 locality points included in KDE analysis (n=11). Interval days (ID): Days between radio-transmitter implant and egress (emigration) from stock tank. Radio Locs: Total number of radio locations. KDE 95/50: Terrestrial home range size in square meters.

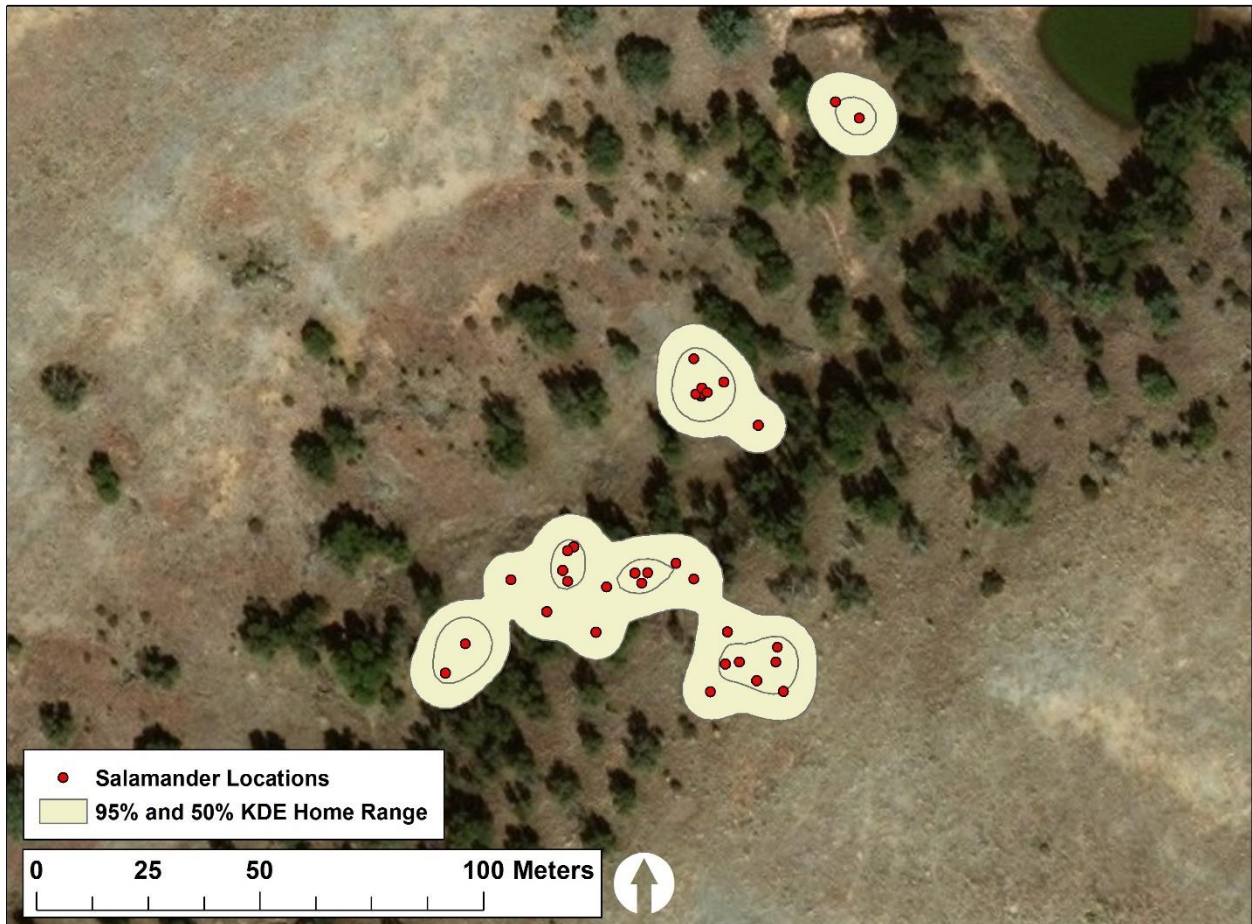
ID	Tank	Sex	Mass (g)	Capture Date	Egress Date	Interval (days)	Radio Locs	KDE 95	KDE 50
D5	Dan	F	59	4/9/2017	5/13/2017	34	37	15086.47	2102.81
D6	Dan	M	46	5/15/2017	6/22/2017	38	46	3007.25	690.74
D27	Dan	M	59.6	6/14/2018	6/19/2018	5	25	222.27	35.03
H3	Huachuca	F	63	5/17/2017	7/3/2017	47	65	716.23	90.80
H6	Huachuca	F	79.1	5/31/2017	7/3/2017	33	51	861.70	158.81
H9	Huachuca	F	64.6	6/13/2017	6/23/2017	10	36	7392.76	1129.33
U5	Upper 13	M	41	5/12/2017	6/23/2017	42	23	46.90	0.26
U8	Upper 13	M	42	5/13/2017	6/8/2017	26	47	955.11	129.45
U12	Upper 13	M	60.5	6/1/2017	6/23/2017	22	49	2678.15	648.04
U18	Upper 13	M	59.6	6/15/2017	7/3/2017	18	32	327.06	70.32
U35	Upper 13	F	42.8	6/7/2018	7/9/2018	32	20	2296.73	498.99

Appendix BII. Average body measurements for radio-transmitter implanted Sonoran tiger salamanders (*Ambystoma mavortium stebbinsi*) in the San Rafael Valley, Arizona (n=78). Mass: Salamander mass before radio-transmitter implant. SVL: Length from snout to posterior of vent.

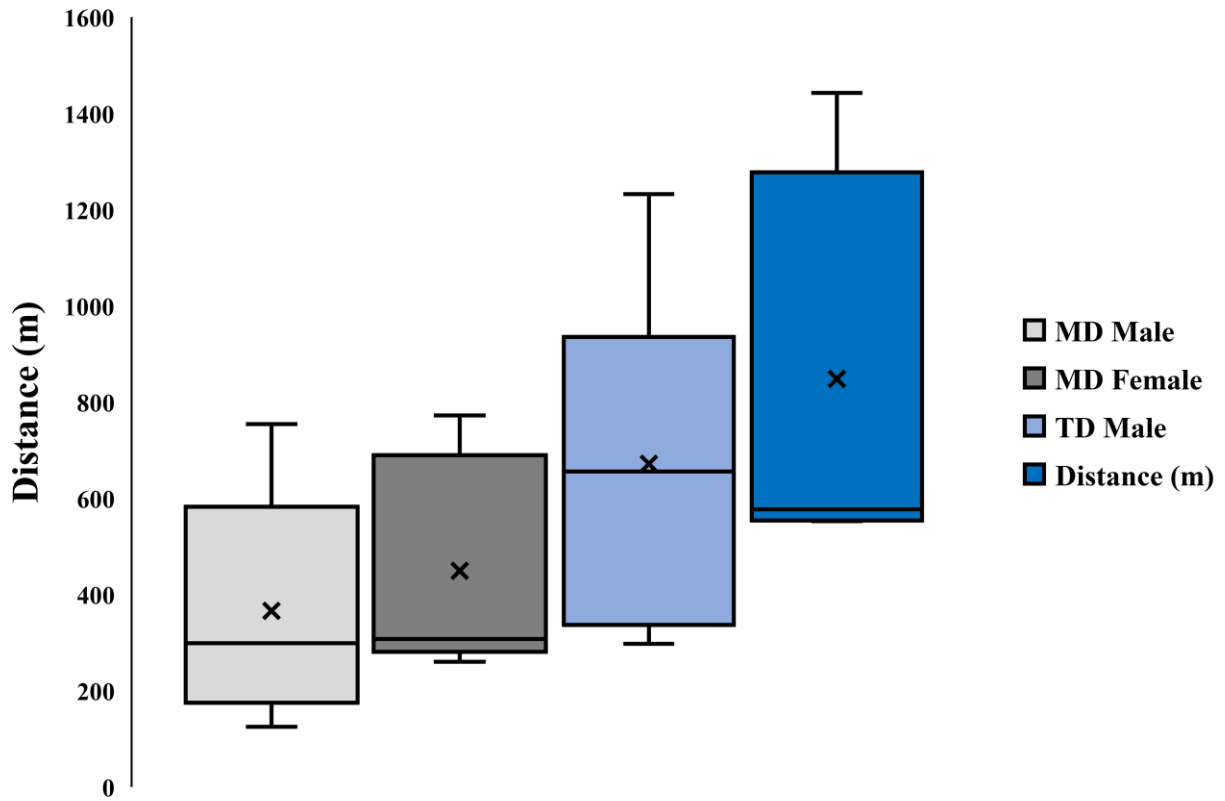
	Male				Female				Total			
	Mean	St. Dev.	Max	Min	Mean	St. Dev.	Max	Min	Mean	St. Dev.	Max	Min
Mass (g)	52.06	10.15	76.6	38.0	63.63	14.21	96.8	39.7	57.70	13.45	96.8	38
SVL (mm)	122.1	5.4	133	106	121.9	6.9	136	107	122	6.1	136	106
Total Length (mm)	228.7	21	265	126	226.1	15.7	251	181	227.4	18.4	265	136



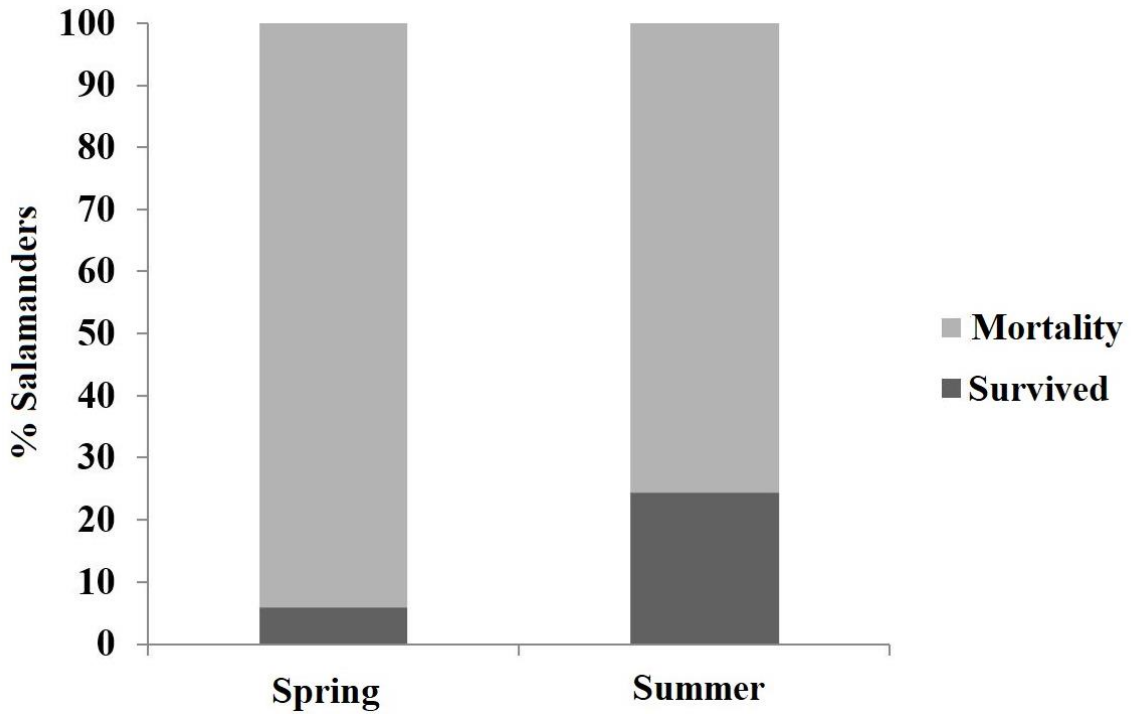
Appendix BIII. Sonoran tiger salamander (*Ambystoma mavortium stebbinsi*) swimming into a stock tank in the San Rafael Valley, Arizona immediately after radio-transmitter implantation and release.



Appendix BIV. Home range map showing total (95%; outer polygon) and core (50%; inner dark circles) home range for a single Sonoran tiger salamander (*Ambystoma mavortium stebbinsi*) (ID# D6) in the San Rafael Valley, Arizona using the fixed kernel density estimator (KDE). Individual localities shown as red dots. 22 June 2017 – 7 Feb 2018.



Appendix BV. Movement differences by sex for radio-transmitter implanted Sonoran tiger salamanders (*Ambystoma mavortium stebbinsi*) in the San Rafael Valley, Arizona. Total terrestrial movement distance (TD) for males (n = 6; light gray) and females (n = 5; dark gray). Maximum linear distance from tank edge (MD) for males (n=6; light blue) and females (n=5; dark blue).



Appendix BVI. Effects of dispersal season (Spring = April + May, Summer = June + July) on radio-transmitter implanted Sonoran tiger salamanders (*Ambystoma mavortium stebbinsi*) in the San Rafael Valley, Arizona that survived (n = 11) or died (n = 47) during 2017 and 2018.