MULTI-YEAR SPACE USE AND SURVIVAL OF HEAD-STARTED MOJAVE DESERT TORTOISES (*GOPHERUS AGASSIZII*) AND FACTORS INFLUENCING RISK OF PREDATION BY SUBSIDIZED PREDATORS

by

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(Under the Direction of Tracey D. Tuberville and Michel T. Kohl)

ABSTRACT

The Mojave desert tortoise (*Gopherus agassizii)* has been the focus of recovery efforts for over 50 years. A major threat to tortoise recovery is reduced juvenile recruitment. Head-starting, the raising of juvenile tortoises to larger sizes to improve survival, is used in areas with limited juvenile recruitment. We quantified multi-year space-use and survival of head-started Mojave desert tortoises following release by radio-tracking tortoises reared with and without an indoor-rearing component. We found that space-use varied by husbandry treatment, but survival did not. Additionally, we used trail cameras to capture predation attempts on 3D-printed tortoise models to evaluate how tortoise size and human infrastructure affect a tortoise's risk of predation in the Eastern Mojave Desert and how risk changes between seasons. By implementing extended monitoring for head-started tortoises and examining the effects of predation on tortoises, we seek to inform recovery efforts for Mojave desert tortoises.

INDEX WORDS: desert, tortoise, *Gopherus agassizii*, head-starting, subsidized predator, space-use, population recovery, conservation

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B.S., Northern Michigan University, 2017

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2022

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The University of Georgia
December 2022

ACKNOWLEDGEMENTS

Funding for this research was provided by the National Park Service (PSAC – CESU Cooperative Agreement number P17AC01606), California Energy Commission (Agreement number EPC-16-038), U.S. Department of Energy under award DE-EM0005228 to the University of Georgia Research Foundation, Bureau of Land Management, the National Fish and Wildlife Foundation, the Warnell School of Forestry and Natural Resources, and the Savannah River Ecology Laboratory. All work was conducted in accordance with permits issued by the U.S. Fish and Wildlife Service (TE-17838A-3), U.S. National Park Service (MOJA- 2018-SCI-0016 [under study MOJA-00258]), and California Department of Fish and Wildlife (SC-0011221). Animal protocols were approved by the University of Georgia under Animal Use Permits A2017 01-021-Y3-A3 and A2020 01-025-Y2-A2.

I thank Dr. Brian Todd for his expertise and for his contribution as a great collaborator and supervisor. For all of their assistance, consultation, and support, I thank Debra Hughson and Neil Darby (National Park Service), Kerry Holcomb and Roy Averill-Murray (USFWS), and Bill Boarman and Tim Shields (Hardshell Labs, Inc.). To those who served on this project before me, Mark Peaden, Melia Nafus, Max Steele, Jacob Daly, Pearson McGovern, and Carmen Candal, thank you all so much for all of the work that has gone into these tortoises. It is an honor to be a part of such an influential crew in tortoise conservation. To Pearson, Carmen, Susanna Mann, and Gabby Barnas, thank you all for being such incredible help, fun in the field, and great people to live with during our times in the desert. To Gabby Barnas especially, your contributions and assistance during my time away from the desert have been invaluable.

I thank my whole committee for their dedication to making me a better scientist. To Jeff Hepinstall-Cymerman, thank you for teaching me to think more broadly and giving me new perspective on my research. To James Martin, thank you for your continued encouragement that began when I was fresh out of my undergraduate degree. I would not be in this position today without the opportunities you gave me. To Kurt Buhlmann, thank you for all your enthusiasm and for ensuring that as ecologists, we remind ourselves why we enter this field and that we maintain an excitement for natural history. To Michel Kohl, thank you for all of the time and commitment you have given to this project. I appreciate you taking me on as a student. I hope to one day make my future lab and research run as smoothly and efficiently as you make yours look! And especially to Tracey Tuberville, thank you for taking a chance on me and allowing me to be a part of this incredible project. I have appreciated your patience and support through this whole process. Thank you for helping me work through ideas and for being such an accessible supervisor. I cannot thank you and my whole committee enough. Beyond my committee, I'd also like to thank Richard Chandler for all of his additional assistance with my analysis.

I also thank Craig Marshall and Joseph Colbert. The two of you have offered so much guidance over the years, both before and during my graduate career. I will always appreciate our conversations and the knowledge that I have not only great scientists, but great people in my corner. Finally, I could not have completed this degree and research without the support of my family and loved ones. To my parents and my sisters, thank you all for your support and encouragement, even when this early career path has seemed winding. Thank you for coming to visit me in all of my interesting field houses and sites. I've always loved showing you all what is going on! And to Emily, thank you for always being there when I needed support or to vent, and for encouraging me to take chances, and for sticking with me during the times that I was far away. Thank you for being a true partner through all of this.

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INTRODUCTION AND LITERATURE REVIEW

Global biodiversity is rapidly declining due to anthropogenic activities (Baillie et al. 2004), with reptiles, specifically turtles, being especially affected (Gibbons et al. 2000, Buhlmann et al. 2009, Stanford et al. 2020). Threats that turtles face include habitat loss and land conversion, poaching and over exploitation, and competition from invasive species (Gibbons et al. 2000). This has led to a number of recovery efforts implemented to slow or reverse population declines. Efforts to combat these losses have included land protection, population augmentation, and legal protections from harvest. However, turtles often show a delayed response to recovery actions due to their long-life histories. Population growth is often driven by adult turtles with high survival, that produce many offspring over their lifetime (Doak et al. 1994, Heppell 1998). However, naturally high juvenile mortality makes replacement of those breeding adults a drawn-out process, as it can take decades for turtles to reach breeding age (Congdon et al. 1993). When those breeding adults are lost, the remaining adults may not produce enough offspring that survive to adulthood, ceasing population growth (Congdon et al. 1993). Pairing mitigation of adult mortality with manipulation of juvenile stages to increase naturally low survival can promote accelerated population recovery (Crawford et al. 2014, Spencer et al. 2017). However, extended monitoring is often necessary to evaluate effort success, as juvenile turtles must be assimilated into breeding populations, which can take decades due to delayed maturity (Griffith et al. 1989, Ashton and Burke 2007, Tuberville et al.

2008). Therefore, studies are needed to examine the long-term success of these conservation efforts in terms of project efficiency and how populations respond to variable recovery actions.

Head-starting is a method of population augmentation that manipulates the juvenile stage of turtles and tortoises to increase juvenile survival (Burke 2015). Head-starting is the process of raising turtles to a size or life stage that is less vulnerable to predation or harsh environmental conditions (Burke 2015), with the goals of creating a self-sustaining population by introducing head-started juveniles to a depleted population (Dodd and Seigel 1991, Seddon 1999). Early head-starting efforts were viewed with controversy, as recovery efforts focused solely on the juvenile stage, and did not address mortality of subadult turtles (Dodd and Seigel 1991, Frazer 1992). However, current recovery efforts now use head-starting with other species conservation actions, addressing causes of decline across the life cycle of the focal species, leading to greater conservation success (Crawford et al. 2014, Spencer et al. 2017). Even with greater head-starting success, head-starting projects can be expensive and labor intensive (Cohn 1999), and identifying the most efficient approaches to meet conservation goals is necessary for head-starting to be a useful tool for turtle recovery.

The Mojave desert tortoise (*Gopherus agassizii*), hereafter “desert tortoise,” is a species native to the desert southwest of North America. Desert tortoise populations have been declining at yearly rates of 3-59% despite four decades of recovery efforts, leading to the species being listed as “Threatened” under the Endangered Species Act in 1990 (USFWS 1990). However, many threats to population viability and recovery remain (USFWS 2011). Efforts to mitigate population declines have included relocation of displaced wild tortoises, installation of fencing and underpasses to mitigate road mortality, predator management, and population augmentation through translocation and head-starting (USFWS 1994, Boarman et al. 1997, USFWS 2011, Shields et al. 2019). Head-starting has only recently been explored as a potential recovery tool for desert tortoises. Head-starting has been used as a successful tool for many turtle species (Gibbs et al. 2014, Buhlmann et al. 2015, Burke 2015), however, it is labor intensive and expensive. Moreover, evaluating the success of head-starting projects has been challenging due to the extended juvenile period and delayed population responses of tortoises (Congdon et al. 1993), and logistical challenges such as naturally low juvenile survival and sample size limitations (Nagy et al. 2015a, Daly et al. 2019). To increase the potential for head-starting to contribute to recovery efforts, it is imperative that head-starting programs be driven by practices that maximize efficiency and directly contribute to conservation success (McGovern et al. 2020a, b). Different head-starting approaches may lead to differences in individual behavior that in turn influence survival, though little information exists regarding how behavior, and subsequent survival, vary past one-year post release.

Head-starting methods for desert tortoises began by raising tortoises in outdoor, predator-proof enclosures (Hazard and Morafka 2002, Nagy et al 2015a). Though these enclosures enhance hatchling and juvenile survival, it can take several years of captive care to produce animals of sufficient size that are likely to survive post-release (Nagy et al. 2015a, Daly et al. 2019, McGovern et al. 2020b). Because tortoises must undergo winter dormancy as they would in the wild, growth rates of tortoises raised in outdoor pens are slow (Daly et al. 2018, Tuberville et al. 2019, McGovern et al. 2020b). The current recommended release size for head-started desert tortoises is 100 mm in midline carapace length (MCL; Nagy et al. 2015a), which can take 5-7 years to reach even with supplemental watering and feeding (Nagy et al. 2015a, Tuberville et al. 2019). However, indoor rearing provides the opportunity for tortoises to skip winter dormancy, thereby allowing year-round growth and reducing time to reach releasable size, which is critical, as tortoise size influences survival (Nagy et al. 2015a, Daly et al. 2019, McGovern et al. 2020b). Recent efforts have explored combination head-starting ("Combo-reared"), in which tortoises are raised indoors their first year to maximize growth, followed by one year of outdoor rearing to promote natural behaviors and learn environmental cues before release (McGovern et al. 2020b). Under combo rearing, tortoises attain the recommended release size of 100 mm MCL within two years, with survival rates as high as 88% in their first-year post-release (McGovern et al. 2020a, Candal 2021). These combo-reared tortoises behave and survive similar to tortoises grown at natural, slow growth rates in their first-year post-release (McGovern et al. 2020a, Candal 2021), but information is lacking in how different pre-release husbandry affects behavior and survival past one-year post-release.

Many head-starting studies only follow released tortoises for the first year following release. However, released animals often exhibit greater movement and surface activity during the first weeks or months following release, which is often referred to as a "settling phase" (Field et al. 2007, Quinn et al. 2018, Daly et al. 2019, McGovern et al. 2020a). The settling phase is also often associated with the greatest mortality risk for several turtle and tortoise species (Epperson and Heise 2003, Pike and Seigel 2006, Quinn et al. 2018). Lack of multi-year monitoring of released tortoises limits the ability to make long-term conclusions on head-started tortoise movement and survival (McGovern et al. 2020a). Further complicating efforts to evaluate the success of head-starting projects are the spatial and temporal variability in post-release survival (Quinn et al. 2018, Daly et l. 2019). Additionally, little information exists on how head-starting methodologies may contribute to differences in movement patterns between the first-year "settling phase" and subsequent years post-release (McGovern et al. 2020a). Without a thorough understanding of the factors that impact post-release survival and movement, we cannot assess the success of head-starting efforts in terms of ensuring long-term juvenile tortoise survival and fidelity to the release site. Head-starting is an iterative process requiring thorough evaluation and refinement of protocols, and extended monitoring gives us the knowledge to continue to improve head-starting and releasing methods as a tool for desert tortoise recovery.

While head-starting of juvenile turtles and tortoises may be becoming an effective management tool, subsidized predators may neutralize these species recovery efforts. Subsidized predators are generalist predator species that adapt to human-made changes on the landscape, taking advantage of human-made subsidies for food, water, and shelter (Goodrich and Buskirk 1995). These predator populations then undergo rapid growth that then spill out from human-dominated areas to natural areas, where they exert increased predation pressure on prey species, termed "spillover predation" (Schneider 2001, Kristan and Boarman 2003). Subsidized predators pose a threat to many imperiled species that may not have serves as a primary prey item (Smith and Quin 1996, O'Neil et al. 2018, Loehr and Keswick 2021), and the temporal and spatial variation in the effects of spillover predation must be understood to properly mitigate losses of threatened species and manage increased predator densities (Goodrich and Buskirk 1995).

A significant hurdle in desert tortoise recovery is increased predation by subsidized predators (Boarman 2002, USFWS 2011, Berry et al. 2020). Both natural juvenile recruitment and head-starting efforts can also be plagued by high mortality rates from common ravens (*Corvus corax,* hereafter "raven") and coyotes (*Canis latrans*; Morafka et al. 1997, Kristan and Boarman 2003, Esque et al. 2010, Daly et al. 2019). There is preliminary research examining how tortoise release size, release location, and timing of releases may contribute to risk of predation (Daly et al. 2019, McGovern et al. 2020a); however, little is known regarding how that risk changes over time since release and changes with distance from human subsidies. Understanding how these factors influence post-release survival of head-started desert tortoises will inform how to modify future releases to increase survival of head-started desert tortoises and their contribution to population persistence.

Ravens represent an increasing threat as they have seen significant population growth over the last 40 years (Boarman and Berry 1995, Sauer and Link 2011) due to the raven's adaptability and generalist habits. Ravens are able to take advantage of anthropogenic food subsidies, such as landfills and roadkill from animal-vehicle collisions (Boarman 2003). The incursion of human-made nesting and perching structures such as power line towers and billboards into natural areas (Boarman 2003), have contributed to raven population growth, and can lead to intense predation pressure on desert tortoises (Boarman 1993, Boarman 2003, Harju et al. 2022).

Ravens present the greatest risk to juvenile tortoises in the spring (March-June), when raven nesting pairs are intensely hunting around their nests to feed their mates and offspring, up to six weeks after the offspring have fledged (Stiehl 1985, Kristan and Boarman 2003). During this time, ravens spend most of their hunting time within 400 m of the nest, however predation events can extend >1 km from the nest (Sherman 1993, Daly et al. 2019). Additionally, ravens are capable of consuming tortoises up to 90 mm MCL (McGovern et al. 2020a). Although desert tortoises are only a small proportion of the raven's diet (Camp et al. 1993), ravens' wide-ranging activity areas and increasing abundance can exert a large demographic impact on local populations of desert tortoises. Individual raven nests and roosting areas have been documented to have as many as 136 tortoise shells of depredated tortoises accumulated under them (Campbell 1983, Berry 1985). Predation by ravens can lead to the loss of up to 72% of head-started tortoises released in some areas (Nagy et al. 2015b). However, little information exists on the impact of raven predation on released juvenile desert tortoises in the eastern Mojave Desert region, where raven populations are lower and less studied than the western Mojave Desert region (Boarman and Kristan 2006).

The Ivanpah Valley, in the eastern Mojave Desert has seen increasing nesting activity by ravens, raising concerns that ravens may begin threatening on-going head-starting efforts (Daly et al. 2019, Tuberville et al. 2019). In 2016, a pair of nesting ravens depredated 26.5% of head-started tortoises released that spring, and hunted tortoises up to 1.6 km from the nest on the powerline towers in the study site (Daly et al. 2019). Since then, nesting raven numbers have continued to rise at the study site (Daly et al. 2019, Tuberville et al. 2019, pers. obs.), threatening head-starting efforts. Spillover predation from subsidized ravens is an increasing problem threatening desert tortoise conservation, regardless of the successes seen from other conservation efforts, and continues to put wild and head-started juvenile desert tortoises at risk.

Similar to ravens, coyotes pose a threat to desert tortoise recovery. Coyotes are very adaptable to human-made changes to the desert southwest of North America, and are able to take advantage of food and water subsidies, as well as use roadways for rapid traversal, as well as for carrion (Esque et al. 2010). The same subsidies ravens use for nesting, such as powerline towers, often have roads for servicing the infrastructure (Kohl et al. 2019), leading to varied predation pressure around these roads (Esque et al. 2010). Coyote predation risk can also vary temporally. Denning season, when coyotes are raising young, can bring increased predation risk on the surrounding landscape (Way et al. 2001). Though less is known about coyote population trends and densities in the eastern Mojave Desert, coyotes are the primary predator of head-started tortoises (McGovern et al. 2020a, Candal 2021), and populations are likely higher due to increased availability of subsidies, as well as the loss of interspecific competition from wolves (Grinnell et al. 1937, Berger and Gese 2007, Hendricks et al. 2016). Predation pressure on desert tortoises can also vary based on climatic shifts. A loss of preferred prey due to a lack of precipitation can cause prey-switching in coyotes, leading to increased predation on desert tortoises (Lovich et al. 2014). Unlike ravens, coyotes are capable of consuming desert tortoises of all sizes (Woodbury and Hardy 1948, Walkup et al. 2019), and pose a threat to even the largest head-started tortoises. Understanding how predation risk from coyotes and ravens varies spatially and temporally is critical for ensuring head-starting effort success, as well as to mitigate predation on wild juvenile tortoises.

Head-starting has proven to be a promising recovery tool for desert tortoises (McGovern et al. 2020a, 2020b, Candal 2021). However, desert tortoises can take up to 20 years to reach sexual maturity (Woodbury and Hardy 1948), and survival and movement vary across life stages of tortoise species (Iverson 1991, Tuberville et al. 2014, Quinn et al. 2018). It is critical to monitor individuals post-release to identify head-starting methods that best balance head-starting efficiency with post-release survival, and to identify how tortoise space-use and survival change over time since release. My objectives were to examine how space-use and survival vary over time since release, and examine the factors that influence predation risk on juvenile tortoises by subsidized predators. In Chapter 2, I quantify the differences in desert tortoise settling time, annual home range size, site fidelity, and survival based on tortoise husbandry treatment over three years post-release. The three head-starting treatments used are Combo-reared (tortoises raised for one year indoors and one year outdoors), Outdoor (tortoises raised for two years outdoors) and Six+ (tortoises raised for over 6 years outdoors prior to release). I hypothesize that older and larger tortoises exhibit greater post-release movement, greater space-use, and lower site fidelity, than younger, smaller tortoises. I hypothesize that space use decreases over time since release and that site fidelity increases over time since release. I also hypothesize that larger tortoises exhibit greater survival than smaller tortoises, and that survival increases with time since release.

In Chapter 3, I examine the factors influencing predation risk on juvenile desert tortoises by subsidized predators, specifically; coyotes and common ravens. I use 3D-printed tortoise models as a proxy for live juvenile tortoises to examine how predation risk varies based on tortoise model size, distance to human infrastructure used by ravens and coyotes, and how predation risk varies due to season (spring, predator reproductive season, vs. fall, non-reproductive season). I hypothesize that predation risk will decrease as the size of tortoise model increases, as well as decrease as distance from human infrastructure increases. I also hypothesize that predation risk will be lower in the fall than in the spring. These studies provide insight on how head-started tortoises assimilate into wild populations and the efficacy of head-starting as a recovery tool, including information on optimal pre-release husbandry for desert tortoises and future release site characteristics. This work also fills in important data for the juvenile stage of desert tortoises, which is lacking basic life-history information. Additionally, knowing how predation risk varies spatially and temporally and how predation risk varies with juvenile tortoise size will help to inform head-starting efforts, as well as identify high-priority release sites and optimal release times to boost juvenile recruitment.

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CHAPTER 2

MULTI-YEAR SPACE USE AND SURVIVAL OF JUVENILE HEAD-STARTED MOJAVE DESERT TORTOISES (*GOPHERUS AGASSIZII*)

Introduction

Biodiversity loss is accelerating globally due to human activities such as habitat destruction and over-exploitation (Baillie et al. 2004). Reptiles, specifically, have undergone precipitous declines, and have begun receiving increased conservation attention in recent decades (Gibbons et al. 2000, Buhlmann et al. 2009, Standford et al. 2020). However, many reptiles, especially turtles, are slow to respond to recovery actions due to their slow life histories characterized by delayed sexual maturity and high juvenile mortality (Griffith et al. 1989, Ashton and Burke 2007, Tuberville et al. 2008). The persistence of turtle populations requires high adult survivorship, providing adults sufficient opportunity to produce enough offspring to eventually replace themselves (Congdon et al. 1993). However, high mortality in the juvenile stage, along with delayed sexual maturation, limits the number of adults that can be recruited into the population. Thus, chronically-high juvenile mortality rates may significantly impede recovery efforts (Congdon et al 1993). Even when sources of mortality to both juveniles and adults are reduced, it can take decades to observe the outcome of recovery actions (Balazs and Chaloupka 2004, Dutton et al. 2005). Delayed response to recovery actions, in combination with the small number of long-term monitoring efforts of recovery actions to date (Germano and Bishop 2009, Burke et al. 2015) have limited our understanding regarding success of species restoration efforts for long-lived species in general, and reptiles specifically (Congdon et al. 1993, Ostermann et al. 2001, Averill-Murray et al. 2012). As such, data regarding the successes and failures of reptile recovery efforts, such as population augmentations, is limited and is now only recently becoming available, as the results from current recovery actions are disseminated (Germano and Bishop 2009).

Population augmentations, such as head-starting, are a critical component of many species' management plans (Tear et al. 1993), with the goal of creating self-sustaining populations (Dodd and Seigel 1991, Seddon 1999). Head-starting is the process of raising an animal to a life-stage that is less vulnerable to mortality from predators or harsh environmental conditions, and is increasingly being explored as a potential recovery tool for imperiled species, including turtles (Burke 2015). The effectiveness of head-starting and other translocation efforts has historically been viewed with skepticism (see Dodd and Seigel 1991, Frazer 1992, Heppell et al. 1996) due to lack of post-release monitoring data or due to translocated animals leaving release areas (Kasworm et al. 2007, Germano and Bishop 2009, Hoy et al. 2020). However, head-starting is becoming recognized as an important recovery tool for turtles, particularly when used in concert with other management approaches (Spencer et al. 2017). Though head-starting shows promise for many turtle species (Gibbs et al. 2014, Buhlmann et al. 2015, Burke et al. 2015), it is labor intensive, often necessitates specialized facilities, and can be costly. Evaluating those head-starting successes, as well as differences in head-starting approaches, also presents a challenge due to the slow population-level responses in most turtle species (Congdon et al 1993).

To increase the potential for head-starting to contribute to recovery efforts, it is imperative that we assess the benefits of head-starting and identify techniques that maximize conservation successes (Burke et al. 2015). Different head-starting or release strategies can influence post-release behavior, with certain strategies minimizing post-release space-use (e.g., soft-release pens; Tetzlaff et al. 2019). These studies have demonstrated that decreased space-use and increased site fidelity by translocated animals are often associated with increased survival (Moehrenschlager and MacDonald 2003, Tetzlaff et al. 2019). Thus, different head-starting approaches impact behavior and space-use by juvenile turtles, and in turn, influence post-release survival.

The Mojave desert tortoise (*Gopherus agassizii*), hereafter "desert tortoise," is a species native to the desert southwest of North America. Desert tortoise populations have declined, leading to its listing as "Threatened" under the Endangered Species Act in 1990 (USFWS 1990). At the time of listing, desert tortoise populations were still declining despite four decades of recovery efforts that preceded the listing decision (USFWS 2011). Mitigation efforts have included relocation of displaced wild tortoises to reduce immediate mortality from human development, installation of fencing and underpasses to mitigate road mortality, predator management, and head-starting (USFWS 1994, Boarman et al. 1997, USFWS 2011, Shields et al. 2019), with efforts aiming to identify the optimal approaches for head-starting of desert tortoises, with the dual goals of reducing costs while maximizing survival.

Early head-starting efforts were limited to the protection of tortoises in outdoor enclosures where they were exposed to natural environmental cues but also experienced long periods of dormancy during which activity and growth ceased (Hazard and Morafka

2002, Nagy et al. 2015). Growth rates of outdoor head-started tortoises often matched those of wild juvenile tortoises, taking 5-9 years to reach the recommended release size of 100 mm midline carapace length (MCL; Nagy et al. 2015). More recent efforts, however, have incorporated an indoor-rearing component (Daly et al. 2018, McGovern et al. 2020a), allowing tortoises to reach the recommended size within one year by promoting year-round activity and growth (McGovern et al. 2020a). This is significant, as tortoise size contributes to survival (Nagy et al. 2015, Daly et al. 2019, McGovern et al. 2020b). McGovern et al. (2020b) compared the post-release fate of tortoises raised solely indoors to similarly-sized tortoises grown outdoors over several years, finding that tortoise size was a significant predictor of survival in the first year following release. Time in captivity was not a significant predictor of survival following release (McGovern et al. 2020b). In addition, initial evidence suggests that post-release movement, space-use, and mortality is driven by size at release, which can vary depending on the head-starting approach (Nagy et al. 2015, Daly et al. 2019, McGovern et al. 2020b). Across the extended juvenile period, which can last 15-20 years (Woodbury and Hardy 1948), survival rates are expected to increase over time, as tortoises become larger in size and less vulnerable to predation and desiccation (Nagy et al. 2015, Murphy et al. 2016, McKee et al. 2021). Additionally, movement, which can influence survival, is often greatest in the first-year post-release (Tuberville et al. 2005, Pille et al. 2018). Although these studies demonstrate the importance of head-starting to tortoise recovery, few studies have greater than one-year of post-release monitoring data (Nagy et al. 2015). As such, the duration of post-release monitoring efforts to date limits our understanding on the long-term outcome of head-starting efforts including the extent that different head starting techniques contribute to conservation successes, such as long-term population persistence.

To fill the aforementioned knowledge gaps and to better guide desert tortoise conservation efforts, we evaluated the outcome of three head-starting approaches by quantifying multi-year post-release movement and survival in desert tortoises. These approaches were: 1) two-year old tortoises raised for one year indoors followed by one year outdoors (**Combo**); 2) same aged but smaller-sized two-year old tortoises raised solely outdoors (**Outdoor**); and 3) similar sized but older, 6- to 7-year-old tortoises raised solely outdoors (**Six+**). Within this context, we quantified the effect of head-starting on space use (settling behavior, home range size, and site fidelity) and annual survival. First, we compared settling dates among tortoises reared under different head-starting treatments, as greater exploratory movements during the settling phase can lead to greater surface activity, which can in turn lead to greater mortality risk due to predation or exposure (Quinn et al. 2018, Daly et al. 2019, Tuberville et al. 2021). Larger, older juvenile tortoises have been shown to exhibit more surface activity than smaller tortoises (McGovern et al. 2020a). Thus, we predicted that settling dates would vary among head-starting treatments with younger, smaller tortoises (Outdoor) settling quicker than Six+ and Combo tortoises. Second, we estimated annual home ranges for each tortoise to evaluate how home range size varied among treatments and over time (i.e., year since release). We predicted that annual home range size would decrease as year since release increased. Additionally, we predicted that older and larger tortoises (Six+ treatment group), would have larger annual home range sizes, as larger tortoises have increased movement and space-use than smaller individuals (Candal 2021). We then compared year-to-year site fidelity among tortoises reared under different head-starting treatments using four metrics – 1) distance between release location and settling location (location associated with settling date), 2) distance between settling location and first year home range center, 3) distance between annual home range centers, and 4) percent annual home range overlap. We predicted that site fidelity would generally increase (i.e., decreased distance between home range centers, increased home range overlap) as year since release increased. However, we predicted that older and larger tortoises (Six+ treatment group), would exhibit lower over-all site fidelity over time relative to smaller and younger tortoises, as larger tortoises tend to undertake larger movements (Candal 2021) and may select new burrows or foraging areas over time post-release.

We quantified annual survival of head-started desert tortoises by treatment group during the first three years post-release. Because survival has been shown to increase with size (Haskell et al. 1996, Nagy et al. 2015, McGovern et al. 2020a, Tuberville et al. 2021), we predicted that survival would be lowest for the Outdoor tortoises, as they are, on average, the smallest group of tortoises of our three treatment groups. We also predicted that the Six+ and Combo tortoises, the treatment groups with the largest tortoises, would have the highest survival. Mortality has also been found to increase with movement and extended settling periods (Germano and Bishop 2009, Daly et al. 2019, McGovern et al. 2020a), which we predicted to be highest in year one. Thus, across groups, we predicted that annual survival probability of released head-started desert tortoises would be lowest during the first-year post-release compared to subsequent years. From this information, we provide insight on how head-started tortoises assimilate into wild populations and how to best apply head-starting as a recovery tool in desert tortoises.

Methods

Study Site

The study was conducted in the Mojave National Preserve (MNP), San Bernardino County, California, USA, in the southern portion of the Ivanpah Valley in the Eastern Mojave Recovery Unit of the Mojave desert tortoise (Nussear et al. 2009, USFWS 2011). Our release areas were located within the northeastern portion of MNP. The release areas were open flats at 940 – 1112 m elevation dominated by creosote (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), little-leaf ratany (*Krameria erecta*), big galleta (*Pleuraphis rigida*), Mojave yucca (*Yucca shigidera*) and cholla cacti (*Cylindropuntia sp.*) and had an abundance of rodent burrows for shelter sites and small rocks for camouflage (Todd et al. 2016). The Eastern Mojave Recovery Unit has the lowest density of juvenile tortoises of the five Mojave Desert Tortoise Recovery Units (Allison and McLuckie 2018).

Obtaining Hatchlings

We reared all tortoises used in this study at the Ivanpah Desert Tortoise Research Facility (IDTRF), which is located 15 km north of our release sites. In May, starting in 2011, we collected wild adult female tortoises that we previously outfitted with VHF radio-transmitters, and used x-radiography to detect the presence of calcified eggs (Gibbons and Greene 1979). We placed gravid females in 5 x 9 m predator-proof nesting pens where they were held to naturally deposit their eggs, after which we returned females to their capture location. The eggs developed *in situ* until they hatched, approximately 90 days after oviposition (Spotila et al. 1994). We marked each hatchling by notching their marginal scutes corresponding to a unique code assigned by USFWS (Cagle 1939). We split hatchlings from each clutch among treatment groups due to potential maternal effects on hatchling size and survival (Nafus et al. 2015a).

Experimental Treatments

Head-started tortoises in this study included individuals from the three aforementioned experimental treatments. The **Combo** treatment consisted of 2-yr old tortoises raised indoors for their first year followed by one year of outdoor rearing. The **Outdoor** treatment, obtained from the same cohort as the Combo treatment, included tortoises raised solely in outdoor pens from hatching to 2 years of age. The Outdoor tortoises dug their own burrows and were inactive during winter months. The **Six+** treatment consisted of tortoises reared solely in outdoor pens from hatching to 6 – 7 years age and were inactive during winter. Because Combo tortoises spent their first winter indoors allowing them to skip the winter dormancy period, they reached sizes comparable to the Six+ tortoises in a single year.

Pre-release Husbandry

We raised Outdoor and Six+ tortoises solely outdoors in 9 x 9 m predator-proof pens in natural desert habitat and outfitted with sprinkler systems, which were run weekly during the active season (Apr. – Oct.) to simulate rainfall. From 2011 to 2015, tortoises only had access to natural forage but received supplemental rain (Tuberville et al. 2019). After 2015, we supplementally fed outdoor-reared tortoises using a mix of leafy greens and Mazuri® Tortoise Diet (Formula 5M21, Mazuri Exotic Animal Nutrition, St. Louis, MO; Daly et al. 2018) during supplemental watering events. We provided artificial burrows (see description in Tuberville et al. 2019) but tortoises were also able to build natural burrows. Tortoise densities in the outdoor pens ranged from 0.1 to 0.13 tortoises/m^2 (further husbandry information: Daly et al. 2018, Tuberville et al. 2019, McGovern et al. 2020b).

During their first year, we reared Combo tortoises indoors in 189 L (50-gallon) mesocosms (Rubbermaid stock tanks, Atlanta, Georgia, USA) with natural desert soil for substrate (Daly et al. 2018). Each mesocosm held eight tortoises at a density of 7.7 tortoises/m^2. We fed tortoises *ad libitum* three times per week using the same leafy greens and Mazuri as outdoor-reared tortoise. Twice weekly, we supplemented tortoise greens with a dusting of Rep-Cal Calcium with Vitamin D3 (Rep-Cal Research Labs, Los Gatos, California, USA). We soaked tortoises once per week in 1 – 2 cm per water for 15 – 30 minutes. Following one year of indoor rearing, we reared Combo tortoises outdoors for one year following the protocols described above. Further husbandry details are provided in McGovern et al. (2020b).

Prior to release, we measured mid-line carapace length (MCL) of all tortoises using vernier calipers (0.1mm precision) as the straight-line distance from the anterior edge of the nuchal scute to the posterior notch on the supracaudal scute. We affixed Outdoor tortoises with 3.1 g R1670 transmitters, and we affixed Combo and Six+ tortoises with 3.6 g R1680 transmitters (Advanced Telemetry Systems, MN, USA), on the fifth vertebral scute of the carapace using 5-minute epoxy (Devcon 5-minute epoxy gel, ITW Engineered Polymers, County Clare, Ireland). Transmitters weighed less than 5% of the body mass of the recipient tortoise at the time of release. To help camouflage the transmitters on the tortoises, we applied a thin layer of sand to the epoxy as it cured (Kazmaier et al. 2002).

Releases

We conducted two releases of juvenile desert tortoises from the three head-starting treatments using similar release protocols. Release 1 occurred on 25 September 2018 (n=78) and release 2 on 19 September 2019 (n=72, Figure 2.1). We released tortoises in an area greater than 4.0 km from heavily trafficked roads to reduce road mortality, and at least 1.6 km from power lines to reduce the risk of depredation from ravens that use power line towers as perching and nesting structures (Daly et al. 2019). For each release, we randomly assigned tortoises to release locations, which were separated into three blocks. For release 1, blocks were spaced 350 m apart from one another for a total size of 150 m x 450 m per block. Within each block in release 1, release locations were spaced 50 m apart from one another. For release 2, we spaced the blocks 350 m apart from one another for a total size of 180 m x 300 m per block. Similar to release 1, we spaced locations 50 m from one another for release 2 (Figure 2.2). Aside from minor differences in block area, release 1 and 2 were carried out under the same protocols. We selected release refugium that consisted of a perennial shrub with an intact rodent burrow underneath within 10 m of each release location (Nafus et al. 2015b; Todd et al. 2016). We placed tortoises facing into these burrows to safely conceal the tortoise upon release (further release information: McGovern et al 2020a, Candal 2021). Due to the low density of juvenile tortoises in the Eastern Mojave Recovery Unit (Allison and McLuckie 2018), the probability of intraspecific competition between wild-recruited and released head-started juveniles is low (McGovern et al. 2020a).

Post-Release Monitoring

During the first-year post-release, we tracked tortoises twice per week (beginning within 24 hours of release) until 31 October, then weekly until winter dormancy (Figure 2.1). We defined tortoises as “Dormant” when they remained in the same burrow for more than two weeks. Once dormant, we tracked tortoises every two weeks through winter dormancy, then weekly following spring emergence in March. Once emerged from winter dormancy, we considered these tortoises as “Active”. After the first year of post-release monitoring, we tracked tortoises weekly during their active season (Mar – Oct) and every two weeks during winter dormancy (Nov – Feb). We used a 3-element Yagi antenna (AF Antronics, Inc., Urbana, IL, USA) and a R1000 receiver (Communications Specialists, Inc., Orange, CA, USA) to conduct radio-telemetry. At each location, we collected UTM coordinates using handheld GPS units with an accuracy of ± 3 m (Garmin model GPSMAP 76, Olathe, KS). If a tortoise was found dead, we recorded the location and any signs of potential predators.

We replaced radio-transmitters each September, with all surviving individuals receiving a 3.6 g R1680 transmitter until September 2020, when we reduced the number of tortoises being monitored via radio-telemetry to 15 tortoises per treatment per release year (n=45). On 1 October 2021, we concluded collecting telemetry data for this study, resulting in three years of monitoring for release 1 and two years for release 2 animals.

Data Analysis: Settling Date

Prior to establishing a home range, tortoises typically exhibit greater movements in the first few weeks following release although the duration of this settling phase can vary among species and individuals (Tuberville et al. 2005, Daly et al. 2015, Quinn et al.

2018, Tuberville et al. 2021). To account for this variation among individuals, we estimated settling date for each released head-start based on their movement behavior. In addition, for each individual we estimated two different settling metrics that capture different movement parameters: daily step-length (settling date$_{DSL}$; meters travelled per day) and daily net distance from release site (settling date$_{DND}$; the straight-line distance from the current location of the tortoise to the release location standardized by the number of days since release). Settling date$_{DSL}$ captured the daily movement of each individual tortoise, indirectly measuring time spent on the surface. Settling date$_{DND}$ identifies the extent to which individual tortoises continue to move away from their initial release location, and may influence the habitat in which the tortoise settles. These metrics are both biologically relevant to head-start project management, as daily step-length corresponds to surface activity, which has been associated with increased risk to mortality (Quinn et al. 2018, Daly et al. 2019, McGovern et al. 2020a), and daily net displacement is necessary to examine final settling location post-release. Settling date$_{DSL}$ was standardized for duration between tracking events, while settling date$_{DND}$ was controlled for days since release to account for animals that survived longer having greater opportunity to move further from the release site.

We then used linear piecewise splines to model an inflection point threshold corresponding to the time point (measured as number of days after release) at which DSL or DND changed for each individual tortoise. Piecewise splines (Wold 1974) are increasingly being used to quantify distinct changes in animal behaviors and survival (e.g., MacNulty et al. 2014, Kohl et al. 2019). We created separate sets of candidate models for each response variable (settling date$_{DSL}$, settling date$_{DND}$), with each set including three model suites: a one-knot, a two-knot, and a linear model. A knot corresponds to the number of days since release that an individual tortoise's movement changed. Individuals for which a one-knot model is the top model would exhibit a single shift in movement behavior, with the single knot representing the settling date. This would occur when an animal's movement slows post-release until a point when movement stabilizes. Two-knot models accommodate multiple distinct shifts in movement behavior by individuals; in these cases, the second knot would correspond to the estimated settling date. For example, this might occur when an animal demonstrates high movement immediately post-release, then declines, then stabilizes. If the linear model was identified as the top model, this would indicate that individual tortoise's movement behavior did not change during the monitoring period and a settling date could not be estimated. For each settling metric (settling date$_{\text{DSL}}$ and settling date$_{\text{DND}}$), we ranked the two-knot, one-knot, and linear models using Akaike's Information Criterion adjusted for small sample sizes (AICc; Burnham and Anderson 2002) to determine the model that best explained settling behaviors for each tortoise (ΔAICc < 2.0). While the one-knot model can identify a settling date, we believe the complex movement patterns of post-release tortoises are best demonstrated in the two-knot model, capturing behaviors such as wandering and exploration that occur post-release and before settling (Germano et al. 2017). If the one-knot or linear model was the best model, we excluded that individual from the analysis due to a lack of defined settling date.

To determine how estimated settling date differed based on the movement metric used, we used an unpaired t-test to compare the mean values of settling date$_{\text{DSL}}$ and settling date$_{\text{DND}}$. We used an unpaired t-test because we could not obtain settling dates from two-knot models for every individual, such as if the two-knot model was not the top model in the initial model suite for each tortoise. Though the settling dates were significantly different from one another, we still constructed candidate model sets for both, as they measure two different patterns of behavior and have different implications regarding release outcome.

We then used linear models to determine how settling date varied in association with treatment group, release year (1 vs. 2), and release MCL. We considered both treatment group and release MCL as covariates in the linear models as head-starting treatment might be expected to influence tortoises beyond affecting their size, such as through duration in captivity and whether they experienced indoor rearing. We log-transformed the response variable of days since release to ensure the data were normally distributed. We used AICc to evaluate model fit (ΔAICc < 7.0). If multiple models were within 7 ΔAICc, we used prediction averaging using the “modavgPred” tool in the “AICmodAvg” package in R (v. 4.1.0) to account for uncertainty in model selection (Mazerolle 2020), then evaluated trends in predicted days since release based on our covariates.

Home Range Size

We estimated home range for each tortoise for each monitoring year. To avoid inflated home range estimates due to exploratory behavior immediately following release, we only included locations post-dormancy for Year 1 calculations, which did not include the initial settling time between release and the first winter post-release. Additionally, we only used locations collected during the “active” season between spring emergence and winter dormancy calculated for each individual separately for subsequent home range calculations. Using these locations, we constructed 95% minimum convex polygons (MCPs; Mohr 1947) to create separate annual home ranges for each tortoise using the “adehabitatHR” package in R (Calenge 2006). A 95% MCP, hereafter “home range”, is the smallest convex polygon that can be built around 95% of the location points of a particular animal (Hayne 1949). This excludes the most extreme exploratory behaviors that can occur with animals exploring novel environments (Burt 1943). Though MCPs can inflate estimates of home range size (Boyle et al. 2008), due to logistics, we were not able to radio-track frequently enough to generate a sufficient number of locations to use other home range estimators. We calculated annual home ranges for any individual tortoise having at least 10 tracking locations in the corresponding active season (range: 10-36 locations). When using MCPs, home range size can be overestimated as the number of locations used to build the home range increases (Anderson 1982). However, given the number of tracking locations and their temporal resolution, we felt that the MCP estimator was the most appropriate home range estimator. Depending on the number of years an individual tortoises survived, up to three annual home ranges could have been constructed for release 1 tortoises (2019, 2020, 2021) and two for release 2 tortoises (2020, 2021).

We then used linear mixed models to examine how home range size differed by treatment group, release year, year since release, and release MCL with home range size (ha) as the response variable and tortoise ID as a random effect (R package “lme4”; Bates et al. 2015) to account for repeated measures of the same individual across years. Home range size was log-transformed prior to analysis to meet assumptions of normality. We used AICc to evaluate model fit (ΔAICc < 7.0). If multiple models were within 7 ΔAICc, we used prediction averaging using the “modavgPred” tool in the “AICmodAvg” package in R (v. 4.1.0) to account for uncertainty in model selection (Mazerolle 2020). We then evaluated trends in predicted home range size based on our covariates.

Site fidelity

We evaluated site fidelity for each individual tortoise using four different metrics: distance between release location and initial settling location, distance between initial settling location and Year 1 home range center, distance between annual home range centers, and home range overlap (proportion of home range$_t$ included in home range$_{t+1}$). We used the settling date$_{DSL}$ to identify the initial settling location (i.e., the location of an individual on the day they were determined to be settled). We then measured the distance between the release location and the settling location, and the distance between settling location to Year 1 home range center. For all metrics, home range center refers to the center point of the 95% corresponding annual home range polygon, calculated using the “sp” package in R (v.4.1.0; Pebesma and Bivand 2005, Bivand et al. 2013). A shorter distance would indicate that a tortoise established its first-year home range closer to its initial settling location. We quantified the extent to which an animal shifted its home range location from year to year by calculating the linear distance between annual home range centers (i.e., the linear distance (m) home ranges for year$_t$ and year$_{t+1}$). A shorter distance between home range centers would indicate that the tortoise did not substantially shift its home range from year to year. Finally, we quantified home range overlap by measuring the proportion of overlap in an individual tortoise’s 95% MCP from year$_t$ to year$_{t+1}$. To do this, we overlayed the home ranges from year$_t$ and year$_{t+1}$ and measured the overlap in hectares, then divided the overlap area by the area of year$_t$ home range using the “rgeos” package in R (v.4.1.0; Bivand and Rundel 2021), with possible values ranging from 0 (no overlap) to 1 (complete overlap) of home range in year_t in home range year_{t+1}. The overlap metric reveals the proportion of a tortoise’s year_t home range used by that individual in the subsequent year, with greater overlap indicating higher site fidelity from year to year.

We built separate model sets for each site fidelity metric. For distance from release location to settling location and settling location to the Year 1 home range center, we used a linear model to examine how distance differed by treatment, release year, and release MCL. For the distance between home range centers and annual home range overlap analyses, we used linear mixed effects models to examine how each site fidelity metric differed based on treatment, release year, years since release, and release MCL. Because of the repeated sampling of individuals, we included tortoise ID as a random effect. We log-transformed all response variables to ensure data were normally distributed and then used AICc to evaluate model fit ($\Delta\text{AICc} < 7.0$). If multiple models in a set were within 7 ΔAICc, we used prediction averaging using the “modavgPred” tool in the “AICmodAvg” package in R (v. 4.1.0) to account for uncertainty in model selection (Mazerolle 2020). We then evaluated trends in predicted home range size based on our covariates. Results for all movement and space use metrics are presented as the mean ± 1 SE of the non-transformed variable.

Survival

We evaluated the effects of head-starting treatment, movement behavior (daily step length (m) during the active season), release MCL, and release year (1 vs. 2) on annual survival using individuals of known fate at the end of the study. We ran a Cox proportional hazard model (Cox 1972) with a weekly binary response (1=alive, 0=died), which included weeks that tortoises were dormant, to examine the effects of different factors (treatment group, daily average step-length, and MCL) on tortoise fate, with release year (1 vs. 2) as a strata variable in the "survival" package in R (Therneau 2022). We used AICc to evaluate model fit (ΔAICc < 7.0), using the "AICcmodavg" packages in R (v. 4.1.0) to account for uncertainty in model selection (Mazerolle 2020).

Results

We collected 12,821 locations on 150 tortoises between 25 Sep 2018 and 01 Oct 2021. Of the 150 tortoises released in September 2018 (release 1; 78 individuals) and September 2019 (release 2; 72 individuals), 51 survived and were radio-tracked until data collection for this thesis ended in September 2021. Twenty-seven tortoises were released from the study in September 2020 to reduce tracking effort; 17 tortoises were lost from the study due to radio failure and their fate was unknown.

Settling Date

We were able to calculate settling date$_{\text{DSL}}$ for 127 tortoises, and settling date$_{\text{DND}}$ for 122 tortoises. We found that settling date$_{\text{DSL}}$ and settling date$_{\text{DND}}$ were significantly different from one another ($t = -4.15$, $df = 247$, $p < 0.05$), but because they measure different movement phenomena, we examined the influences of predictor variables on each metric. Overall, mean settling date$_{\text{DSL}}$ was 6.6 ± 0.5 days post-release and ranged from 2 – 33 days post-release (Table 2.1). Mean settling date$_{\text{DSL}}$ was not different among treatment groups, between releases, or as a function of release MCL (Figure 2.3). None of the seven candidate models for the settling date$_{\text{DSL}}$ gathered >0.36 of the AICc model weight, indicating high uncertainty in the model selection (Table 2.2). There was no significant difference in settling date$_{DSL}$ among treatment groups.

Overall, mean settling date$_{DND}$ was 9.5 ± 0.5 days and ranged from 2 – 40 days post-release (Table 2.1). None of the seven candidate models for the settling date$_{DND}$ gathered >0.24 of the AICc model weight, indicating high uncertainty in the model selection (Table 2.2). Mean settling date$_{DND}$ was not significantly different among treatment groups, though the smaller tortoises from the Outdoor treatment settled about one day earlier (settling date$_{DND}$ = 8.3 ± 0.8 days) than tortoises from the Combo (10.6 ± 0.8) and Six+ treatments (9.6 ± 1.2 days). Mean settling date$_{DND}$ was not significantly different between releases or as a function of release MCL (Figure 2.4).

Home Range Size

Mean annual home range size across all tortoises and all years of monitoring was 0.7 ± 0.3 ha (n= 276) and ranged from 0.0 – 54.8 ha (Table 2.1). When model predictions were averaged (Table 2.2), home range size differed by treatment and years since release. Tortoises in the Six + treatment had larger home ranges (1.6 ± 0.8 ha) than the Combo (0.2 ± 0.0 ha) and Outdoor treatment groups (0.2 ± 0.1 ha, $p<0.05$). Additionally, home range size decreased with each year since release (Figure 2.5). Annual home range size did not differ by release year.

Site Fidelity

Across all treatment groups, the mean distance between the release location and the settling location was 203.5 ± 32.4 m and ranged from 2.2 – 2,867.1 m (Table 2.1). When model predictions were averaged (Table 2.2), distance from release to settling location differed among treatment groups. Six+ tortoises and Outdoor tortoises settling further from their release points (349.0 ± 80.1 m, 152.7 ± 26.4 m, respectively) than did Combo tortoises (92.5 ± 26.0 m, Table 2.1, Figure 2.6). Distance between release and settling location did not differ between releases or vary by MCL at release.

Across all treatment groups, the mean distance between the settling location and Year 1 home range center was 104.5 ± 14.2 m (n= 136) and ranged from 3.9 – 1,380.8 m (Table 2.1). Model predictions for distance between settling location and Year 1 home range were averaged (Table 2.2). Although the mean distance between settling to Year 1 home range center was 100.4 ± 16.8 m for the Combo treatment, 132.8 ± 39.8 m for the Outdoor treatment, and 84.1 ± 12.0 m for the Six+ treatment, we did not find a significant difference among treatments. Distance between the settling location and Year 1 home range center was explained by interaction between MCL and release year as predictors, indicating that the distance between the initial settling location and Year 1 home range center was different between release 1 and release 2 and increased as tortoise size increased for tortoises in release 2 (Figure 2.7).

Across treatments and years, the distance between annual home range centers ranged from 1.1 – 1269.9 m with a mean of 41.2 ± 11.1 m (n= 139, Table 2.1). Site fidelity as measured by distance between annual home range centers differed by treatment and year since release. Model predictions for distance between annual home range centers were averaged (Table 2.2). Distance between home range centers was greater in the Six+ tortoises (83.1 ± 31.2 m) than the Combo (20.4 ± 2.3 m) and Outdoor treatments (17.7 ± 2.6 m, Table 2.1, Figure 2.8). Finally, distance between home range centers decreased with time since release (Figure 2.8). Distance between home range centers did not vary by MCL at release, and only decreased slightly between release 1 and 2.

The mean home range overlap across treatments and years was 30.12 ± 2.08% (n= 136) and ranged from 0.00 – 100% (Table 2.1). When predictions were averaged (Table 2.2), home range overlap was not significantly different among treatment groups, but differed among release years, with the tortoises in release 2 having less overlap than tortoises from release 1 (Figure 2.9).

Survival

A total of 55 tortoises were confirmed to have died over the course of the study, with all mortalities attributed to predation: five (9.1% of known mortalities) to an avian predator, 48 (87.3%) to mammalian predators, and two (3.6%) to unidentified predators. Post-release survival to the end of the study (September 2021) for release 1 was 0.45, with annual survival ranging from 0.55 to 0.98 over three years across all treatments (95% CI, 0.34 – 0.60, Figure 2.10). Post-release survival to the end of the study for release 2 was 0.63, with annual survival ranging from 0.72 to 0.87 over two years across all treatments (95% CI, 0.51 – 0.77, Figure 2.10, Table 2.3). Most of the mortalities (32 of 55) occurred in 2021 (Year 3 for release 1, Year 2 for release 2, Figure 2.11).

Our best fitting Cox proportional hazards model included an interaction between daily step length (m) and treatment. The top model gained 0.95 of the AICc weight and included daily step length, treatment group, and their interaction as covariates (Table 2.2). There was no significant difference in survival due to treatment alone. There was, however, a significant effect of movement per day on risk to mortality on the Combo treatment ($\beta = 0.33$, 95% CI = 0.17, 0.48, Table 2.4). The hazard ratio for this effect is

1.38 (95% CI: 1.19 – 1.62), indicating an increase in risk of mortality of 38% for every additional meter moved per day. There was not a significant difference in risk of mortality for the Outdoor and Six+ treatment groups compared to the Combo treatment group (β = -0.10, 95% CI = -0.12, 1.76, β = -0.24, CI = -0.64, 1.32, respectively, Table 2.4). While the interaction was also not significant among treatment groups, we observed a lower risk of death for both Outdoor and Six+ tortoises as movement per day increased relative to Combo tortoises. Release year and years since release were not significant predictors of tortoise survival.

Discussion

Head-starting is a conservation practice increasingly being used for desert tortoise recovery. Different husbandry treatments may impact space-use and survival; factors that directly contribute to restoration success. However, multi-year post-release monitoring is rarely implemented for head-starting projects (Germano and Bishop 2009, Nagy et al. 2015). By monitoring head-started tortoises from three different treatment groups for multiple years, we sought to fill knowledge gaps in the ecology of juvenile tortoises and to examine how husbandry treatment influences spatial behavior and survival to direct future conservation efforts. We found that Outdoor tortoises settled slightly earlier than Six+ and Combo tortoises. Six+ tortoises had larger home ranges than both Combo and Outdoor tortoises. Additionally, home range size decreased over time since release. While home range overlap did not differ among treatment groups, distance between home range centers was larger in the Six+ tortoises than the Combo and Outdoor treatment groups, indicating that the older Six+ tortoises also tended to shift the location of their home ranges year to year more than other treatment groups. Finally, annual survival was not significantly different among treatment groups but tended to be higher in the treatment groups with larger tortoises (i.e., the Combo and Six+ groups).

Settling

Estimated settling date differed significantly between the two settling date metrics, settling date$_{DSL}$ and settling date$_{DND}$, with settling date$_{DSL}$ occurring on average 3 days before settling date$_{DND}$. It is unsurprising that the means of these metrics differed, as they are measuring two different behaviors. Settling date$_{DSL}$ is an indirect measure of time spent on the surface and exposed to predators or harsh conditions during the initial settling period, whereas settling date$_{DND}$ takes into account the distance that the tortoise is moving away from the release location, influencing what habitat a tortoise finally settles within. Tortoises tended to reduce their daily movement between tracking events within one week of release, resulting in an earlier settling date$_{DSL}$, but took slightly longer to stop moving further away from the release location. Our two settling date metrics differ from previous studies of post-release tortoise movement, where settling has been defined as “time to first burrow construction” (Candal 2021, McGovern et al. 2021) or movement around a central location (Nafus et al. 2017). Due to the later settling date that was calculated, settling date$_{DND}$ was a more conservative metric than settling date$_{DSL}$ in our study, and by identifying differences among treatment groups, may serve as a better tool for quantifying settling behavior in future translocation and head-starting studies.

Settling date$_{DND}$ differed among treatment groups, with Outdoor tortoises settling a day earlier than Combo and Six+ tortoises. Settling date$_{DSL}$ did not differ among treatment groups, and none of our covariates served as significant predictors of settling date$_{DSL}$. Rather, all tortoises may have been reducing their daily step-length around the same time post-release. However, while Outdoor tortoises began to move around a central location while maintaining overall movement levels, Combo and Six+ tortoises continued to move farther from their release locations. Overall, tortoises in our study settled within 10 days of release. Post-release settling behavior has been shown to be influenced by both intrinsic and extrinsic factors. Hazard and Morafka (2002) reported similar settling times (~7 days post-release) for neonate and head-started desert tortoises, though older juveniles moved more often. Nafus et al. (2017) found that most translocated juvenile desert tortoises (65%) settled within two weeks of release and that settling behavior was most influenced by habitat characteristics such as the presence of desert washes, and substrate composition. Habitat characteristics also have been shown to influence settling behavior in a variety of translocated species, such as cane toads (*Rhinella marina*; Pettit et al. 2017) and elk (*Cervus elaphus*; Larkin et al. 2004). In combination, this suggests that post-release settling behavior is likely influenced by both pre-release factors, such as age and size of the individuals, time and care in captivity, and the quality of the habitat in that they are released (Stamps and Swaisgood 2007, Garnier et al. 2021). Additionally, our releases were conducted in the fall, which may have helped facilitate settling behavior, as the onset of winter dormancy encouraged tortoises to become less active on the surface as temperatures cool (Pille et al. 2018, Daly et al. 2019).

Home Range Size

In addition to taking longer to settle and settling further from their release location, Six+ tortoises consistently had the largest home ranges compared to the Combo and Outdoor tortoises. While the Six+ tortoises were similar in size to the Combo tortoises, they were over five years older than the Combo and Outdoor tortoises, suggesting that post-release home range size may be driven by age rather than tortoise size. Annual home ranges averaged 0.7 ha for head-started tortoises, with many of the home ranges being below 0.5 ha, consistent with the few home range estimates available for other *Gopherus* species (Diemer 1992, Wilson et al. 1994). Home ranges of immature tortoises tend to be smaller than for adult tortoises, as observed in Sonoran Desert tortoises (*Gopherus morafkai*; Averill-Murray et al. 2020). Indeed, the juveniles in our study had much smaller home ranges than the 6 – 26 ha home ranges previously reported for adult Mojave desert tortoises (Sullivan et al. 2016). The larger home ranges we observed in older Six+ juveniles may indicate that these tortoises may be reaching the subadult stage at which they may be forced to disperse, either due to potential competition with adult tortoises, or to eventually seek mating opportunities (McRae 1981, Tuberville et al. 2014).

As we predicted, however, annual home range estimates decreased over time (i.e., time since release) in each treatment group. Similar space use behavior has been observed in other translocation studies, with home range size decreasing after the first year following release in both desert tortoises (Field et al. 2007, Nussear et al. 2012), gopher tortoises (Heise and Epperson 2005, Tuberville et al. 2005) and other species (ornate box turtles, *Terrapene ornata*; Doroff and Keith 1990, timber rattlesnakes, *Crotalus horridus*; Reinert and Rupert 1999). Our results confirm those of Nussear et al. (2012), that space use will decrease over time when tortoises are released in suitable habitat, and that decrease in space use occurs regardless of tortoise size or pre-release husbandry. Additionally, due to the intense drought in 2021, tortoises may have used less space than previous years due to a lack of foraging resources available.

Site Fidelity

We assessed site fidelity using four different metrics, and the factors driving site fidelity differed based on the metric considered. Six+ and Outdoor tortoises moved further between their initial release location and their settling locations than Combo tortoises. After settling, tortoises across all treatments and release years established initial (Year 1) home range centers near their settling locations. Although the distance between settling location and Year 1 home range center varied widely among individuals (1.1 – 1269.9 m), tortoises on average established their initial home range centroid within ~ 105 m of the settling location. However, this distance increased with MCL and was farther (~20 m) for tortoises from release 2 than release 1. Similarly, both Nagy et al. (2015) and Nafus et al. (2017) reported that head-started desert tortoises generally settle within 100 – 200 m of their initial release location.

Though the Six+ treatment group had larger distances between annual home range centers than Combo and Outdoor tortoises, the distance between home range centers decreased between years in all three treatments. The combination of decreased home range size and distance between annual home range centers with time since release indicates that tortoises – regardless of treatment – exhibit increased site fidelity over time. Even in the Six+ group, which exhibited the greatest shift in home range location, the average distance between annual home ranges was only 83 m. The high site fidelity exhibited by head-started desert tortoises in our study may in part be due to the habitat characteristics of the release site, which supported high quality habitat with preferred plant communities and was fairly homogenous (Nussear et al. 2012, Todd et al. 2016). While estimates of site fidelity over multiple years post-release are limited for tortoises, our results mirror previous studies that also observed tortoises showing increased site fidelity over time post-release (Nussear et al. 2012).

The mean home range overlap – our third metric of site fidelity – was 30.1% across all tortoises and years monitored. Overlap was similar among treatments and did not differ between years. Because of the paucity of home range data for juvenile desert tortoises, there are no published estimates with which to compare our results. The amount of home range overlap we observed in head-started tortoises was low compared to values reported for adult Mojave (78%; Harless et al. 2009) and Sonoran desert tortoises (*G. morafkai*, 78 – 84%; Sullivan et al. 2016, Averill-Murray et al. 2020) but this may be because our juvenile tortoises use much less space than adult desert tortoises.

Overall, we found that between-year site fidelity was high but exhibited extensive variability – some of which could be attributed to tortoise size or husbandry treatment. However, some of the site fidelity metrics varied between release 1 and release 2. Tortoises from release 2 exhibited less home range overlap than tortoises from release 1. Similar to our settling data, the difference between release 1 and release 2 may be due to differences in weather when tortoises were emerging from dormancy burrows, as winter and spring precipitation in March and April of 2020 was almost 3x average levels (9.6 mm average, 26.1 mm in spring 2020; USDC 2022). This increase in precipitation likely brought increased spring forage availability that allowed for the tortoises in release 2 (Fall 2019) to move farther from their release location in their first year than tortoises in release 1 (Fall 2018) due to a relative abundance of forage and water. However, the following spring, 2021, was characterized by a total lack of precipitation, which likely led to decreased movement of all released tortoises (Duda et a. 1999). Because release 1 tortoises had two years-worth of time on the landscape before the 2021 spring drought, they had more time to settled into preferred home ranges than tortoises in release 2. As such, the release 2 tortoises likely stayed sedentary through the 2021 spring drought, instead of returning to previously used burrows or foraging areas. We also saw a difference in distance between home range centers between release 1 and release 2. Again, this may have been due to annual differences in precipitation during each release year, which can drastically alter desert tortoise behavior and may allow for greater movement due to increased forage and hydration (pers. obs, Wilson et al. 2001).

Survival

Our annual survival rates prior to 2021 were higher than those previously reported for head-started and translocated juvenile desert tortoises (0.44 – 0.79; Nagy et al. 2015, Nafus et al. 2017, Daly et al. 2019, Tuberville et al. 2019. The larger size of tortoises released in the current study (mean=107.1 mm MCL) may have contributed to the higher overall annual survival we observed. McGovern et al (2020a) found that size was an important predictor of survival of head-started desert tortoises during their first year following release, but size is not always the most important predictor (Candal 2021). We found that annual survival was influenced by an interaction of treatment group and daily step length. Although treatment alone did not influence annual survival, the interaction between movement and treatment group was the most significant predictor of survival in our study. As movement per day increased, the risk of mortality also increased. Increased movement likely resulted in increased surface activity time, which has been associated with mortality risk in head-started desert tortoises and gopher tortoises (Quinn et al.

2018, Daly et al. 2019, McGovern et al. 2020a). While this interaction between movement and survival was not significantly different among treatment groups, Combo tortoises had higher risk to mortality as movement per day increased than the Outdoor and Six+ tortoises. Prior to release, all tortoises in our study were reared at least one year in naturalistic outdoor enclosures and may have thus experienced a form of pre-release conditioning, which has been shown to decrease post-release movement (Tetzlaff et al. 2019) and could lead to increased survival when compared to non-conditioned animals, though more time outside may be required to reduce the increased risk to mortality with increased movement in Combo tortoises.

Most tortoise mortalities in our study were attributed to mammalian predators, as has been reported in previous studies, including earlier releases at our study site (Nagy et al. 2015, McGovern et al. 2020a, Candal et al. 2021). In contrast, Daly et al. (2019) reported common ravens (*Corvus corax*) served as the primary predator in the first releases at our study site and showed that mortality risk due to ravens extended 1.6 km from powerlines that served as perching and nesting structures (Daly et al. 2019). The preponderance of mammalian predation in the current study likely stems from two factors. First, following the recommendations of Daly et al. (2019), we released all tortoises ≥ 1.6 km away from the nearest powerline (Daly et al. 2019), thereby mitigating potential raven predation. Second, the greatest mortality was observed in the final year of monitoring (Year 3 for release 1, Year 2 for release 2), which coincided with a marked decrease in precipitation (2021). An average of 7.6 – 12.7 cm of rainfall occurs annually on Mojave National Preserve, with most occurring in the spring (Mar – Apr; USDI 2022). However, in spring of 2021, our study area received no rain and tortoises delayed emergence from their winter dormancy burrows. With the onset of the summer monsoon, however, tortoises emerged *en masse*, making them particularly vulnerable to predators. In addition, coyotes (*Canis latrans*) are known to become more reliant on desert tortoises as a food source during drought years when jackrabbits (*Lepus californicus*), their primary prey, become less abundant (Esque et al. 2010, USFWS 2011). Annual survival of all treatment groups in release 1 dropped from 0.98 in 2020 to 0.55 in 2021, and survival of all treatment groups in release 2 dropped from 0.87 in 2020 to 0.72 in 2021. The increase in predation events during the summer of 2021 appeared to have occurred irrespective of tortoise size and may have masked any significant differences in survival among our three treatment groups. Our results followed a similar pattern to Nagy et al. (2015) where survival rates increased with size and over time since release, until harsh drought conditions lead to increased predation to all released tortoises, regardless of size.

We did not observe any direct evidence of mortality caused by desiccation in our study, even during the dry conditions of 2021. Desiccation has been reported as a significant cause of mortality in previous studies of head-started and translocated juvenile tortoises (Nagy et al. 2015, Nafus et al. 2017, Daly et al. 2019, Tuberville et al. 2019). The lack of exposure-related mortalities in our study may be driven by releasing larger tortoises with greater water retention abilities (Wilson et al. 2001, Murphy et al. 2016), allowing them to better survive harsh desert conditions, even when exacerbated during drought conditions. However, lack of water may have driven tortoises out of burrows, where they were exposed to predators, or some individuals died due to dehydration and may have been subsequently scavenged by predators.

Conclusions

This study presents a novel examination of space-use and survival for head-started tortoises for up to three years following release. Overall, head-started tortoises – regardless of treatment, showed high site fidelity to the release site, with fidelity increasing in subsequent years. Annual survival was also high except in the final year of monitoring when head-starts experienced severe drought conditions. Most differences in space use among treatments were associated with larger home ranges and less between-year site fidelity in the oldest tortoises, which had been head-started for six or seven years prior to release. The Combo-reared tortoises attained release sizes similar to the Six+ treatment but with only two years of head-starting investment. Thus, our results corroborate the results of McGovern et al. (2020a, 2020b, 2021) and Candal (2021), showing that combination rearing (one year of indoor rearing following by one year of outdoor rearing) continues to be a viable head-starting method for producing large juvenile tortoises in a relatively short amount of time without altering behavior or compromising survival. By incorporating an indoor rearing component into tortoise husbandry, wildlife managers and conservationists can improve the efficiency of head-starting projects, thereby making head-starting a more feasible recovery approach that can be more broadly implemented.

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Tables

Table 2.1. Means, standard errors, and ranges of settling dates, home range size, and site fidelity metrics for head-started desert tortoises (*Gopherus agassizii*) on Mojave National Preserve, California, USA from 2018 – 2021. *2019 home ranges and site fidelity metrics could only be calculated for tortoises in release 1.

		Combo	**Outdoor**	**Six+**	**Release 1**	**Release 2**	**All**
Settling Date							
DSL	Mean (days) ± SE	6.9 ± 0.7	5.5 ± 0.6	7.1 ± 1.0	6.2 ± 0.4	6.9 ± 0.9	6.5 ± 0.5
	Range (days)	2 – 20	2 – 17	2 – 33	2 – 18	2 – 33	2 – 33
DND	Mean (days) ± SE	10.5 ± 0.8	8.3 ± 0.8	9.6 ±1.0	8.8 ± 0.6	10.3 ± 1.0	9.5 ± 0.6
	Range (days)	3 – 22	2 – 24	3 – 40	3 – 24	2 – 40	2 – 40
Home Range Size							
Year 1 Home Range	Mean (ha) ± SE	0.3 ± 0.1	0.3 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.2 ± 0.1	0.4 ± 0.1
	Range (ha)	0 – 3.4	0 – 4.4	0 – 5.7	0 – 5.7	0 – 3.4	0 – 5.7
Year 2 Home Range	Mean (ha) ± SE	0.1 ± 0.0	0.1 ± 0.0	3.8 ± 2.1	2.3 ± 1.2	0.2 ± 0.1	1.4 ± 0.7
	Range (ha)	0 – 0.7	0 – 0.5	0 – 54.8	0 – 54.8	0 – 3.4	0 – 54.8
Year 3 Home Range*	Mean (ha) ± SE	0.1 ± 0.0	0.1 ± 0.0	0.3 ± 0.1	0.2 ± 0.0	–	–
	Range (ha)	0 – 0.3	0 – 0.5	0 – 0.8	0 – 0.8	–	–
Site Fidelity							
Release to Settling	Mean (m) ± SE	92.5 ± 26.0	152.7 ± 26.4	349.0 ± 80.1	231.2 ± 55.3	175.8 ± 34.0	203.5 ± 32.4
	Range (m)	4.1 – 1184.7	2.2 – 957.1	4.5 – 2867.1	4.1 – 2867.1	2.2 – 1494.2	2.2 – 2867.1
Settling to Year 1 Center	Mean (m) ± SE	100.4 ± 16.8	132.8 ± 39.8	84.1 ± 12.0	102.7 ± 17.9	106.3 ± 22.1	104.5 ± 14.2
	Range (m)	4.9 – 533.0	3.9 – 1380.8	5.7 – 402.5	4.9 – 795.3	3.9 – 1380.8	3.9 – 1380.8
Year 1-Year 2 Center	Mean (m) ± SE	22.4 ± 2.8	18.6 ± 3.1	105.7 ± 42.3	73.4 ± 25.6	17.3 ± 1.8	50.4 ± 15.3
	Range (m)	4.6 – 76.7	2.0 – 76.5	3.1 – 1269.9	3.9 – 1269.9	2.0 – 45.5	2.0 – 1269.9
Year 2-Year 3 Center*	Mean (m) ± SE	15.2 ± 3.3	15.6 ± 5.0	22.0 ± 3.6	17.6 ± 2.3	–	–
	Range (m)	1.7 – 39.0	1.1 – 71.8	6.9 – 45.8	1.1 – 71.8	–	–
Overlap Year 1-Overlap Year 2	Mean (%) + SE	27.3 ± 4.3	28.0 ± 4.3	35.4 ± 4.7	38.6 ± 3.6	18.5 ± 2.8	30.4 ± 2.6
	Range (%)	0.1 – 99.9	1.0 – 97.2	0.0 – 100.0	0.0 – 100.0	0.0 – 62.6	0.0 – 100.0
Overlap Year 2-Overlap Year 3*	Mean (%) + SE	27.0 ± 5.8	23.5 ± 4.3	38.1 ± 6.7	29.5 ± 3.4	–	–
	Range (%)	0.0 – 72.1	4.8 – 54.9	10.4 – 70.5	0.0 – 72.1	–	–

Table 2.2. Model ΔAICc values used for space use and survival of head-started Mojave desert tortoises (*Gopherus agassizii*) on Mojave National Preserve, California, USA from 2018 – 2021. The response variables of the model sets are the columns across the top. Squares indicate that the model covariate was not in the candidate set for each response variable. MCL is "midline carapace length" in mm. **Bold** is the top model of each set.

Linear Models	Settling Date: DSL	Settling Date: DND	Home Range Area	Settling to Year 1 Center	Home Range Centers	Home Range Overlap	Post-Release Survival
Null	**0.00**	0.38	□	5.31	□	□	□
MCL	1.82	1.11	□	3.99	□	□	□
MCL*Release	4.36	2.83	□	**0.00**	□	□	□
MCL+Release	3.80	2.82	□	6.01	□	□	□
Release	1.90	2.17	□	7.40	□	□	□
Release*Treatment	2.79	1.35	□	5.01	□	□	□
Release+Treatment	3.96	1.94	□	10.40	□	□	□
Treatment	2.01	**0.00**	□	8.24	□	□	□
Nonlinear Models							
Null	□	□	29.57	□	12.19	9.33	30.94
MCL	□	□	24.39	□	11.50	21.49	30.31
MCL*Release	□	□	□	□	22.97	15.57	□
MCL*Year	□	□	18.69	□	21.15	37.66	□
MCL+Release	□	□	□	□	11.82	11.40	□
MCL+Year	□	□	6.56	□	12.67	26.62	□
Movement	□	□	□	□	□	□	11.89
Movement*MCL	□	□	□	□	□	□	9.54
Movement*Treatment	□	□	□	□	□	□	**0.00**
Movement+MCL	□	□	□	□	□	□	8.89
Movement+Treatment	□	□	□	□	□	□	7.51
Release	□	□	6.58	□	9.49	**0.00**	□
Treatment	□	□	16.12	□	4.67	18.43	31.10
Treatment*Release	□	□	□	□	6.39	13.25	□
Treatment*Year	□	□	7.10	□	13.07	29.57	□
Treatment+Movement+MCL	□	□	□	□	□	□	9.62
Treatment+Release	□	□	□	□	3.59	9.37	□
Treatment+Year	□	□	**0.00**	□	6.62	23.55	□
Year	□	□	11.47	□	13.76	14.36	□
Year+Release	□	□	□	□	5.23	4.35	□
Year+Treatment+Release	□	□	□	□	**0.00**	□	□

Table 2.3. Summary of survival rates for head-started Mojave desert tortoises (*Gopherus agassizii*) on Mojave National Preserve, California, USA from 2018 – 2021.

		Annual Survival			**Cumulative Survival**
		2018 – 2019	2019 – 2020	2020 – 2021	
Release 1	Combo	0.88	1.00	0.60	0.53
	Outdoor	0.71	1.00	0.40	0.28
	Six+	0.9	0.96	0.65	0.56
	All	0.83	0.98	0.55	0.45
Release 2	Combo	-	0.88	0.63	0.55
	Outdoor	-	0.92	0.65	0.60
	Six+	-	0.83	0.92	0.76
	All	-	0.87	0.72	0.63

Table 2.4. Model estimate values used for survival of head-started Mojave desert tortoises (*Gopherus agassizii*) on Mojave National Preserve, California, USA from 2018 – 2021. Combo is the reference group for this model set; thus, no coefficient estimate is provided in a categorical analysis. **Bold** is significant differences between the covariate and the model intercept, * denotes the model's intercept value.

Cox Model Variables	**Post-Release Survival**
Treatment	
Combo	
Outdoor	0.823
Six+	0.303
Movement:Treatment Combo	**0.327***
Movement:Treatment Outdoor	-0.102
Movement:Treatment Six+	-0.241

Figures

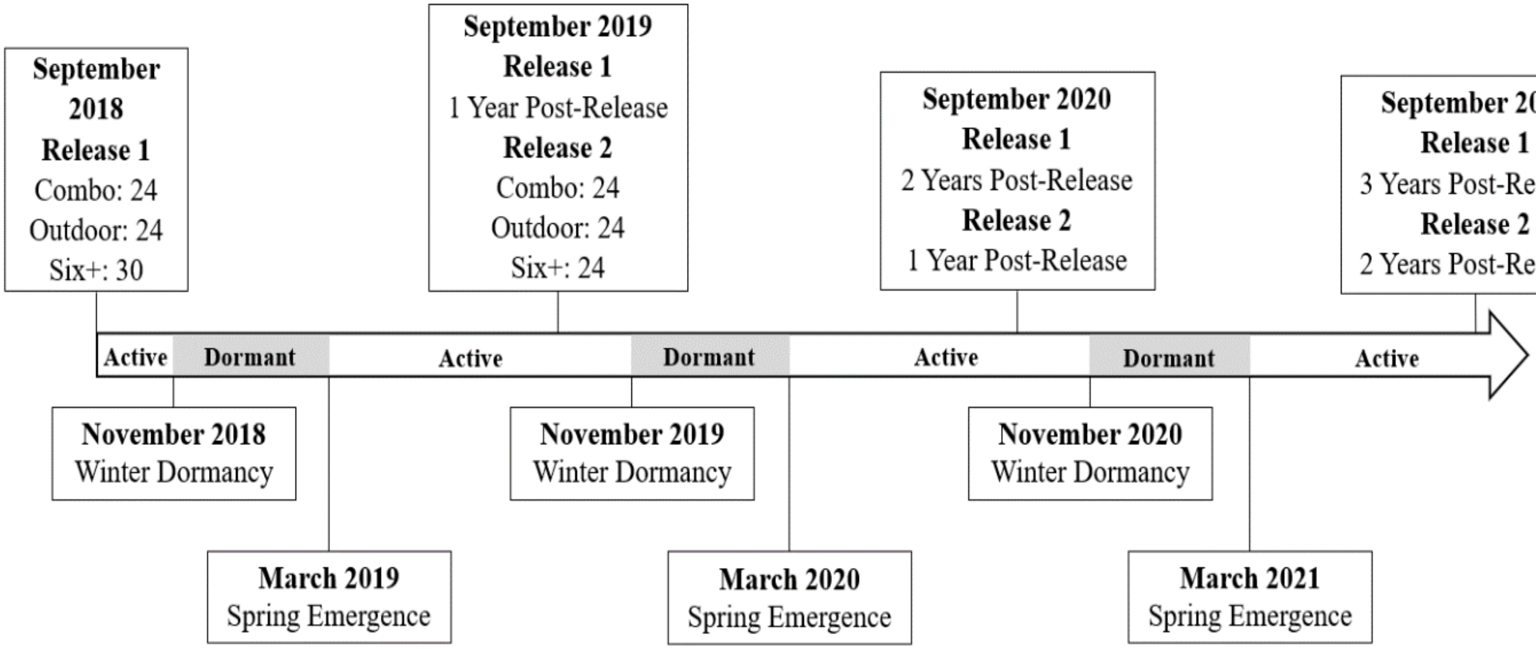

Figure 2.1. Release and radio-telemetry data collection timeline for post-release head-started Mojave desert tortoises (*Gopherus agassizii*) in Mojave National Preserve, CA from 2018

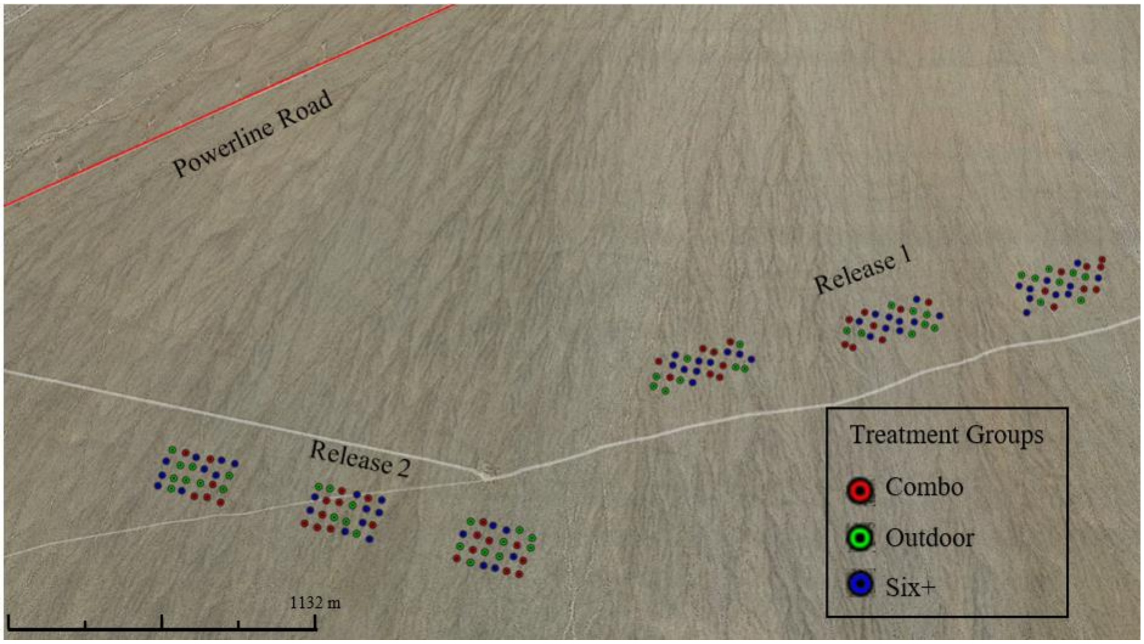

Figure 2.2. Release blocks for releases 1 and 2 of head-started desert tortoises in Mojave National Preserve, CA in 2018 and 2019. Each circle represents a tortoise release location, with the color corresponding to treatment group.

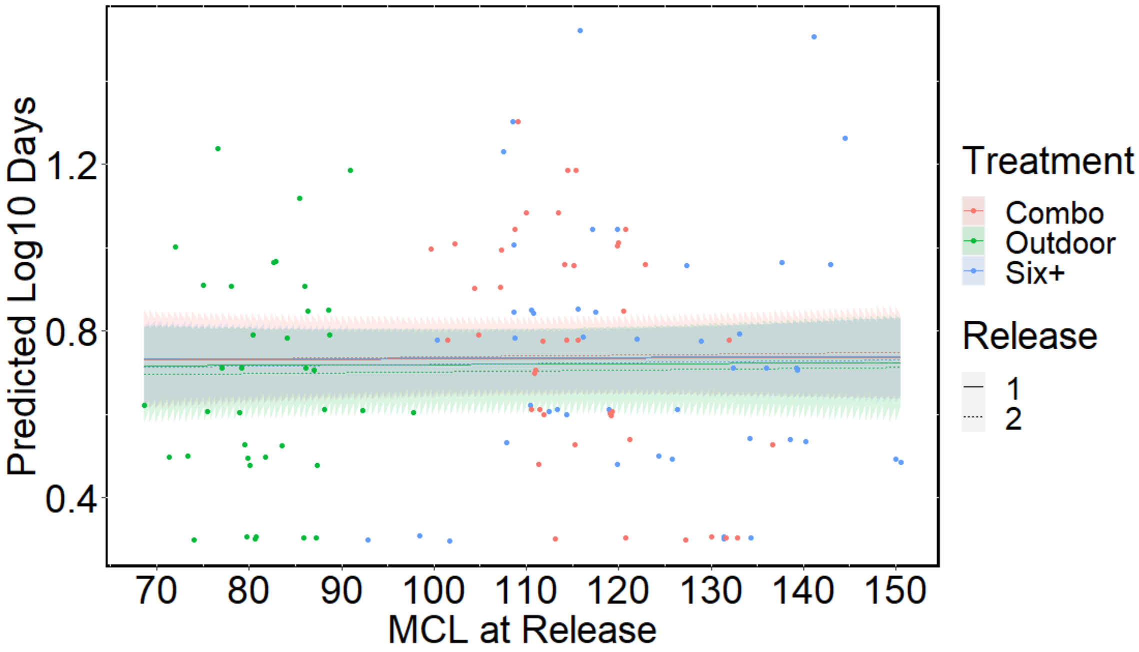

Figure 2.3. Prediction averaged log10 days to settled calculated using settling date$_{\mathrm{DSL}}$ for head-started Mojave desert tortoises (*Gopherus agassizii*) released in Mojave National Preserve, California, USA. Days to settled did not differ by head-starting treatment group, release year, or vary by midline carapace length (MCL) at release.

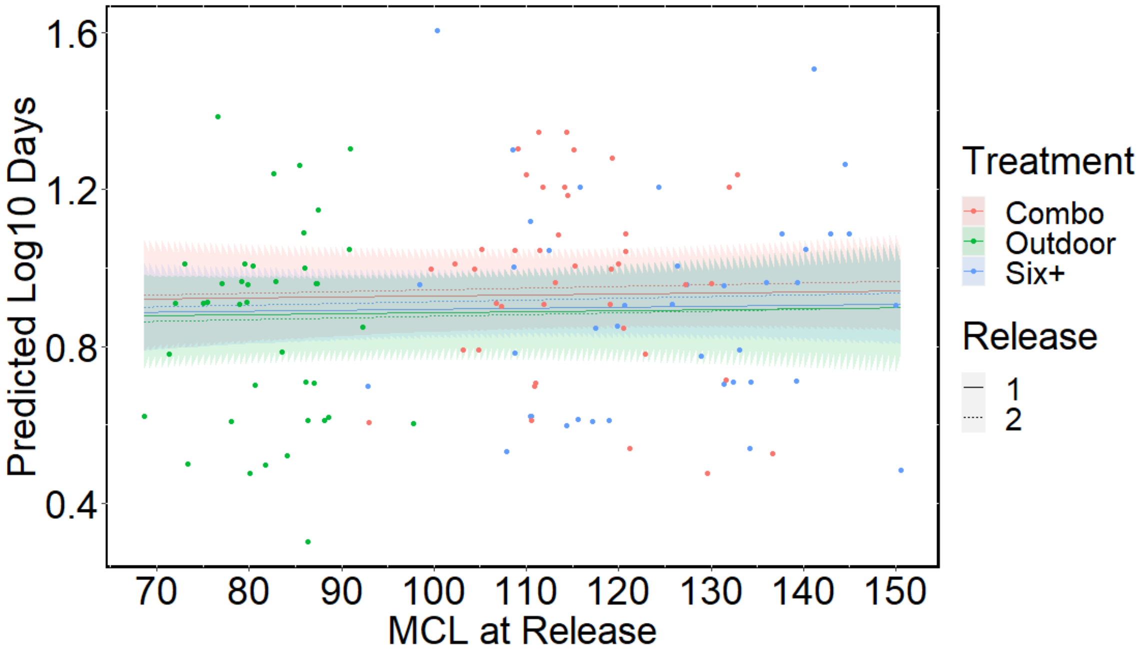

Figure 2.4. Prediction averaged log10 days to settled calculated using settling date$_{\mathrm{DND}}$ for head-started Mojave desert tortoises (*Gopherus agassizii*) released in Mojave National Preserve, California, USA. Days to settled did not differ by head-starting treatment group, release year, or vary by midline carapace length (MCL) at release.

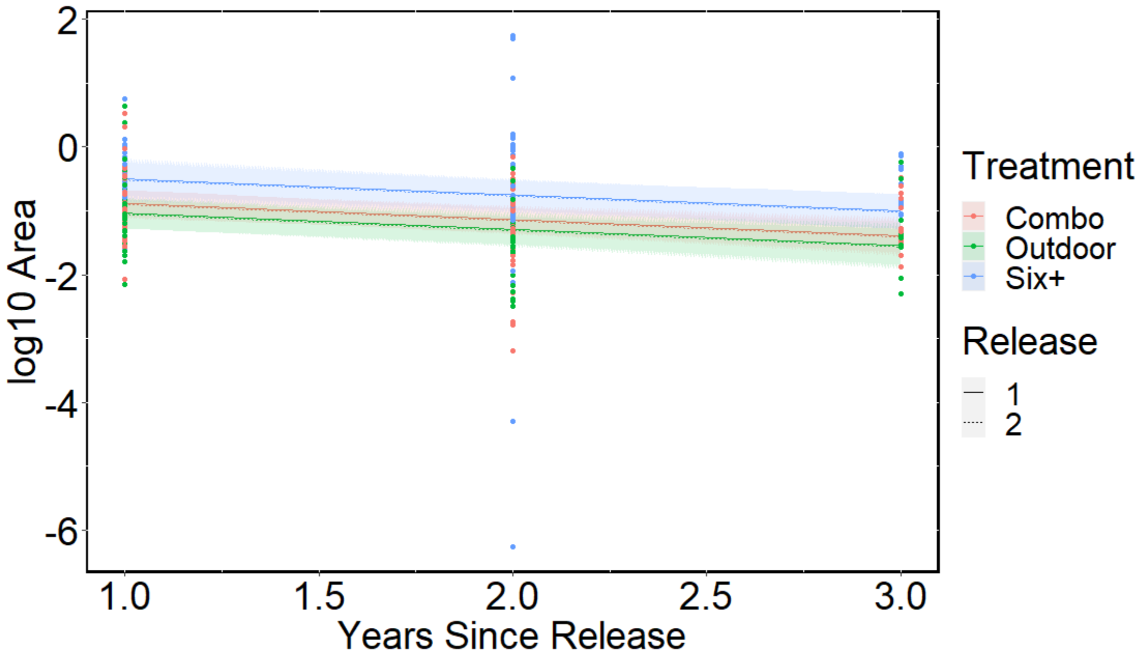

Figure 2.5. Prediction averaged change in log10 annual home range area (ha) over time (years since release) for each head-start treatment group for head-started Mojave desert tortoises (*Gopherus agassizii*) released in Mojave National Preserve, California, USA. Tortoises in the Six+ treatment group had larger home ranges than Combo and Outdoor treatment tortoises, with home range size decreasing over time in each head-starting treatment group.

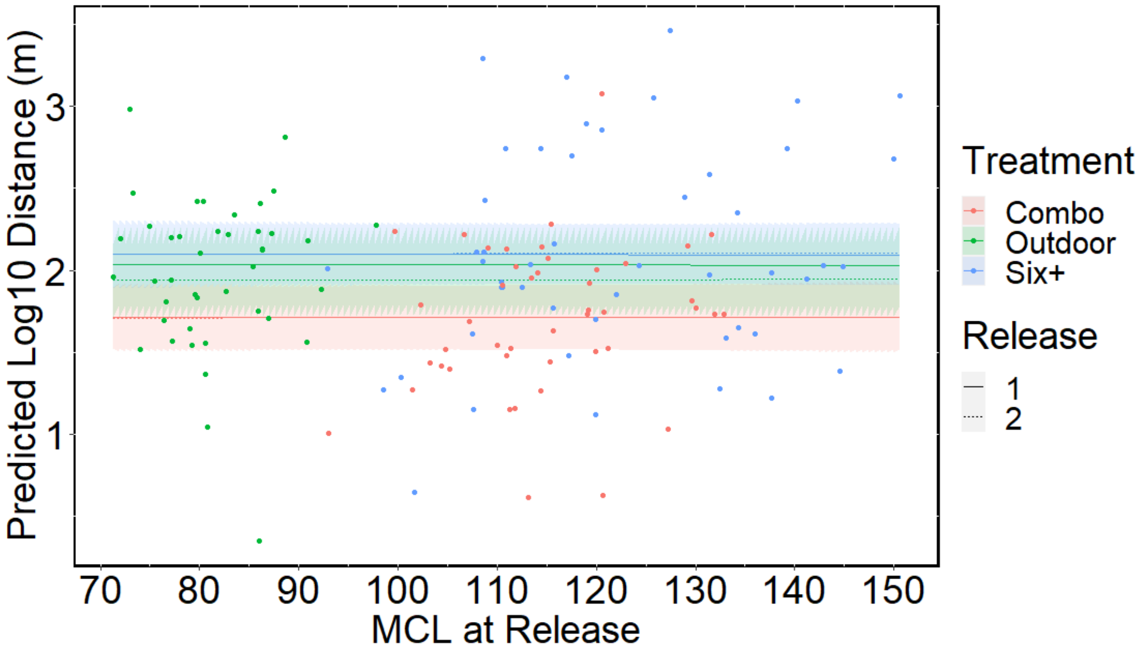

Figure 2.6. Prediction averaged log10 distance (m) between release location and settling location for each head-start treatment group and release year for head-started Mojave desert tortoises (*Gopherus agassizii*) released in Mojave National Preserve, California, USA. Tortoises in the Six+ and Outdoor treatment groups had larger distances between release and settling locations than Combo treatment tortoises. Distance did not vary by release year or midline carapace length (MCL) at release.

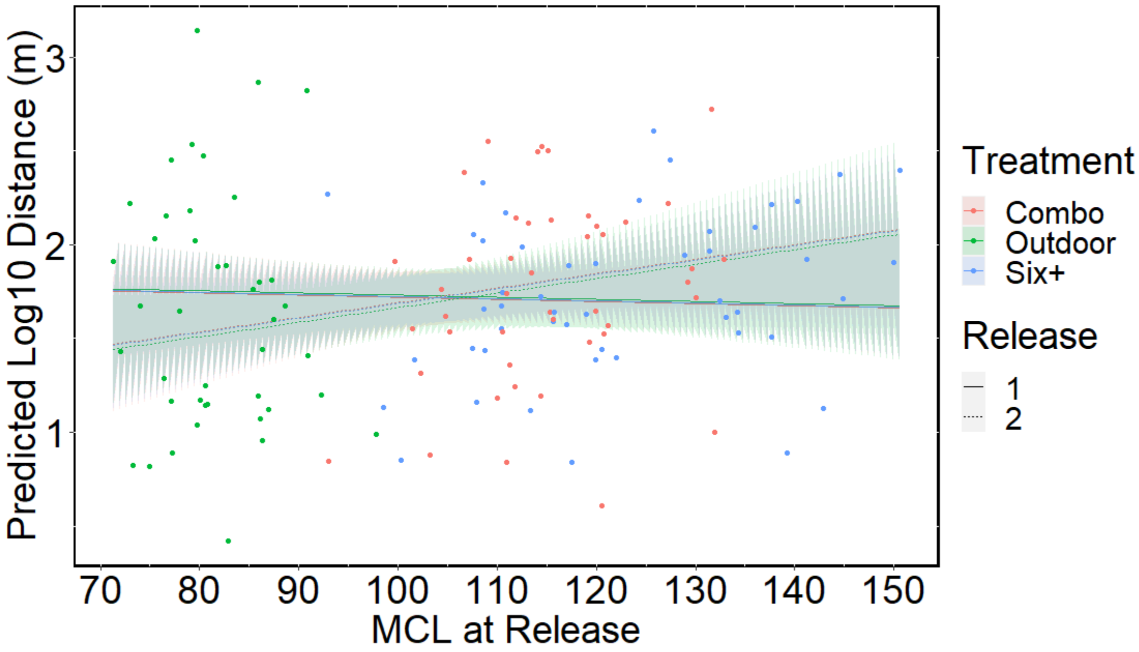

Figure 2.7. Prediction averaged log10 distance (m) between settling location and Year 1 home range center for each head-start treatment group and release year for head-started Mojave desert tortoises (*Gopherus agassizii*) released in Mojave National Preserve, California, USA. Tortoises in release 2 had greater distances between settling location and Year 1 home range center compared to tortoises in release 1 and distance that increased with midline carapace length (MCL) at release. Distance did not vary by head-starting treatment group.

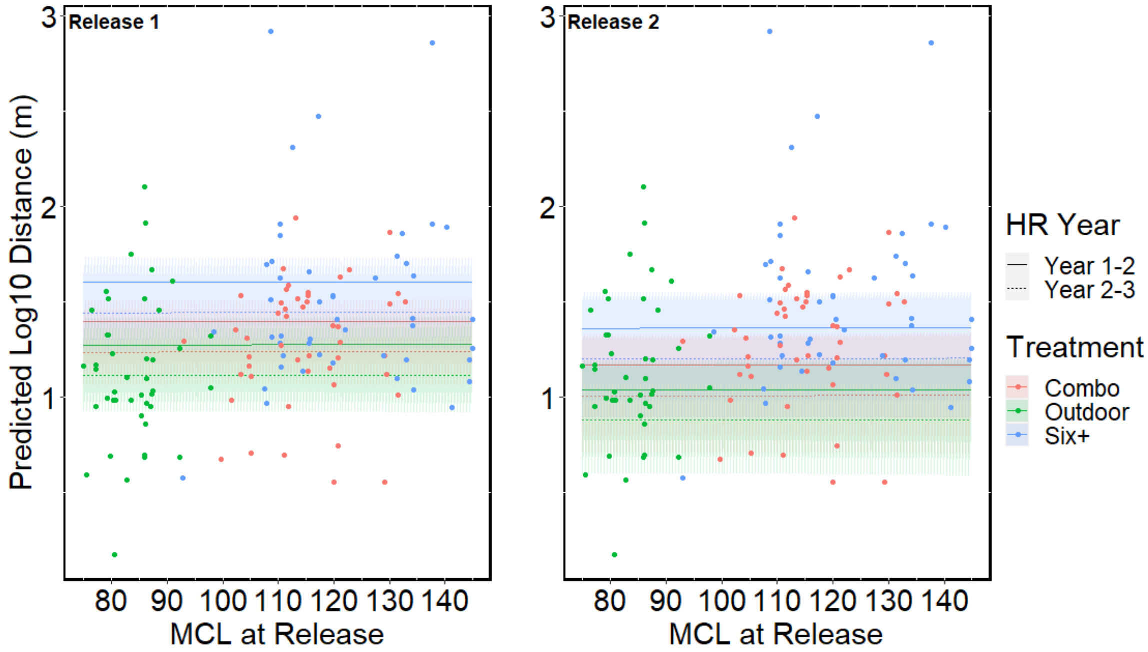

Figure 2.8. Prediction averaged log10 distance (m) between annual home range centers for each head-start treatment group for head-started Mojave desert tortoises (*Gopherus agassizii*) released in Mojave National Preserve, California, USA. Distance between home range centers was greater in Six+ tortoises than the tortoises in the Combo and Outdoor treatment groups. Distance between home range centers decreased with time since release (HR Year), but did not change with midline carapace length (MCL).

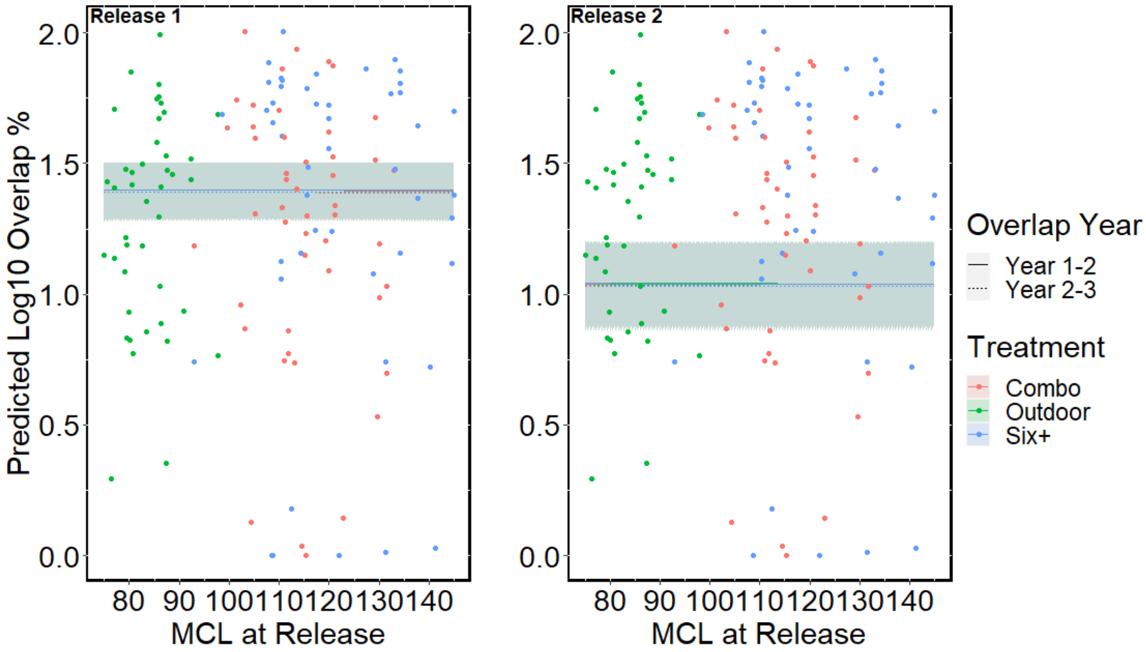

Figure 2.9. Prediction averaged log10 overlap of annual home range (%) for each head-start treatment group for head-started Mojave desert tortoises (*Gopherus agassizii*) released in Mojave National Preserve, California, USA. Overlap did not differ by treatment group or years since release (Overlap Year) or change with midline carapace length (MCL). Tortoises in release 2 had less home range overlap than tortoises in release 1.

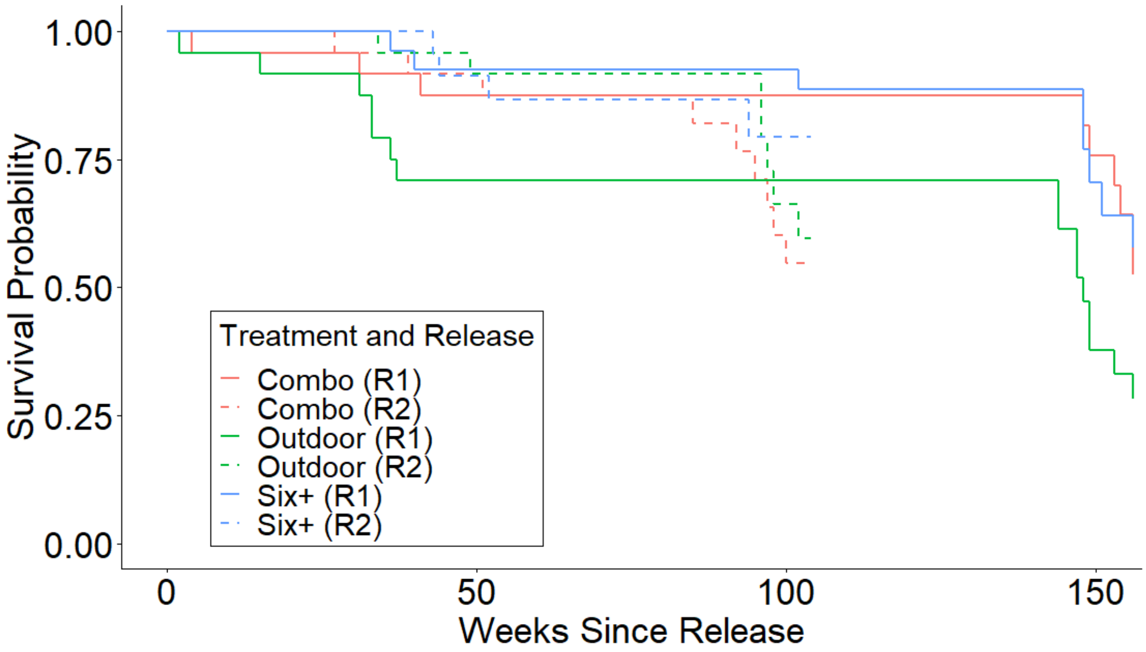

Figure 2.10. Cox survival curve for head-started Mojave desert tortoises (*Gopherus agassizii*) tortoises from three head-start treatment groups and two different releases in Mojave National Preserve, California, USA from 2018 – 2021. Release 1 included 78 tortoises released in 2018 and radio-tracked for up to three years; release 2 included 72 tortoises released in 2019 and followed up to two years. on. There was no significant difference in annual survival among treatments ($p>0.05$), however there was a significant interaction between daily step length (m) and treatment ($p<0.05$).

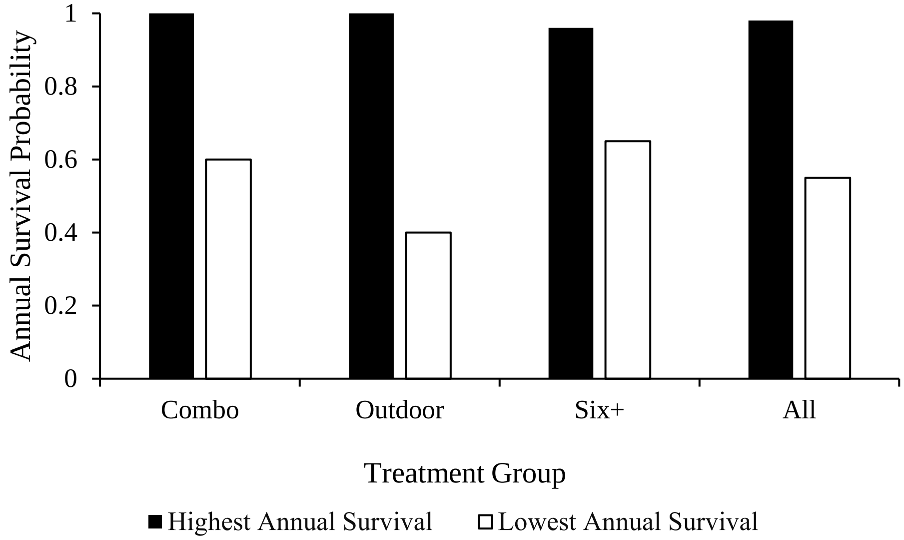

Figure 2.11. Range of annual survival probability of head-started for head-started Mojave desert tortoises (*Gopherus agassizii*) tortoises from three treatment groups in Mojave National Preserve, California, USA from 2018 – 2021. Lowest annual survival for all three treatment groups occurred in 2021.

CHAPTER 3

FACTORS INFLUENCING RISK OF PREDATION BY SUBSIDIZED PREDATORS ON MOJAVE DESERT TORTOISES (*GOPHERUS AGASSIZII*)

Introduction

As global biodiversity declines and recovery efforts are implemented to mitigate loss, managers and conservationists must continually monitor conservation efforts and adapt to changing threats to ensure population viability (Gibbons et al. 2000, Germano and Bishop 2009, Burke et al. 2015). As humans continue to encroach on natural areas, some generalist species are able to adapt to and take advantage of habitat changes that offer supplemental resources. By using anthropogenic resources, or benefitting from the protection of human habitation, densities of generalist species can increase (Goodrich and Buskirk 1995). Supplemental resources can drastically increase the density or alter the distribution of species. When increased resources alter the density and distribution of predator species, it can lead to "spillover predation" in which increased predation pressure on the surrounding landscape negatively affects populations of prey items (Schneider 2001, Kristan and Boarman 2003). By taking advantage of human-made resources or subsidies, these "subsidized predators" can severely jeopardize the recovery efforts of imperiled species that historically served as secondary or non-prey items (Smith and Quin 1996, O'Neil et al. 2018, Loehr and Keswick 2021). In these cases, targeted management actions are needed to control subsidized predators. However, the effects of predation by subsidized predators can vary spatially and temporally (Harju et al. 2018, Daly et al. 2019, Harju et al. 2022), and knowledge of predation risk is necessary to implement effective management actions (Goodrich and Buskirk 1995).

Subsidized populations of corvids have been implicated in the decline of many species worldwide (Rees et al. 2020, Harju et al. 2022, Loehr and Keswick 2022). The common raven (*Corvus corax,* hereafter "raven") represents a significant hurdle in the recovery of many species in North America, including Mojave desert tortoises, (*Gopherus agassizii*), marbled murrelets (*Brachyramphus marmoratus*), and greater sage-grouse (*Centrocercus urophasianus*; Peery and Henry 2010, USFWS 2011, Harju et al. 2018). Though they are native to western North America, raven population densities have grown exponentially due to their ability to take advantage of food, water, and nesting subsidies associated with human expansion (Boarman 2003, Harju et al. 2022). For example, in the deserts of western North America, ravens did not historically have access to nesting structures within the sage-brush and creosote vegetation communities that harbor greater sage-grouse or Mojave desert tortoises. However, as electrical transmission lines have been erected in these habitats, ravens have used these towers as elevated platforms to nest and forage, facilitating incursion of ravens into large, otherwise unfragmented landscapes (Boarman 2003, Harju et al. 2018). Ravens present the greatest risk as predators in the spring (March-June), when nesting pairs are intensely hunting around their nests to feed their mates and offspring (Stiehl 1985, Kristan and Boarman 2003). During this time, ravens spend most of their hunting time within 400 m of the nest, however predation events can extend >1 km from the nest (Sherman 1993, Daly et al. 2019) contributing to landscape-scale predation risk to imperiled species. However, after the nesting season, predation risk declines as ravens leave nesting areas to forage elsewhere in the late summer and fall (Boarman et al. 2006).

Coyotes (*Canis latrans*) are also a subsidized predator of many imperiled taxa across North America. Facilitated by the loss of North American wolves (*C. lupus, C. rufus, C. lycaon*) and human-altered landscapes, coyotes rapidly spread throughout North American over the last century (Hody and Kays 2018). Coyotes, like ravens, are capable of adapting to human-influenced environments and can take advantage of food and water subsidies such as landfills, or highway carrion (Esque et al. 2010), and have been identified as a potential threat to the recovery of certain imperiled species, including the Mojave desert tortoise (USFWS 2011), pygmy rabbit (*Brachylagus idahoensis*; Crawford et al. 2010), and least tern (*Sterna antillarum*; Atwood et al. 1988). Coyotes are highly mobile predators, with roads serving as corridors that facilitate travel by coyotes through critical habitat for imperiled species, or by providing food subsidies through roadkill (Esque et al. 2010). Human infrastructure that may be used by ravens for nesting substrate, like powerline towers, is often accompanied by a service road, (Kohl et al. 2019), causing predation risk from coyotes to vary spatially and temporally near human infrastructure. Predation risk may decrease as distance from human infrastructure increases (Esque et al. 2010). During the reproductive season (March-June), predation risk may also increase closer to denning areas, where coyote pairs care for young (Way et al. 2001).

The Mojave desert tortoise (“desert tortoises”), a species of tortoise native to the desert southwest of North America, was federally listed as “Threatened” in 1994 (USFWS 1994). A significant hurdle in desert tortoise recovery is increased predation by subsidized predators (Boarman 2002, USFWS 2011, Berry et al. 2020), especially ravens and coyotes. Although desert tortoises comprise a small proportion of the raven's diet (Camp et al. 1993), their wide-ranging activity areas and increasing abundance can exert a large demographic impact on local populations of desert tortoises. Head-starting, the process of raising hatchling tortoises to a life-stage that is less vulnerable to mortality from predators or harsh environmental conditions, is currently being explored as a potential recovery tool for desert tortoises (USFWS 2011, Burke 2015). However, predation by ravens can lead to the loss of up to 72% of head-started tortoises released in some areas (Nagy et al. 2015a). Little information exists on the impact of raven predation on post-release juvenile desert tortoises in the eastern Mojave Desert region, where raven populations are lower than those in the western Mojave Desert (Boarman and Kristan 2006). Coyotes too can impart severe predation pressure on juvenile tortoises, resulting in limited recruitment and hindered tortoise recovery efforts (Esque et al. 2010). Additionally, predation by coyotes on desert tortoises can be exacerbated during drought or by novel disease spread (e.g., RHV2, *Lagovirus europaeus*; USGS 2020) that negatively impacts rabbits - one of their preferred mammalian prey items, and causing coyotes to switch to less common prey such as desert tortoises (Peterson 1994, Lovich et al. 2014).

Raven population densities are increasing across the range of the desert tortoise (Harju et al. 2022), however, relative abundance differs across the western and eastern regions of the Mojave Desert, with increased raven density occurring in the west compared to the east (Boarman et al. 2006). The Ivanpah Valley in the Eastern Mojave Recovery Unit for desert tortoises, supports lower densities of ravens than the western region of the Mojave Desert but has seen increasing nesting activity by ravens (Boarman and Kristan, 2006, Harju et al. 2022). The eastern Mojave Recovery Unit has the lowest juvenile desert tortoise densities of the desert tortoise recovery units (Allison and McLuckie 2018) and head-starting has been implemented as a way to recover populations, though subsidized predators can limit effectiveness of this recovery action. This was particularly evident as one pair of nesting ravens in the head-start release site depredated 26.5% of the tortoises released in 2016, with predation events occurring up to 1.6 km from a powerline nest (Daly et al. 2019). Since then, nesting raven abundance has continued to increase along the powerline in Mojave National Preserve (Daly et al. 2019, Tuberville et al. 2019, pers. obs.), which may hinder recovery efforts there.

Less is known about the spatial and temporal trends of coyote abundance in the region, though coyotes serve as the primary predator of released head-starts (McGovern et al. 2020, Candal 2021, Chapter 2). Coyote predation rates on tortoises likely reflect higher than natural, unsubsidized levels due to historic wolf presence and interspecific competition in the Southwestern United States (Grinnell et al. 1937, Berger and Gese 2007, Hendricks et al. 2016). Additionally, predation pressure from coyotes in the eastern Mojave region likely increase during drought years and can vary seasonally with coyote reproduction (Peterson 1994, Way et al. 2001, Lovich et al. 2014). Subsidized predators are an increasing problem threatening desert tortoise conservation, regardless of the successes seen from other conservation efforts, and continue to put wild and head-started juvenile desert tortoises at risk. However, identifying factors associated with risk of predation could help identify head-starting or release practices that might improve post-release survival of head-started desert tortoises.

To evaluate the risk of predation by subsidized predators on juvenile desert tortoises in the Mojave National Preserve in an area where head-started desert tortoises are being released, we examined how mortality risk of 3-dimensionally printed tortoise models (Figure 3.1) varies based on model size, distance from human-made nesting structures, and season. Juvenile tortoise survival increases with size (midline carapace length, MCL), and common ravens are capable of killing juveniles <90 mm MCL (Nagy et al. 2015b, McGovern et al. 2020), thus we predicted that risk to predation from ravens would decrease as tortoise size increased. We also predicted that risk to raven predation would decrease as distance from powerlines (i.e., potential nesting platforms) increased. We also predicted that juvenile tortoise risk to predation from ravens would be higher in the spring (raven nesting season) than the fall (non-nesting season) because ravens are intensely hunting around their nesting areas in the spring (Boarman 2003, Daly et al. 2019). We predicted that juvenile tortoise risk to predation from coyotes would not change as tortoise size increases, because even adult desert tortoises are vulnerable to predation by coyotes (Woodbury and Hardy 1948). We also predicted that we would see a difference in predation risk from coyotes with distance from the powerline because, as coyotes may preferentially travel on roads associated with powerlines, and predation risk may decrease with distance from the powerline road (Esque et al. 2010). We predicted that juvenile tortoise risk to predation from coyotes would be similar in the spring and the fall. Though coyotes reproduce in the spring leading to increased predation risk near denning areas (Way et al. 2001), pups disperse in the fall, while adult territories likely remain the same in our study area, as coyotes consistently use open habitat over the course of a year (Koehler and Hornocker 1991) and thus, may serve as a year-round predation risk to tortoises. Understanding how risk of raven and coyote predation vary with tortoise size can provide best management practices for ideal size at release for head-starting efforts to maximize survival probability. Additionally, knowing how predation risk varies spatially and temporally will help to identify high-priority release sites and optimal release times to boost juvenile recruitment and effectiveness of head-starting outcomes, as well as tailor predator management to protect wild juvenile tortoises.

Methods

Study Site

The study was conducted on Mojave National Preserve (MNP), San Bernardino County, California, USA, in the southern portion of the Ivanpah Valley, in the Eastern Mojave Recovery Unit of the Mojave Desert Tortoise (Nussear et al. 2009, USFWS 2011). The study area was characterized by open flats interspersed by desert washes, with vegetation dominated by creosote (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), little-leaf ratany (*Krameria erecta*), big galleta (*Pleuraphis rigida*), Mojave yucca (*Yucca shigidera*) and cholla cacti (*Cylindropuntia sp.*; Todd et al. 2016). The area has low densities of wild juvenile tortoises and has served as a release site for head-started tortoises (Allison and McLuckie 2018, Daly et. al 2019). Post-release monitoring of head-started desert tortoises revealed high mortality risk from ravens near powerline transmission towers, which ravens use as roosting and nesting substrates and near which they hunt prey to provision their young (Daly et al. 2019). Raven densities in the range of the desert tortoise have increased over the last 50 years, with raven abundance in the east Mojave Desert increasing by 1% per year, though exact population densities and growth rates in our study area are yet to be determined (Boarman and Kristan 2006, Harju et al. 2022). Three power lines (two SCE 200kV lines, and one SCE 500 kV line, California Energy Commission) extend 10 km through our study area (Figure 3.2). A service road runs below these three power lines; it is rarely trafficked by vehicles (<1 per day) but is frequently used by small and medium sized vertebrates, including desert tortoises and potential predators such as coyotes and badgers (*Taxidea taxus*; pers. obs).

Model and Camera Trials

We quantified the risk of predation by ravens and coyotes on juvenile tortoises by measuring attack rates on 3D-printed tortoise models (“Techno-Torts”; Hardshell Labs, Inc. Joshua Tree, CA), which were composed of hard plastic and airbrushed to closely resemble a live tortoise with their legs retracted into their shell (Figure 3.1). We compared predation risk as a function of tortoise size (75, 100, or 125 mm MCL), distance from powerline (250, 750, and 1250 m), and season of year (spring vs. fall, corresponding to the raven nesting and non-nesting season) using trail camera arrays. We deployed two arrays per trial, with individual trials lasting for two weeks. We conducted serial trials through the raven nesting (April-June) and non-nesting season (September-October) in 2020 and 2021.

Each array contained 9 stations (Figure 3.2). We placed a tortoise model of each size (75, 100, 125 mm) at each of three distances (250, 750, 1250 m) from the powerline, randomly assigning each model to one of the nine stations corresponding to each model size*distance combination. We anchored both the tortoise models into the ground using thick, clear monofilament tied to a 20 cm galvanized steel spike, driven into the ground, and covered in soil.

At each station, we measured attack rate using a Cuddeback H-1453 Trail Camera (Cuddeback 2016, De Pere, WI, USA) placed 2 m from the model. We set the cameras to take a two-photograph burst when triggered, followed by a 30-second video to capture predator interactions with the tortoise model. We mounted the cameras 60 cm off the ground on a 1 m U-Post on the opposite side of a creosote shrub from the power line to help conceal it from ravens scanning the landscape from the powerline, though we did not fully camouflage the cameras from ravens as in other studies (Coates et al. 2008). As the tortoise models were set completely in the open at each location, we felt that the concealment of the cameras behind shrubbery would be enough to ensure ravens were approaching due to attraction or curiosity towards the models rather than the cameras. Within an array, we set stations at each distance 200 m apart from one another to ensure independence of observations. We fit 16 arrays along the northwest and southeast sides of the powerline road (Figure 3.3). We separated arrays by 600 m to ensure independence in observations among arrays.

We recorded the following for each photo or video obtained by cameras: tortoise model size, distance from powerline, image date and time, the potential predator species that appears in the photographs or videos, and if the predator "attacked" the tortoise model. We considered any appearance on camera by a raven or coyote as an attempted predation event if the animal approached the tortoise model within 1.5 meters, which would likely result in an attack if the animal encountered a live tortoise. Because we could not identify individual ravens or coyotes, any raven or coyote that left the camera frame for 20 minutes between photos or videos was considered a unique individual.

Statistical Analysis

Using the "survival" package in R (Therneau 2022), we ran a Cox proportional hazard model (Cox 1972) with a daily binary response (1=alive, 0=died), to examine the effects of tortoise model size, distance from the powerline, and season on tortoise model fate during each 14-day trial. Once a tortoise model was attacked, its status was "0" for the rest of the trial and was not available for predation again. By censoring the tortoise model after the first attack, we treated the tortoise model as if it was a live tortoise that would then be consumed by the attacking predator. We also used year (2020 vs. 2021) as a strata variable to account for differences in predator activity or abundance from year to year**.** We built a model set for all predator species combined, as well as separate model sets for ravens and coyotes. To build the model sets for separate predator species, we censored attacks by the opposite predator to remove that tortoise model as a potential "prey item" for the focal predator. We built univariate models for tortoise model size, distance from the powerline, and season, as well as an additive model for tortoise model size and distance, an additive model for tortoise model size, distance, and season, and an interactive model of tortoise model size and distance. We then used AICc to evaluate model fit, selecting models using the "AICmodAvg" package for any models within two ΔAICc (ΔAICc < 2.0), in R (v. 4.1.0) to account for uncertainty in model selection (Mazerolle 2020).

Results

Over the course of 22 trials (14 Spring, 8 Fall), we monitored a total of 396 tortoise model stations. 43 tortoise models were "attacked" over the course of our study, 16 (37.2% of attacks, six in 2020, 10 in 2021) were by ravens, while the remaining 27

(62.8%, 15 in 2020, 12 in 2021) were by coyotes. The overall survival rate for tortoise models during trials (14 days) ranged from 0.82 in Spring 2020 to 0.97 in Fall 2021 (Table 3.1). Several non-subsidized predator species of desert tortoises were observed on camera over the course of the study, including kit foxes (*Vulpes macrotis*), badgers (*Taxidea taxus*), bobcats (*Lynx rufus*), and red-tailed hawks (*Buteo jamaicensis*). None of these animals exhibited any predatory interest toward the models. However, kit foxes often marked the tortoise model with urine or feces.

When considering attacks by both coyotes and ravens combined, our best fitting model was the null model, gaining 0.37 of the AICc weight (Table 3.2), indicating that there was no significant effect of tortoise model size, distance from the powerline, or season on the survival of tortoise models. Our best fitting model for raven-specific predation included season as its only covariate, gaining 0.5 of the AICc weight (Table 3.2). There was no significant difference between spring and fall ($\beta = 1.42$, 95% CI: -0.06, 2.90; Figure 3.4). Though the difference was insignificant, the hazard ratio for spring was 4.14 (95% CI: 0.94, 18.22), indicating an increase in risk of mortality from ravens of 414% in spring raven nesting season relative to fall non-nesting season. Our best fitting model for coyote predation was the null model, gaining 0.35 of the AICc weight (Table 3.2). There was no significant effect of tortoise model size, distance from the powerline, or season on the survival of tortoise models from coyotes (Figure 3.5).

Discussion

Increased predation by subsidized predators represents a significant obstacle in desert tortoise recovery, as it inhibits population persistence through the loss of juvenile recruitment (Boarman 2003, USFWS 2011). We aimed to quantify the risk of predation from ravens and coyotes to juvenile desert tortoises and examine how that risk varies based on tortoise size, distance from potential raven nesting platforms (powerline towers), and season to inform future desert tortoise conservation efforts. Survival of tortoise models – when considering attacks from both coyotes and ravens combined— was not driven by any of the factors we considered. We observed a total of 43 attacks on tortoise models over the course of this study. The overall low visitation rate by predators may have masked any patterns of predation risk when considering both predator species combined. Additionally, patterns may have been masked due to the differences in raven and coyote foraging strategies, as ravens are flighted, diurnal, visual predators, while coyotes are terrestrial, hunt during the day and night, and rely on olfaction in addition to visual acuity to hunt (Boarman 2003, Wells 1978, Grinder and Krausman 2001). Additionally, fluctuations in the populations of primary prey items of coyotes, such as jackrabbits (*Lepus californicus*) over the course of the study, may have led to variation in attack rates on tortoise models.

Risk to predation by ravens was not significantly different between spring and fall. This is surprising given raven nesting and foraging behavior. Each spring, breeding ravens select nesting sites, and spend their time hunting near their nest to feed offspring (Sherman 1993). Previous studies have shown that predation risk from ravens then decreases as juveniles fledge and adults move away from nesting territories (Stiehl 1985). In the fall, ravens often join larger flocks and will move away from nesting areas to more productive feeding areas (Boarman et al. 2006). In our study area in the Ivanpah Valley, ravens are observed occasionally traveling across our study area after the nesting season but most do not remain residents in the fall but instead appear to migrate to other areas in the Mojave Desert, where both adult and juvenile ravens gather at human-made subsidies to forage during the fall (Boarman et al. 2006, pers. obs.).

Similar to the lack of significant difference between predation risk from ravens in the spring and fall, neither the size of the tortoise models nor the distance of tortoise model from powerlines influenced risk of raven attack in our study, despite our initial predictions. Previous research has demonstrated that tortoise size is a driving factor in post-release mortality, and that desert tortoises under 90 mm in carapace length are vulnerable to raven predation (Nagy et al. 2015b, McGovern et al. 2020). Although size was not a significant predictor of raven attacks on tortoise models in our study, half of the attacks were on the smallest models (75 mm) compared to only 25% on each of the larger sized models (100 and 125 mm). Thus, the size of the models that experienced greatest risk of raven attack was the only size of model smaller than the 90 mm threshold reported for raven predation on wild juvenile desert tortoises. The distance at which the tortoise model was located from powerlines also was not a significant driver of survival of tortoise models from raven predation, at least over the range of distances we tested. While the majority of the raven attacks on tortoise models occurred at 250 m (5 of 16 attacks) and 750 m (7 of 16 attacks), we observed raven attacks on models placed as far as 1250 m from the powerline (4 of 16 attacks). Daly et al. (2019) reported increased predation risk by ravens to released head-started tortoises extending out as far as 1600 m from raven nesting sites. In the current study, we intentionally selected station locations < 1600 m from the powerline in an attempt to refine the distance at which predation risk by ravens extends from the powerlines towers where they often nest. Although we observed a low attack rate on models and thus obtained a small sample size, our results suggest that predation risk by ravens extends beyond 1250 m and may indeed extend as far as reported by Daly et al. (2019).

Over the course of this study, we observed only 16 attacks on our tortoise models from ravens. The low attack rates by ravens may have been driven by two factors. First, though curious and intelligent (Merrell 2012), ravens are visual predators (Conover et al. 2010) and because the tortoise models did not move, ravens may not have been enticed to visit the tortoise models or did not return after learning the tortoise models were not a potential prey item. Second, while raven numbers are increasing across the Mojave Desert, the eastern region of Mojave Desert, where our study was conducted, has not experienced the dramatic increases in raven density and abundance like that of the western Mojave Desert (Boarman and Kristan 2006). The western region has been subject to more human development than the east Mojave, resulting in earlier colonization and growth of raven populations (Boarman 2003, Boarman and Kristan 2006). Additionally, the east Mojave, where our study took place, does not have the same anthropogenic subsidies to support high densities of ravens year-round, which may have led to the low attack rates by ravens. Camera trials conducted in areas of greater raven abundance might reveal a clearer understanding of the patterns of predation risk to juvenile Mojave desert tortoises.

Risk to predation of tortoise models by coyotes was not driven by tortoise size, distance from powerline, or season of year. Coyotes have been shown to exhibit temporal variation in landscape presence in other studies, with pup dispersal in fall potentially altering predation risk on the landscape (McClure 1993) though we did not observe temporal variation in coyote predation risk in this study. Additionally, although tortoise size can influence survival of juvenile desert tortoises (Nagy et al. 2015b, McGovern et al. 2020), even the largest of the tortoise models we tested (125 mm) are within the size of tortoises vulnerable to coyote predation (Woodbury and Hardy 1948, McGovern et al. 2020, Candal 2021, Chapter 2). Distance from the powerline was also not a significant predictor of risk to coyote predation. Intuitively, the powerline towers do not offer coyotes the same resource subsidy they offer ravens, however, they do use the service roads located near or underneath powerline towers for travel efficiency (Grubbs and Krausman 2009), and if the road along our powerline towers were more heavily trafficked, there may be roadkill that could serve as a food subsidy. Coyotes are highly mobile, can have extensive territories up to >100 km^2 in the Southwest United States, and are able to cover >6 km in one night (Grinder and Krausman 2001). Though coyotes frequently use roads or other linear pathways for travel or to forage on roadkill (Grubbs and Krausman 2009, Esque et al. 2010), our tortoise models sat 250 m from the road, and with no olfactory attractants to lure coyotes off the pathway, this likely led to the lack of effect of distance from the powerlines.

Though our tortoise models were not scented to provide olfactory cues to mammalian predators like coyotes, we observed more attacks on tortoise models by coyotes than ravens (27 vs. 16 attacks). The results of our camera trials largely mirror findings from radio-telemetry monitoring of head-started desert tortoises released in the same general area, with greater predation by coyotes than ravens (McGovern et al. 2020, Candal et al 2021, Chapter 2). Coyotes, like ravens, are primarily visual predators but also depend on their keen sense of smell while foraging (Wells 1978). Future studies that include tortoise-scented models may lead to increased visitation and attack frequency, helping elucidate the factors that influence risk of predation by coyotes to juvenile desert tortoises.

Several studies have used animal models to examine predator behavior or estimate risk of predation to live animals. For example, Tetzlaff et al. (2020) examined risk of predation in eastern box turtles (*Terrapene carolina*) using 3D models, finding that raccoons (*Procyon lotor*) were the primary predator, and that predation risk was most influenced by habitat type. Recently, 3D models of animals have been employed to train potential predators to avoid focal species of interest to aid in conservation efforts. Prior to the reintroduction of the endangered Southern Corroboree frog (*Pseudophryne corroboree*; Umbers et al. (2020) conducted serial deployments of 3D clay frog models and found that the number of attacks between model deployments decreased, thereby teaching predators that the 3D models, and potentially the live frogs, are not a viable food source. Additionally, tortoise models like the ones used in our study, are being used in combination with avian irritants to deter raven predation (Hardshell Labs, Inc. Joshua Tree, CA; Peebles and Spencer, 2020). Thus, the use of tortoise models are potentially useful conservation tools in both their utility in examining factors that influence predation risk and their role actively reducing landscape-scale predation risk to juvenile desert tortoises through aversive training of subsidized predators such as ravens or coyotes

Conclusions

Subsidized predators, such as common ravens and coyotes, represent a growing challenge for desert tortoise conservation (USFWS 2011) and can critically impair recovery efforts of threatened species (Smith and Quin 1996, Boarman 2003, O’Neil et al. 2018, Loehr and Keswick 2021). Predation risk to juvenile desert tortoises is increasing due to elevated densities of predators that have taken advantage of human-made subsidies, and can lead to a loss of juvenile recruitment of desert tortoises (Boarman 2003). Our data supports previous findings that predation risk from common ravens decreases in the fall (Stiehl 1985, Daly et al. 2019), and we continue to recommend fall releases for head-started or translocated juvenile tortoises to reduce mortality. Future research should continue to examine how predation risk varies over spatial scales and the influence of human subsidies on predation of juvenile tortoises, in addition to examining using 3D-printed models, such as tortoise models as a potential tool for predator avoidance. However, reducing access to human-made subsidies, as well as coordinated, informed, and humane predator control may be the only way to effectively reduce spillover predation on juvenile desert tortoises (Goodrich and Buskirk 1995, Shields et al. 2019) and limit further population declines and global biodiversity loss.

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Tables

Table 3.1. Summary of survival rates for tortoise models over 14-day trials examining risk to predation by common ravens (*Corvus corax*) and coyotes (*Canis latrans*) on Mojave desert tortoises (*Gopherus agassizii*) conducted in spring and fall of 2020 and 2021 on Mojave National Preserve, California, USA

		Model Survival			
		2020		2021	
		Survival	95% CI	Survival	95% CI
Spring	Overall	0.92	0.88 – 0.97	0.86	0.80 – 0.92
	Ravens	0.96	0.93 – 1.0	0.93	0.88 – 0.97
	Coyote	0.96	0.93 – 1.0	0.93	0.88 – 0.97
Fall	Overall	0.82	0.74 – 0.91	0.97	0.94 – 1.0
	Ravens	0.99	0.96 – 1.0	0.99	0.96 – 1.0
	Coyotes	0.83	0.75 – 0.92	0.99	0.96 – 1.0

Table 3.2. Model AICc values used for survival tortoise models during 14-day trials conducted during Spring and Fall of 2020 and 2021 on Mojave National Preserve, California, USA. **Bold** is the top model of each set.

	Survival Models	AICc	ΔAICc	Cumulative Weight
Overall	**Null**	**450.15**	**0**	**0.37**
	Size	451.17	1.02	0.59
	Season	452.1	1.96	0.72
	Dist.	452.16	2.01	0.86
	Size+Dist.	453.19	3.04	0.94
	Size*Dist.	455	4.85	0.97
	Season+Size+Dist.	455.16	5.02	1
Ravens	**Season**	**164.95**	**0**	**0.5**
	Season+Size+Dist.	167.28	2.33	0.65
	Null	167.85	2.9	0.77
	Size	168.25	3.31	0.86
	Size*Dist.	169.34	4.39	0.92
	Dist.	169.75	4.8	0.96
	Size+Dist.	170.17	5.22	1
Coyotes	**Null**	**282.5**	**0**	**0.35**
	Season	282.91	0.41	0.63
	Size	284.43	1.93	0.76
	Dist.	284.47	1.97	0.89
	Size+Dist.	286.41	3.91	0.94
	Season+Size+Dist.	286.84	4.34	0.98
	Size*Dist.	288.09	5.59	1

Figures

Figure 3.1. The three sizes of tortoise models: 75 mm, 100 mm, and 125 mm MCL, from left to right used to examine risk to predation by common ravens (*Corvus corax*) and coyotes (*Canis latrans*) on Mojave desert tortoises (*Gopherus agassizii*) during spring and fall 2020, and spring and fall 2021 in Mojave National Preserve, California, USA.

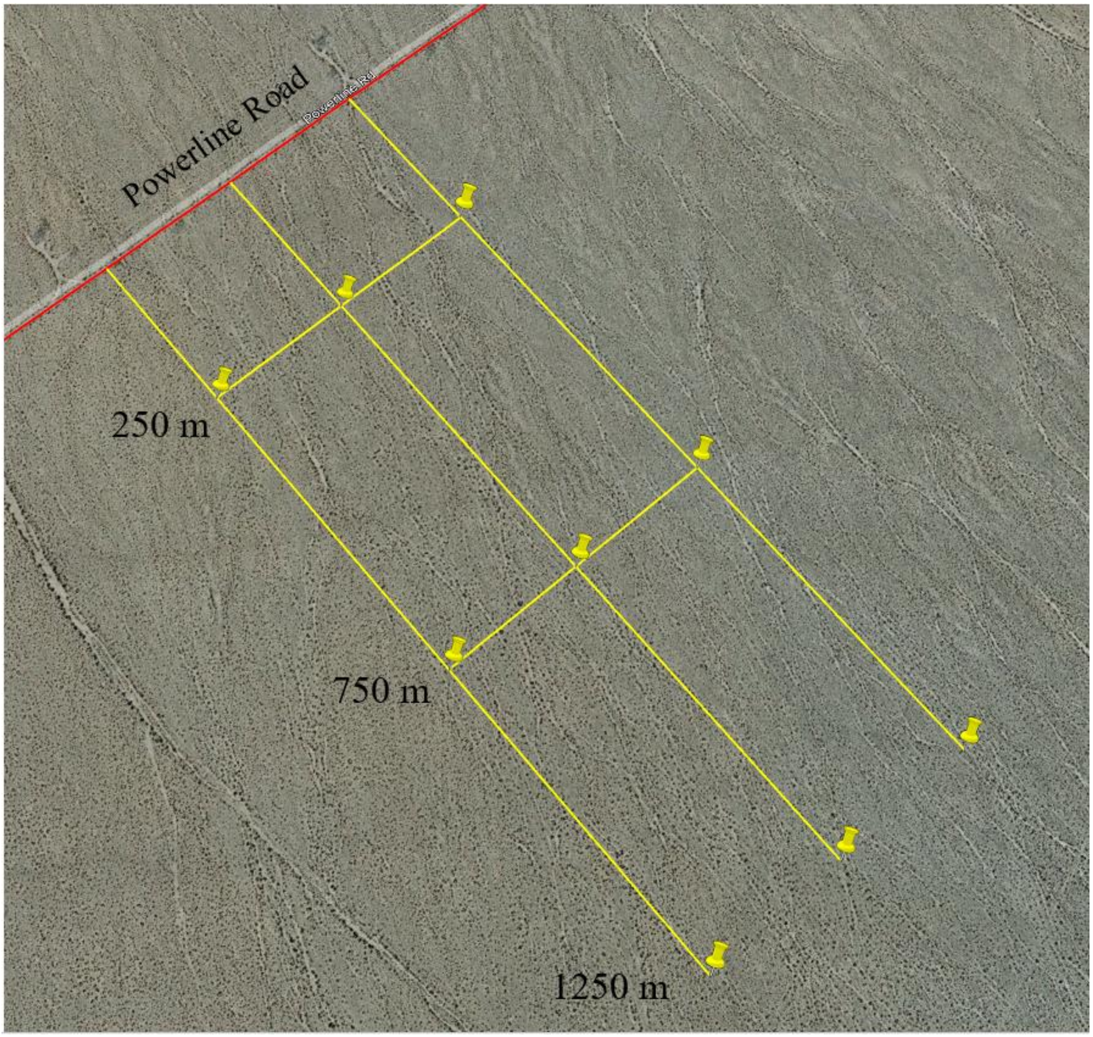

Figure 3.2. Map of one array showing the 10 stations of each camera, with 3-D tortoise models placed at three different distances from the powerline for 14-day trials examining risk to predation by common ravens (*Corvus corax*) and coyotes (*Canis latrans*) on Mojave desert tortoises (*Gopherus agassizii*) conducted in spring and fall of 2020 and 2021 on Mojave National Preserve, California, USA. The powerline road is displayed in red.

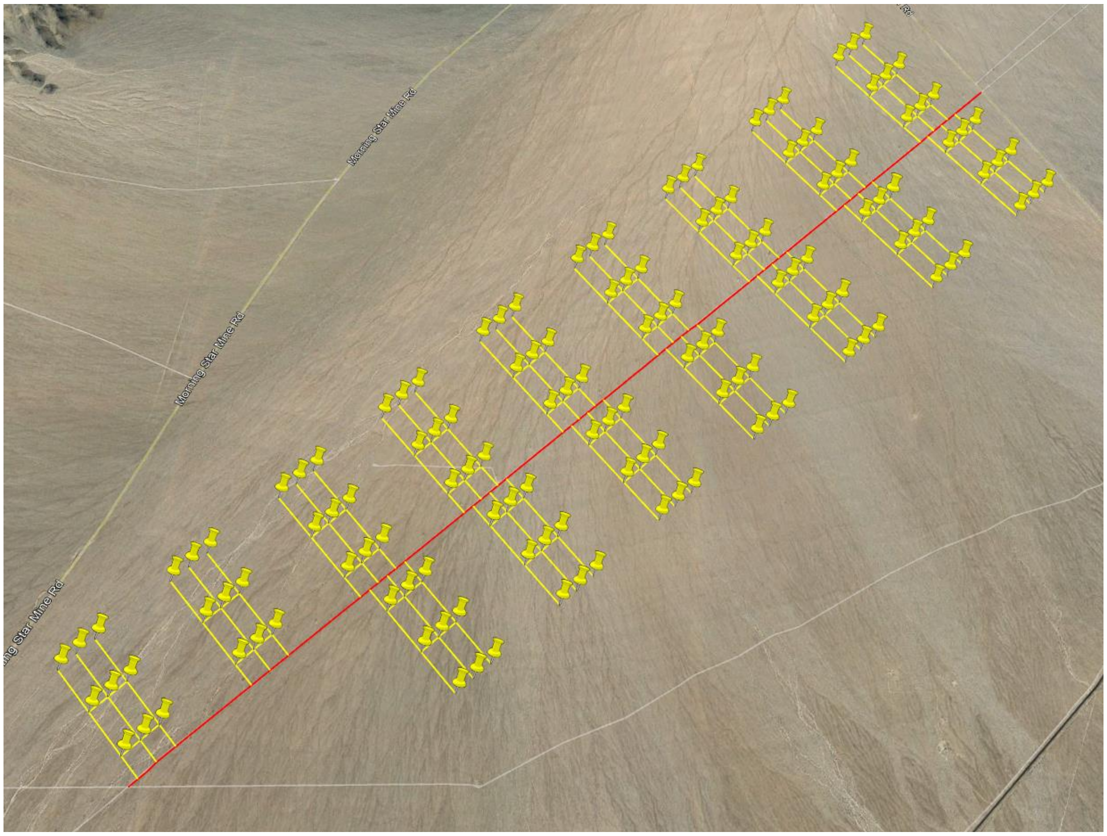

Figure 3.3. The 10 km stretch of power line within our study area, with all 16 array stations shown, used for 14-day trials examining risk to predation by common ravens (*Corvus corax*) and coyotes (*Canis latrans*) on Mojave desert tortoises (*Gopherus agassizii*) conducted in spring and fall of 2020 and 2021 on Mojave National Preserve, California, USA. The powerline road is displayed in red.

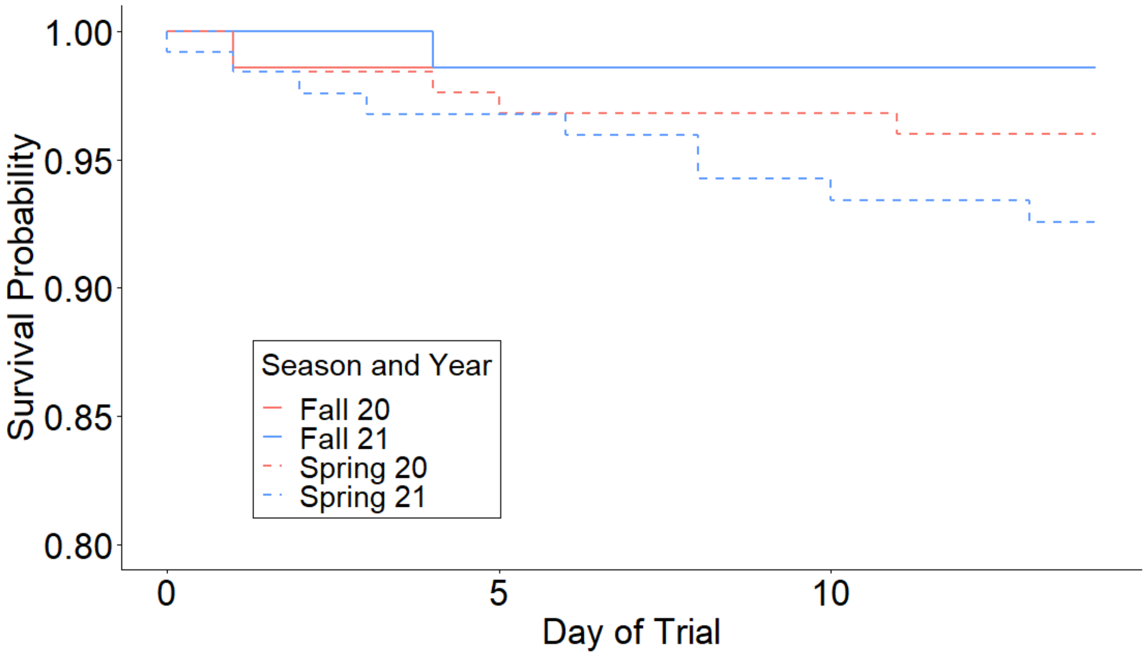

Figure 3.4. Cox survival curve for tortoise models on Mojave National Preserve, California, USA attacked by common ravens (*Corvus corax*) during 14-day trials examining predation risk by common ravens on Mojave desert tortoises (*Gopherus agassizii*). There was no significant difference between seasons (p>0.05).

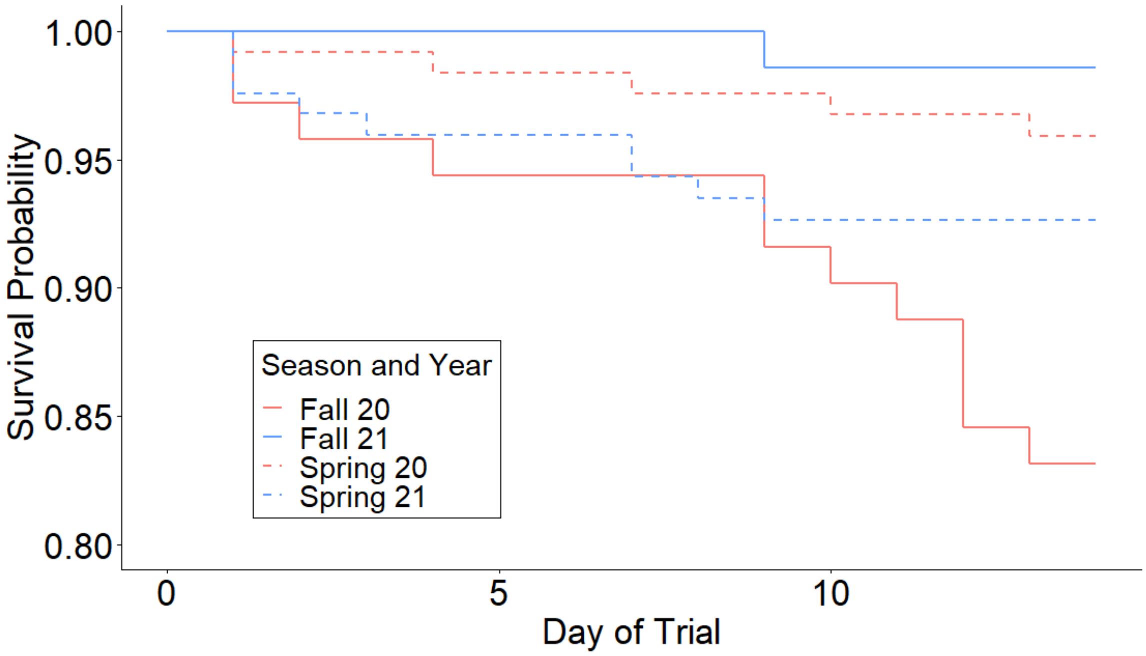

Figure 3.5. Cox survival curve for tortoise models on Mojave National Preserve, California, USA attacked by coyotes (*Canis latrans*) during 14-day trials examining predation risk by coyotes on Mojave desert tortoises (*Gopherus agassizii*). There was no significant difference between seasons (p>0.05).

CHAPTER 4

SUMMARY AND CONCLUSIONS

Desert tortoises, like many turtle and tortoise species around the world, are declining and have been subject to extensive conservation and recovery actions (Gibbons et al. 2000, USFWS 2011, Stanford et al. 2020). My thesis research informs desert tortoise recovery through the evaluation of head-starting as a population management tool and by examining the risk to juvenile tortoises to predation by subsidized predators. Recent efforts have demonstrated that head-starting is a promising recovery tool with released juveniles capable of experiencing high survival during their first year following release (McGovern et al. 2020). Desert tortoises, however, are long-lived and slow to mature, which has limited our knowledge of tortoise movement and survival during the long and vulnerable juvenile stage, ultimately hindering any evaluation of longer-term success of head-starting efforts. We monitored post-release space use and survival of head-started tortoises reared under three different head-starting protocols for up to three years following release. Additionally, as subsidized predators continue to threaten desert tortoise recovery actions including head-starting (Boarman 2003, USFWS 2011, Harju et al. 2022), research is needed to examine spatial and temporal trends in predation risk from subsidized predators. To address this need, we quantified predation risk over a spatial gradient from human infrastructure and quantified how predation risk varies based on season. By determining risk to predation from subsidized predators, we can then inform head-starting and release protocols, and incorporate head-starting and predator research with other recovery actions to maximize conservation success (Spencer et al. 2017).

In Chapter 2, we examined differences in settling time, space use, site fidelity, and survival among three head-start treatment groups. We also examined how these metrics change over time since release. We found that tortoises from all treatment groups settled shortly following release (i.e., within 10 days), with Outdoor tortoises settling slightly earlier. Tortoises across all three treatment groups decreased their space-use over time since release and also exhibited high site fidelity between years, with most individuals shifting their annual home range centers ≤100 m from year to year. The Six+ tortoises had the largest annual home ranges and exhibited the lowest site fidelity of the three treatments. Survival did not vary significantly among the treatment groups, however, Combo and Six+ tortoises, the largest two treatment groups, did have ~20% greater annual survival during 2021, when there was a severe spring and summer drought. Similar to McGovern et al. (2020) and Candal (2021), we found that Combo-reared tortoises experienced comparable survival rates as the older but same-sized Six+ group and exhibited similar space use as the same-aged but smaller Outdoor tortoises for up to three years post-release. Thus, our results provide further evidence that combo-rearing method is an both an efficient and efficacious method of producing head-started tortoises.

In Chapter 3, we examined the factors that influence predation risk to juvenile tortoises by subsidized predators, using 3D models of tortoises as a proxy for live juvenile tortoises. In our study area, as well as across the Mojave Desert, subsidized ravens and coyotes represent a major hurdle for desert tortoise recovery, due to their negative impact on juvenile recruitment of both head-started and wild juveniles (USFWS 2011, Daly et al. 2019). When considering both coyote and raven attacks combined, we did not observe any difference in predation risk based on model size, distance from the powerline towers and associated service road, or season. We did observe a difference in predation risk by ravens based on season, with higher risk of predation occurring in the spring (i.e., raven nesting season) compared to the fall (non-nesting season). These results provide further support for conducting releases of juvenile tortoises in the fall to avoid increased predation risk from nesting ravens (Daly et al. 2019). However, the lack of an effect of distance from powerline on predation risk suggests that juvenile tortoises are at equal risk of predation over the distances we tested (250 – 1250 m), corroborating a previous study that showed that the risk of predation by ravens on head-started desert tortoises extended up to 1600 m from powerlines (Daly et al. 2019). Additionally, all sizes of tortoise models in our study incurred similar risk of predation. Post-release survival of juvenile desert tortoises has previously been shown to be positively correlated with size at release, with tortoises ≤90 MCL being vulnerable to ravens, although coyotes were able to predate larger tortoises (McGovern 2020). More recently, coyotes have become the primary predator of released head-starts, likely due to a combination of our efforts to minimize raven predation by releasing tortoises further from potential nesting structures and due to raven mitigation being conducted by management agencies at our release site. Further research is needed to determine the best way to minimize predation by coyotes on head-started desert tortoises. Better information on densities and population trends of subsidized predators could help inform predator management actions, such as lethal removal or predator aversion tactics, and guide timing and location of future releases of head-started tortoises.

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