

FIRE EFFECTS ON SMALL MAMMALS: IMPLICATIONS AND SOLUTIONS  
FOR ENDANGERED MT. GRHAM RED SQUIRRELS

by

Marina Morandini

---

Copyright © Marina Morandini 2022

A Dissertation Submitted to the Faculty of The  
SCHOOL OF NATURAL RESOURCES AND THE ENVIRONMENT

In Partial Fulfillment of the Requirements

For the Degree of

DOCTOR OF PHILOSOPHY  
WILDLIFE CONSERVATION & MANAGEMENT

In the Graduate College  
THE UNIVERSITY OF ARIZONA

2022

THE UNIVERSITY OF ARIZONA  
GRADUATE COLLEGE

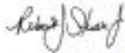
As members of the Dissertation Committee, we certify that we have read the dissertation prepared by: Marina Morandini  
titled: Fire effects on small mammals: implications and solutions for endangered Mt. Graham red squirrels

and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy.



John Koprowski

Date: Aug 10, 2022



Robert Steidl

Date: Aug 10, 2022

*R. William Mannan*

R. William Mannan

Date: Aug 12, 2022



Lucas Wauters

Date: Aug 12, 2022

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

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



John Koprowski  
School of Natural Resources & the Environment

Date: Aug 10, 2022

## **Acknowledgments**

Nature have always been inspiring to me and leaves me with questions and an open mind. I always felt peaceful and happy being in nature and especially observing mammals. For a long time, I thought only being a vet would allow me to work with animals, but as soon as I discovered the profession of a wildlife conservationist, I decided that this was my dream job. I want to make an impact helping to conserve endangered species, and not just aiding individuals. As a wildlife conservationist I am able to fully realize my passion, being surrounded by nature which is close to my heart while making a difference in the world and helping whole species that are endanger from various threats. Very few people in the world are able to discover fully what their calling in life is, much less it be something that aligns with their passions. I found both.

John L. Koprowski allowed me to start this journey and welcomed me in the Conservation Research Laboratory of University of Arizona. I want to thank Prof. John Koprowski for the constant financial and academic support during this long journey and for teaching me that catastrophic events can be seen as opportunity. After the Frye Fire, which destroyed all of the study area and my entire first project, John taught me to look at the picture from different perspective and see how science does not stop despite various types of changes, positive or negative. Sincere thanks go to the graduate committee members Bill Mannan, Robert Steidl, and Lucas Wauters, who provided wisdom throughout my journey. Robert Steidl always has provided insightfulness to the statistical analysis, and Lucas never turned down any meeting despite being from Italy frequently had been on evening time. I also need to give a special thanks to Javan Bauder, who immensely helped me with the analysis of the last chapter and taught me great basis of movement analysis. Javan's generosity with his time, advice, and repartee has been invaluable.

I would also like to thank all of the Koprowski Conservation Research Laboratory members for the continuous support during this journey. Fieldwork tasks could not have been completed without the ever willing and resourceful Melissa Merrick and Vicki Greer. We would like to thank the Mt. Graham Red Squirrel Research Program graduate and undergraduate research assistants for valuable help in the field. Data collection across Arizona's wild mountains would not have been possible without research assistants Adelyne Blanchette, Jeff Dolphin, Meagan Bethel, Alexis Blair, Elizabeth Grube, Anne-Laure Blanche, Kelsi Thacker, Britt Dobroslavic, Kacy Jo

Lewis, Helena Yomantas, Samantha Johnson, Alexis Culbertson, Ruby Meyer, Lucero Anais Barraza, Camille McCollum. All lab colleagues provided inspiration along the way, my sincere thanks to: Brian Blais (especially for the numerous brain storming lunches), Alexandra Burnett (for all the nice work done side by side at the Green Valley experimental range), Colin Brocka, Neil Dutt, Kira Hefty, Shambhu Praudel, Amanda Veals, Mauro Vela Vargas, and Stuart Wells. Thanks also for the support of many friends and roommates, Travis Mattson, Saverio Cambioni, Ali Hassani, Artin Majdi. A special thanks for Maria Vittoria Mazzamuto, who initially supported me in the decision of accepting this position, and she has always provided great advice and a friendship that will last forever.

Logistics and field support by Arizona Game and Fish, especially by Ronald Logan who always made sure I was safe at the end of the long fieldwork day and numerous time he helped me with logistics. We thank the agency partner Arizona Game and Fish Department and the University of Arizona School of Natural Resources and the Environment. This research was supported by grants to JLK from the University of Arizona, Arizona Game and Fish Department (grants no. I18005 and I16002), and T & E Inc. Grants for Conservation Biology.

I could not have reached this stage without the love and support of my parents, my sisters, my grandparents, and I thank them for having faith in me. In the past two years I have been blessed meeting my husband William, who never stopped supporting, encouraging me and believing in me.

## **Dedication**

“Ai miei genitori che mi hanno sempre incoraggiato a seguire i miei sogni,  
in particolare a mio padre che mi ha insegnato ad amare la natura e gli animali.”

“To my parents, who always encourage me to follow my dream,  
in particular my dad who taught me the love for nature and for animals.”

# Table of contents

List of figures .....	8
List of tables .....	10
Abstract .....	12
Introduction .....	13
Present study .....	16
References .....	17
<b>Appendix A: Foraging behavior, response of small mammals to different burn severities .....</b>	<b>21</b>
Abstract.....	21
Introduction .....	23
Material and method.....	25
Results.....	28
Discussion .....	29
Acknowledgment.....	32
References .....	33
<b>Appendix B: Using a substitute species to inform translocation of an endangered territorial mammal</b>	<b>46</b>
Abstract.....	46
Introduction .....	47
Methods and study area .....	49
Results.....	52
Discussion .....	54
Acknowledgments .....	61
References .....	62
<b>Appendix C: Post-translocation movements and the important of conspecific distribution to settlement site selection in a territorial species .....</b>	<b>73</b>
Abstract.....	73
Introduction .....	75
Materials and methods.....	77

Results..... 83  
Discussion ..... 85  
Acknowledgments ..... 90  
Supplemental material ..... 109

## List of figures

- Figure 1.1: Grams of sunflower seeds collected from the trays (therefore non-eaten by animals = high GUD) in the 3 burn severity patches (CB=completely burned, PB= partially burned, NB=non-burned). ..... 37
- Figure 1.2: The PCA transformation of the vegetation characteristics at burned severity patches, explained 78% of the variation in the first 3 PCs. The first PC emphasized the change from more open areas of dead or dying trees to healthy small and large trees, with higher canopy cover. The second PC emphasized the change from numerous logs and less grass cover to less volume of logs and higher grass cover..... 38
- Figure 1.3: Box plot of the number of species of vertebrates detected in each tray per burn severity (CB=completely burned, PB= partially burned, NB=non-burned)..... 39
- Figure 1.4: Species composition in each patch type, characterized by different burn severity (NB= non burned, PB= partial burned, CB= complete burned)..... 40
- Figure 1.5: Percentage of presence of each species (Abert's squirrel - *Sciurus aberti*, cliff chipmunk - *Tamias dorsalis*, Mt Graham red squirrel - *Tamiasciurus fremonti grahamensis*, mouse - *Peromyscus sp.*, Mexican woodrat - *Neotoma mexicana*, rock squirrel - *Otospermophilus variegatus*, long-tailed vole - *Microtus longicaudus*) at the 3 different burn severity patches (Complete, partial and non-burned)..... 41
- Figure 2.1: Number of red squirrels *Tamiasciurus fremonti fremonti* per different fate by sex and season (winter and fall), after translocation. The different fate has been identified as dead, establish (settled in a new area, different from the original home range), missing (when the animals was not trackable by telemetry and not possible to locate again), home (animals able to homing after being translocated)..... 66
- Figure 2.2: Cox Model survival curve of red squirrels *Tamiasciurus fremonti fremonti* after translocation, from the first day of release until 60 days after the release (usually corresponding also to the end of the field season). On the x-axis is represented the time in days after translocation, while on the y-axis is represented the survival probability, starting as 1 the day of the animal release and decreasing until just below 0.5 after 40 days..... 67
- Figure 2.3: In blue the variation in body mass of translocated red squirrels *Tamiasciurus fremonti fremonti* (N=10), expressed as percentage of body mass change after translocation in respect to the weight at release. In red the variation in body mass of non-translocated animals (N=9), expressed as percentage of body mass change between two trapping sections in respect to the weight of the first trapping event (as a control group)..... 68
- Figure 2.4: Plot of mean, sd, minimum and maximum distance of settlement site to release site (Fall: mean 1752, sd 1472, maximum 5162, minimum 233. Winter: mean 364, sd 421, maximum 1494, minimum 0 (one squirrel stayed at the release site), and number of days passed before

squirrel (*Tamiasciurus fremonti fremonti*) settled (Fall: mean 23, sd 13.6, maximum 57, minimum 8. Winter: mean 6, sd 2.45, maximum 11, minimum 3). ..... 69

Figure 3.1: Distance (m) from the release point as a function of days post-release for translocated red squirrel (*Tamiasciurus fremonti fremonti*) in the White Mountains, Arizona, USA, from 2018 to 2020. The orange dots represent the telemetry points while the animals were dispersing after translocation, while the blue dots are the telemetry points when the animals settled. .... 97

Figure 3.2: Use of habitat features during different behaviors (Foraging, resting, traveling) by translocated squirrels (*Tamiasciurus fremonti fremonti*) during dispersal after translocation in the White Mountains, Arizona, USA, from 2018 to 2020 ..... 98

Figure 3.3: Distributions of distance moved (locations separated by < 24 hours) or movement rates (locations separated by ≥24 hours) between telemetry locations during exploratory and settlement behavioral phases for translocated red squirrel (*Tamiasciurus fremonti fremonti*) in the White Mountains, Arizona, USA, from 2018 to 2020. Curves were estimated using generalized Pareto distributions. .... 99

Figure 3.4: Model support (AICc weight) across spatial scales testing for selection of environmental features by translocated red squirrel (*Tamiasciurus fremonti fremonti*) in the White Mountains, Arizona, USA, from 2018 to 2020, during the exploratory phase of post-release dispersal ..... 100

Figure 3.5: Model support (AICc weight) across spatial scales testing for differences in environmental covariates between red squirrel (*Tamiasciurus fremonti fremonti*) settlement locations (n = 12) and 5000 random available points in the White Mountains, Arizona, USA; and model support (AICc weight) across spatial scales testing for differences in mean distance among middens and midden density (middens /area of buffer) between red squirrel (*Tamiasciurus fremonti fremonti*) settlement locations (n = 12) and 83 ground-based random points from within forest habitat in the White Mountains, Arizona, USA ..... 101

Figure 3.6: Plots of principal components analyses versus environmental features (with the best supported spatial scale) used in describing settlement point selection by translocated red squirrel (*Tamiasciurus fremonti fremonti*) in the White Mountains, Arizona, USA, from 2018 to 2020. .... 102

Figure 3.7: Boxplot of settlement site, original midden, and release site characteristics (PC1, PC3, and number of middens) used by red squirrel (*Tamiasciurus fremonti fremonti*) during different phases of translocation in the White Mountains, Arizona, USA, from 2018 to 2020. .... 103

Figure 3.8: Distance (m) from the release point as a function of days post-release for translocated red squirrel (*Tamiasciurus fremonti fremonti*) in the White Mountains, Arizona, USA, from 2018 to 2020, that dies or went missing after translocation, but before settlement behavior was observed. .... 109

## List of tables

Table 1.1: Results of generalized linear mixed model (Binomial distribution, logit link), examining the effect of burn severity, year, and total volume of logs on the GUD (grams of seeds left at the tray). Area was entered as a random effect in the model .....	42
Table 1.2: Results of linear mixed model (Gaussian distribution, identity link), examining the effect of burn severity, year, and total volume of logs on the GUD (grams of seeds left at the tray). Area was entered as a random effect in model. ....	43
Table 1.3: Results of linear mixed models, examining the effect of vegetation characteristics on the GUD (grams of seeds left at the tray) in different burned severity patches. Area was entered as a random effect in the model .....	44
Table 1.4: Number of trays where each species has been detected during the experiment (60 trays for 3 rounds) and percentage of each species detected over the total amount of trays during the entire experiment (180 trays). ....	45
Table 2.1: Total number of red squirrels, <i>Tamiasciurus fremonti fremonti</i> translocated in the White Mountains (Arizona, USA) from 2018 to 2020, by sex, season (fall and winter), and translocation type (soft and hard) .....	70
Table 2.2: Estimate regression parameters, standard errors, z values and P values for the generalized linear to examine the effect of season (fall or winter), type of release, and body mass on two response variables: time to settlement (d) and distance to settlement (m) from release site. ....	71
Table 3.1 Results of generalized mixed models with gaussian distribution and identity link, to understand the effect of sex, days from the release event, settlement, and number of telemetry points respectively on daily distance (m/day), speed (m/h), and turning angle of translocated animals on the White Mountains, AZ, USA, from 2018 to 2020. Animal ID has been included as random effect for each model. ....	104
Table 3.2: The two models selected with AICc to explain point selection by translocated red squirrel ( <i>Tamiasciurus fremonti fremonti</i> ) in the White Mountains, Arizona, USA. We measured availability using empirically derived generalized Pareto distribution (GPD) kernels centered on telemetry locations. PSF has been fitted using Cox proportional hazard regression model with the coxph function of the survival package. ....	105
Table 3.3: Results of principal components analyses describing variation in environmental features used in describing settlement point selection by translocated red squirrel ( <i>Tamiasciurus fremonti fremonti</i> ) in the White Mountains, Arizona, USA, between 2018 and 2020. Distance values represent the best supported spatial scale (i.e., buffer radius) for each covariate. ....	106
Table 3.4: The two models selected to explain settlement selection by translocated red squirrel ( <i>Tamiasciurus fremonti fremonti</i> ) in the White Mountains, Arizona, USA. The models are	

generalized linear model, with binomial family and logit link. The variables in the model are for the first model PC1 and PC3, while for the second model PC1, PC3, and PC2. .... 107

Table 3.5: model selected to explain settlement selection by translocated red squirrel (*Tamiasciurus fremonti fremonti*) in the White Mountains, Arizona, USA, when density of red squirrel residents is included. The model is a generalized linear model, with binomial family and logit link. The variables in the model are PC1, PC3 and local density around a buffer of 100m from the settlement or random point. .... 108

Table 3.6: Comparisons of spatial scales (canopy cover, tree height, slope, TPI, TRASP) during exploratory movements, testing for differences in environmental covariates between red squirrel (*Tamiasciurus fremonti fremonti*) telemetry locations and the average covariate value within a specific buffer in the White Mountains, Arizona, USA. Models were ranked using Akaike’s Information Criterion adjusted for small sample sizes (AICc) and w is AICc model weight. .... 109

Table 3.7: Rankings of candidate models for point selection functions by translocated red squirrel (*Tamiasciurus fremonti fremonti*) in the White Mountains, Arizona, from 2018 to 2020, USA during exploratory movements. Covariates include tree height, percent slope, topographic position index (TPI) and topographic radiation aspect index (TRASP). K is the number of model parameters and w is the AICc model weight. .... 110

Table 3.8: Comparisons of spatial scales (canopy cover, tree height, slope, TPI, TRASP) during settlement movements, testing for differences in environmental covariates between red squirrel (*Tamiasciurus fremonti fremonti*) settlement locations (n = 12) and 5000 random available points in the White Mountains, Arizona, USA. Midden density and average midden distance have been instead compared between settlement locations and 43 random available points. Models were ranked using Akaike’s Information Criterion adjusted for small sample sizes (AICc) and w is AICc model weight. .... 114

Table 3.9: Rankings of candidate models for settlement site selection by translocated red squirrels (*Tamiasciurus fremonti fremonti*) in the White Mountains, Arizona, USA, between 2018 and 2020, with available habitat features measured at 5000 random points throughout our study area. Covariates include the first three components of a principal components analysis using GIS-based vegetation and topographic covariates measured at settlement points and random available points. K is the number of model parameters and w is the AICc model weight. .... 117

Table 3.10. Rankings of candidate models for settlement site selection by translocated red squirrel (*Tamiasciurus fremonti fremonti*) in the White Mountains, Arizona, USA, from 2018 to 2020, with available habitat features measured at 43 available points in forested areas throughout our study area. Covariates include the first three components of a principal components analysis using GIS-based vegetation and topographic covariates, mean midden density, and mean inter-midden distance measured at settlement points and available points. K is the number of model parameters and w is the AICc model weight. .... 118

## Abstract

Climate change has already impacted biodiversity worldwide by shaping species habitat range, their survival, resource availability and interactions among species. Climate change is also the cause of more frequent extreme weather events, including wildfires. These cause profound challenges for animals to overcome, especially forest-dwelling mammals, due to reliance on specific vegetation types. We studied the impact on small mammal foraging behavior of Frye Fire that in 2017 burned 20,000 ha and ranged in elevation from 1,219 to above 3,000 m. Different burned severity affects perceived predation risk, reflecting in the amount of time spent foraging by small mammals, where in completely burned patches, small mammals spend less time foraging than partially- and non-burned patches. Fires affect foraging behavior of small mammals but does not impact all species in the same way. Generalists, such as *Peromyscus* sp., seem to forage across all burn severities, while specialist species, such as tree squirrels, including the endangered species Mt Graham red squirrel (*Tamiasciurus fremonti grahamensis*), tend to avoid the completely burned patches. The fire caused a drastic decrease in the abundance and distribution of the endangered Mt Graham red squirrels. This made necessary the need for studying translocation techniques to identify factors that could lead to improving the chances of success by potentially augmenting the population from *ex situ* bred stock. We used a surrogate subspecies, *Tamiasciurus fremonti fremonti* to test different translocation techniques to inform potential management actions on the endangered Mt. Graham red squirrel. We fitted VHF radio collars to 54 animals, and we monitored their survival and movements until individuals settled on a new territory. Survival probability averaged 0.48 after 60 days from the translocation event and was not affected by season or translocation technique; 54% of the mortality was caused by predation. Distance moved and number of days to settlement varied with season, where winter was characterized by shorter distances (average of 364 m in winter versus 1752 m in fall) and a smaller number of days (6 in winter versus 23 in fall). We also analyzed the movement and habitat selection of the animals after translocation. The importance of understanding dispersal behavior in reintroduction biology is well recognized to improve conservation translocations. However, few studies have accounted for differences in behavioral state, even if they can substantially change conclusions on post release habitat selection. Post-release movements of translocated red squirrels represent at least two different behavioral phases characterized by differences in movement patterns and the scale of selection for environmental features. During the first phase (hereafter “exploratory phase”),

squirrels made long rapid movements and selected areas with taller trees and valley bottoms at relatively broad spatial scales (i.e., 500-600 m). In contrast, during the second behavioral phase (hereafter ‘settlement phase’), squirrels appeared to act like resident squirrels by displaying shorter movements within a smaller area, caching food, and defending their middens. Squirrels still selected primarily forested areas in valley bottoms and fewer conspecific middens, but the scale of response was much lower than during the initial phase. Translocated squirrels select areas with fewer conspecifics, highlighting the importance of considering the role of conspecifics, as well as environmental features, also in translocations of solitary species.

## Introduction

Earth is currently in a period of mass global species extinction (Ceballos et al., 2015). Current and projected rates for the extinction of species exceed normal geological background rates by several orders of magnitude (Barnosky et al., 2011; Ceballos, Ehrlich, & Dirzo, 2017). Also species considered at no risk, are experiencing a dramatic loss of their geographic ranges, up to 80% in the period 1900–2015 (Ceballos, Ehrlich, & Dirzo, 2017). The ultimate drivers of this phenomenon are human overpopulation and overconsumption (Ceballos, Ehrlich, & Dirzo, 2017), acting through habitat alteration, climate change, overexploitation, species invasions, along with other lower-ranked threats (Gurevitch & Padilla, 2004; Hoffmann et al., 2010; Maxwell et al., 2016; Ducatez & Shine, 2017). In this context, studying the threats to endangered species can provide science-based information to guide managing actions, and a contribution for ensuring the long-term persistence of endangered species (Wiens & Hobbs, 2015; Scheele et al., 2018).

Climate change has already impacted biodiversity worldwide by shaping species habitat range (Colwell et al., 2008), their survival (Chamailé-Jammes et al., 2006), resource availability (Visser & Both, 2005) and interactions among species (Moritz & Agudo, 2013). Anthropogenic climate change has also already led to more frequent extreme weather events, for example wildfires, floods, tornados (Bouwer, 2019), which can have greater environmental consequences than changes in climate means (Maron et al., 2015; Bailey & Pol, 2016; McKenzie & Littell, 2017). In particular, the increase in magnitude and occurrences of wildfire is quite alarming, considering the profound changes caused by fire in the composition and abundance of plant and animal species (Smucker, Hutto, & Steele, 2005; Lindenmayer et al., 2016; Camargo et al., 2018), as well as animal ecology due to habitat loss and environmental changes (Whelan, 2002; Koprowski et al.,

2006; Engstrom, 2010). Post disturbance impacts often come later in the form of changes to vegetation structure and composition, quantity and distribution of resources, or possible increase of predation (Engstrom, 2010; Lawes et al., 2015). Changes in cover availability can influence predation risk and subsequently alter the behavior, demographics, and growth rates of prey populations. The ability to adapt to those changes is reflected in fitness, and ultimately on the entire population affected by fire (Whelan, 2002; Forsman, 2015).

The post fire landscape offers heterogeneities in hazards and opportunities, with patches characterized by higher concentration of resources, but also patches with high visibility (high predator risk), due to the reduction of canopy cover. Predators do not only influence prey by killing them, but also by creating a landscape of fear that influences activity times, foraging tactics, and microhabitat selection of prey (Cowlshaw, 1997; Schmitz, Beckerman, & O'Brien, 1997). Several studies have investigated the influence of fire and fuel management treatments on small mammal abundance (e.g., (Fisher & Wilkinson, 2005; Converse et al., 2006; Amacher et al., 2008; Lawes et al., 2015; Hutchen et al., 2017). However, research focused on how disturbances affect animal behavior is scarce and the response is not always clear on burned patches (Reed, 1982).

Fires affect greatly isolated populations or populations with small geographic ranges, threatening the potential for recovery (Gerber & Hilborn, 2001). A common technique to mitigate the loss and depletion of endangered species is translocation: the intentional movement of animals for conservation purposes (Blumstein & Fernández-Juricic, 2010; Drake & Temple, 2012; Resende et al., 2020). However, numerous examples worldwide have shown failures for translocation programs across a wide variety of species (Drake and Temple 2012; Nafus et al. 2017). An experimental approach may help identify and mitigate factors that influence the outcome of translocations, which could reduce translocations failures (Bubac et al., 2019). However, such an approach may not be feasible for endangered taxa that ethically should not and legally may not be used for experimentation in the wild (National Research Council, 1995; Gannon & Sikes, 2007). In this context, using ecologically and genetically similar species (i.e., substitute species) to test management strategies is a valuable tool to avoid disturbance of species already facing numerous challenges (Caro, Eadie, & Sih, 2005; Murphy, Weiland, & Cummins, 2011).

Extensive post-release movements after translocations are often the cause for failure (Harrington et al., 2013; Berger-Tal, Blumstein, & Swaisgood, 2020). These movements are energetically

costly and often expose individuals to numerous hazards including increased predation risk, road mortality, and negative intra-specific interactions with resident conspecifics (Linklater & Swaisgood, 2008; Yott et al., 2011). Translocated animals face a unique situation of encountering a completely novel environment (Frair et al., 2007). They will initially explore their surroundings to gain knowledge to survive, usually performing long and linear movements (Berger-Tal & Saltz, 2014). As translocated individuals become more familiar with their environment, individuals will shift their movements from exploratory movements to more localized movements reflecting the spatial distribution of resources and their exploitation (Eliassen et al., 2007; Berger-Ta & Saltz, 2014). This process of shifting behavior over time after translocation has been called post release behavioral modification (PRBM) by Berger-Tal and Saltz (2014).

Post release behavioral modification has implications for understanding post-release habitat selection (Picardi et al., 2022) as different behavioral states may correspond to different resource priorities and scales at which individuals respond to landscape features. Therefore, it is important to consider the different behavioral phases when modeling habitat selection in post-translocated animals (Picardi et al., 2022). Habitat selection is not influenced only by landscape characteristics, but also by the presence of conspecifics. They can attract a disperser, acting as a cue for good habitat quality (Serrano & Tella, 2003; Harrison et al., 2015), or, alternatively, can cause intraspecific competition and prompt some individuals to depart (Dolev et al., 2002). Understanding the role of intra-specific interactions in habitat selection by translocated individuals is important, particularly for territorial species where the presence of resident conspecifics may limit habitat availability (Stamps, 2001; Stamps & Krishnan, 2005).

We use the Frye Fire wildfire that in 2017 burned 20,000 ha and ranged in elevation from 1,219 to above 3,000 m. It impacted the upper elevation spruce-fir forest as well as the lower elevation mixed-conifer forest and strongly altered habitat structure and availability of non-burned habitat patches over most of the mountain. The fire impacted the community of wildlife and vegetation inhabits this sky island and caused a drastic decrease in the abundance and distribution of the endangered Mt Graham red squirrels (*Tamiasciurus fremonti grahamensis*). Herein, we present a study that explores the behavioral responses of small mammal species to a wildfire. Next, we analyze how translocation of individuals from a territorial arboreal mammal affects their behavioral responses, including movement and habitat selection, after release in new areas. In fact, the Frye Fire caused the declined of the population of Mt Graham red squirrel to 35 animals

(Merrick et al. 2021), creating the need for scientific data that evaluate the impact of translocation on behavior, survival, and movements. We used a substitute species, (*T. f. fremonti*, Hope et al. 2016) to investigate how different factors play their role in translocation, and in particular: translocation technique (hard vs soft), season (winter vs fall), individual characteristics (sex, body size). We also analyzed the post-release movement and the effect of different behavioral stages on habitat selection after translocation. This study will support development of conservation and protection strategies for the recovery of the endangered subspecies Mt Graham red squirrel, extending to other territorial species.

### ***Present study***

This dissertation comprises three manuscripts.

The first manuscript, intended for submission to the journal *Fire*, “Foraging behavior response of small mammals to different burn severities” aims to address the impact of different types of burn severity forest areas on foraging behavior of small mammals. We studied the perceived predation risk through giving up density experiments, and we determined if different species are impacted differently by the fire. We also explored how different vegetation characteristics can contribute to the perceived predation risk inside each burn severity area.

The second manuscript, submitted for consideration in PLoS One, “Using a substitute species to inform translocation technique for an endangered territorial mammal”, analyzed different translocation techniques to inform management actions on the endangered Mt. Graham red squirrel (*Tamiasciurus fremonti grahamensis*). We used a surrogate subspecies, (*Tamiasciurus fremonti fremonti*) to test the effect of season, translocation technique, and body mass on the subsequent survival, distance moved after release, and time to settlement of translocated animals.

The third manuscript, “Post-translocation movements and the important of conspecific distribution to settlement site selection in a territorial species.”, studied the post-release movement and habitat choice of red squirrels (*T. f. fremonti*) following translocation. In particular we wanted to determine how many behavioral phases can be recognized after translocation and how habitat selection corresponds to each. We also explored if squirrels selected the new settlement site based on habitat attributes experienced in their original midden, and if the density of conspecific can affect this decision.

## References

- Amacher, A. J., Barrett, R. H., Moghaddas, J. J., & Stephens, S. L. (2008). Preliminary effects of fire and mechanical fuel treatments on the abundance of small mammals in the mixed-conifer forest of the Sierra Nevada. *Forest Ecology and Management* 255, 3193–3202.
- Bailey, L. D., & Pol, M. van de. (2016). Tackling extremes: challenges for ecological and evolutionary research on extreme climatic events. *Journal of Animal Ecology* 85, 85–96.
- Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B., & Ferrer, E. A. (2011). Has the Earth's sixth mass extinction already arrived? *Nature* 471, 51–57.
- Berger-Tal, O., Blumstein, D. T., & Swaisgood, R. R. (2020). Conservation translocations: a review of common difficulties and promising directions. *Animal Conservation* 23, 121–131.
- Berger-Ta, O., & Saltz, D. (2014). Using the movement patterns of reintroduced animals to improve reintroduction success. *Curr Zool* 60, 515–526.
- Blumstein, D. T., & Fernández-Juricic, E. (2010). A primer of conservation behavior. Sunderland, Mass: Sinauer Associates.
- Bouwer, L. M. (2019). Observed and projected impacts from extreme weather events: Implications for Loss and Damage. In R. Mechler, L. M. Bouwer, T. Schinko, S. Surminski, & J. Linnerooth-Bayer (Eds.), *Loss and Damage from Climate Change: Concepts, Methods and Policy Options*. pp. 63–82. Cham: Springer International Publishing.
- Bubac, C. M., Johnson, A. C., Fox, J. A., & Cullingham, C. I. (2019). Conservation translocations and post-release monitoring: Identifying trends in failures, biases, and challenges from around the world. *Biological Conservation* 238, 108239.
- Camargo, A. C. L., Barrio, R. O. L., de Camargo, N. F., Mendonça, A. F., Ribeiro, J. F., Rodrigues, C. M. F., & Vieira, E. M. (2018). Fire affects the occurrence of small mammals at distinct spatial scales in a neotropical savanna. *Eur J Wildl Res* 64, 63.
- Caro, T., Eadie, J., & Sih, A. (2005). Use of substitute species in conservation biology. *Conservation Biology* 19, 1821–1826.
- Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances* 1, e1400253.
- Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences* 114, E6089–E6096.
- Chamaillé-Jammes, S., Massot, M., Aragón, P., & Clobert, J. (2006). Global warming and positive fitness response in mountain populations of common lizards *Lacerta vivipara*. *Global Change Biology* 12, 392–402.
- Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C., & Longino, J. T. (2008). Global Warming, Elevational Range Shifts, and Lowland Biotic Attrition in the Wet Tropics. *Science* 322, 258–261.
- Converse, S. J., White, G. C., Farris, K. L., & Zack, S. (2006). Small mammals and forest fuel reduction: national-scale responses to fire and fire surrogates. *Ecological Applications* 16, 1717–1729.

- Cowlishaw, G. (1997). Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour* 53, 667–686.
- Dolev, A., Saltz, D., Bar-David, S., & Yom-Tov, Y. (2002). Impact of repeated releases on space-use patterns of Persian fallow deer. *The Journal of Wildlife Management* 66, 737–746.
- Drake, D., & Temple, S. A. (2012). Captive propagation and translocation. In *The Wildlife Techniques Manual*. Silvy, N.J., pp. 293–306. Baltimore: Johns Hopkins University Press.
- Ducatez, S., & Shine, R. (2017). Drivers of extinction risk in terrestrial vertebrates. *Conservation Letters* 10, 186–194.
- Eliassen, S., Jørgensen, C., Mangel, M., & Giske, J. (2007). Exploration or exploitation: life expectancy changes the value of learning in foraging strategies. *Oikos* 116, 513–523.
- Engstrom, T. R. (2010). First-order fire effects on animals: review and recommendations. *Fire Ecology* Vol. 6, 115–130.
- Fisher, J. T., & Wilkinson, L. (2005). The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Review* 35, 51–81.
- Forsman, A. (2015). Rethinking phenotypic plasticity and its consequences for individuals, populations and species. *Heredity* 115, 276–284.
- Frair, J. L., Merrill, E. H., Allen, J. R., & Boyce, M. S. (2007). Know the enemy: experience affects elk translocation success in risky landscapes. *The Journal of Wildlife Management* 71, 541–554.
- Gannon, W. L., & Sikes, R. S. (2007). Guidelines of the American Society of Mammologist for the use of wild mammals in research. *Journal of mammology* 88, 15.
- Gerber, L. R., & Hilborn, R. (2001). Catastrophic events and recovery from low densities in populations of otariids: implications for risk of extinction. *Mammal Review* 31, 131–150.
- Gurevitch, J., & Padilla, D. K. (2004). Response to Ricciardi. Assessing species invasions as a cause of extinction. *Trends in Ecology & Evolution* 19, 620.
- Harrington, L. A., Moehrensclager, A., Gelling, M., Atkinson, R. P. D., Hughes, J., & Macdonald, D. W. (2013). Conflicting and complementary ethics of animal welfare considerations in reintroductions. *Conservation Biology* 27, 486–500.
- Harrison, P. M., Gutowsky, L. F. G., Martins, E. G., Patterson, D. A., Cooke, S. J., & Power, M. (2015). Personality-dependent spatial ecology occurs independently from dispersal in wild burbot (*Lota lota*). *Behav Ecol* 26, 483–492.
- Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T. M., Butchart, S. H. M., Carpenter, K. E., Chanson, J., Collen, B., Cox, N. A., Darwall, W. R. T., Dulvy, N. K., Harrison, L. R., Katariya, V., Pollock, C. M., Quader, S., Richman, N. I., Rodrigues, A. S. L., Tognelli, M. F., Vié, J.-C., Aguiar, J. M., Allen, D. J., Allen, G. R., Amori, G., Ananjeva, N. B., Andreone, F., Andrew, P., Ortiz, A. L. A., Baillie, J. E. M., Baldi, R., Bell, B. D., Biju, S. D., Bird, J. P., Black-Decima, P., Blanc, J. J., Bolaños, F., Bolivar-G., W., Burfield, I. J., Burton, J. A., Capper, D. R., Castro, F., Catullo, G., Cavanagh, R. D., Channing, A., Chao, N. L., Chenery, A. M., Chiozza, F., Clausnitzer, V., Collar, N. J., Collett, L. C., Collette, B. B., Fernandez, C. F. C., Craig, M. T., Crosby, M. J., Cumberlidge, N., Cuttelod, A., Derocher, A. E., Diesmos, A. C., Donaldson, J. S., Duckworth, J. W., Dutson, G., Dutta, S. K., Emslie, R. H., Farjon, A., Fowler, S., Freyhof, J., Garshelis, D. L., Gerlach, J., Gower, D. J., Grant, T. D., Hammerson, G. A., Harris, R. B., Heaney, L. R., Hedges, S. B., Hero, J.-M., Hughes, B., Hussain, S. A., Icochea M., J., Inger, R. F., Ishii, N., Iskandar, D. T., Jenkins, R. K. B., Kaneko, Y., Kottelat, M., Kovacs, K. M., Kuzmin, S. L., La Marca, E., Lamoreux, J. F., Lau, M. W. N., Lavilla, E. O., Leus,

- K., Lewison, R. L., Lichtenstein, G., Livingstone, S. R., Lukoschek, V., Mallon, D. P., McGowan, P. J. K., ... Stuart, S. N. (2010). The impact of conservation on the status of the world's vertebrates. *Science* 330, 1503–1509.
- Hutchen, J., Volkmann, L. A., Hodges, K. E., Hutchen, J., Volkmann, L. A., & Hodges, K. E. (2017). Experimental designs for studying small-mammal responses to fire in North American conifer forests. *International Journal Wildland Fire* 26, 523–531.
- Koprowski, J. L., Leonard, K. M., Zugmeyer, C. A., & Jolley, J. L. (2006). Direct effects of fire on endangered Mount Graham red squirrels. 51, 59–63.
- Lawes, M. J., Murphy, B. P., Fisher, A., Woinarski, J. C. Z., Edwards, A. C., & Russell-Smith, J. (2015). Small mammals decline with increasing fire extent in northern Australia: evidence from long-term monitoring in Kakadu National Park. *International Journal Wildland Fire* 24, 712.
- Lindenmayer, D. B., Blanchard, W., MacGregor, C., Barton, P., Banks, S. C., Crane, M., Michael, D., Okada, S., Berry, L., Florance, D., & Gill, M. (2016). Temporal trends in mammal responses to fire reveals the complex effects of fire regime attributes. *Ecological Applications* 26, 557–573.
- Maron, M., McAlpine, C. A., Watson, J. E. M., Maxwell, S., & Barnard, P. (2015). Climate-induced resource bottlenecks exacerbate species vulnerability: a review. *Diversity and Distributions* 21, 731–743.
- Maxwell, S. L., Fuller, R. A., Brooks, T. M., & Watson, J. E. M. (2016). Biodiversity: The ravages of guns, nets and bulldozers. *Nature* 536, 143–145.
- McKenzie, D., & Littell, J. S. (2017). Climate change and the eco-hydrology of fire: Will area burned increase in a warming western USA? *Ecological Applications* 27, 26–36.
- Moritz, C., & Agudo, R. (2013). The future of species under climate change: resilience or decline? *Science* 341, 504–508.
- Murphy, D. D., Weiland, P. S., & Cummins, K. W. (2011). A critical assessment of the use of surrogate species in conservation planning in the Sacramento-San Joaquin Delta, California (U.S.A.). *Conservation Biology* 25, 873–878.
- National Research Council. (1995). *Science and the Endangered Species Act*. National Academies Press.
- Picardi, S., Coates, P., Kolar, J., O'Neil, S., Mathews, S., & Dahlgren, D. (2022). Behavioural state-dependent habitat selection and implications for animal translocations. *Journal of Applied Ecology* 59, 624–635.
- Reed, T. M. (1982). Interspecific territoriality in the chaffinch and great tit on islands and the mainland of Scotland: Playback and removal experiments. *Animal Behaviour* 30, 171–181.
- Resende, P. S., Viana-Junior, A. B., Young, R. J., & de Azevedo, C. S. (2020). A global review of animal translocation programs. *Animal Biodiversity and Conservation* 43, 221–232.
- Scheele, B. C., Legge, S., Armstrong, D. P., Copley, P., Robinson, N., Southwell, D., Westgate, M. J., & Lindenmayer, D. B. (2018). How to improve threatened species management: An Australian perspective. *Journal of Environmental Management* 223, 668–675.
- Schmitz, O. J., Beckerman, A. P., & O'Brien, K. M. (1997). Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78, 1388–1399.
- Serrano, D., & Tella, J. L. (2003). Dispersal within a spatially structured population of lesser kestrels: the role of spatial isolation and conspecific attraction. *Journal of Animal Ecology* 72, 400–410.

- Smucker, K. M., Hutto, R. L., & Steele, B. M. (2005). Changes in bird abundance after wildfire: importance of fire severity and time since fire. *Ecological Applications* 15, 1535–1549.
- Stamps, J. (2001). Habitat selection by dispersers: integrating proximate and ultimate approaches.
- Stamps, J., & Krishnan, V. V. (2005). Nonintuitive cue use in habitat selection. *Ecology* 86, 2860–2867.
- Visser, M. E., & Both, C. (2005). Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B*. 272, 2561–2569.
- Whelan, R. J. (2002). Managing fire regimes for conservation and property protection: an Australian response. *Conservation Biology* 16, 1659–1661.
- Wiens, J. A., & Hobbs, R. J. (2015). Integrating conservation and restoration in a changing World. *BioScience* 65, 302–312.

# Appendix A: Foraging behavior, response of small mammals to different burn severities

Marina Morandini<sup>1</sup> & John L. Koprowski<sup>2</sup>

<sup>1</sup> School of Natural Resources and the Environment, University of Arizona, Tucson, AZ, USA

<sup>2</sup> Haub School of Environment and Natural Resources, University of Wyoming, Laramie, WY, USA

Corresponding Author:

Marina Morandini<sup>1</sup>

7777 NY-30, Paul Smiths, NY, 12970, USA

Email address: mmorandini@paulsmiths.edu

## ***Abstract***

Wildfires cause profound challenges for animals to overcome, especially forest-dwelling mammals, due to reliance on specific vegetation types. This study addresses the impact of 3 types of burn severity forest areas (completely, partially, and non-burn areas) on foraging behavior of a small mammals in the Pinaleño Mountains (Arizona) using the giving up density experiment approach (GUD). Overall, burned severity affects perceived predation risk (reflected in the GUD), where in completely burned patches, small mammals spend less time foraging than partially- and non-burned patches. Vegetation characteristics influence GUD in the 3 burn severity patches. Higher canopy cover indicated an increased in perceived predation risk (higher GUD) in partial and non-burn patches, while cover provided by logs or small trees correspond to lower GUD (increased foraging) in non-burned and completely burned patches. This suggests complicated interactions between levels of vegetation characteristics (ground, medium and upper level) in the perception of predation risk related to burned severity. Fires affect foraging behavior of the small mammals but does not impact all species in the same way. Generalists, such as *Peromyscus* sp., seem to forage across all burn severities, while specialist species, such as tree squirrels, tend to

avoid the completely burned patches. Clarifying complex impacts of fires on small mammals foraging behaviours contribute to our understanding of the intricate interactions, at micro-habitat levels, between vegetation structure, and behavior responses of animals.

## ***Introduction***

Climate change is increasing the magnitude of extreme environmental events (Bailey and Pol 2016, Stott 2016), such as wildfire severity and occurrences (Jolly et al. 2015, Littell et al. 2016, McKenzie and Littell 2017). In the western United States, fires are estimated to increase at a rate of 7 additional large events each year (Dennison et al. 2014). This phenomenon is quite alarming, considering the profound changes caused by fire in the composition and abundance of plant and animal species (Smucker et al. 2005, Lindenmayer et al. 2016, Camargo et al. 2018). Direct effects of wildfire, such as death due to injury, extreme temperature, or smoke inhalation (Whelan 2002, Engstrom 2010), is not an exhaustive description of the wildfire consequences in wildlife. Indirect effects, including habitat loss and environmental changes, arise later, but can extensively impact animal ecology (Whelan 2002, Koprowski et al. 2006, Engstrom 2010).

The largest obstacle for all animals effected by fires to overcome is dealing with an instantaneously new environment, including changes to vegetation structure and composition, quantity and distribution of resources, possible increase of predation (Engstrom 2010, Lawes et al. 2015). Changes in cover availability can influence predation risk and subsequently alter the behavior, demographics, and growth rates of prey populations (Arthur et al. 2004, Spencer and Thompson 2005). For example, fires influence forage availability and quality, consequently affecting bison (*Bison bison*) feeding behavior, with an increase in bite mass and instantaneous intake rate of individual bison in periodically burned grassland (Raynor et al. 2015). Woodpeckers (*Picoides sp.*) tend to select burned areas after fire due to an increase of insects in dead logs (Kreisel and Stein 1999). The ability to adapt to those changes is reflected in fitness, and ultimately on the entire population affected by fire (Whelan 2002, Forsman 2015).

The effects of fire on wildlife, depend upon the ecology of the species (Haim et al. 1996, Sutherland and Dickman 1999, Horn et al. 2012). For example, the population of the insectivore rodents *Akodon cursor* increased after the fire, whereas frugivore/granivore *Oecomys concolor* decreased until disappearing in some area after the fire (De Souza Lima Figueiredo and Fernandez 2004). Usually, fires affect greatly isolated populations or populations with small geographic ranges, threatening the potential for recovery (Gerber and Hilborn 2001). Fires also have a larger effect on habitat specialists, such as small to medium forest-dwelling mammals, because of their narrow niche breadth and reliance on specific vegetation community types (Merrick et al. 2021).

Small mammals are a crucial component of forest ecosystems; they play an important role in the dispersal of plant seeds and spores of mycorrhizal fungi and are prey for many avian and mammalian predators (Converse et al. 2006, Boone et al. 2022). Therefore, any changes in small mammal abundance and behavior due to disturbances, such as fires, may affect forest ecosystem function. Fire creates a mosaic landscape of different degrees of burn severity, which influences the foraging behavior of rodents (Doherty et al. 2015). The post fire landscape offers heterogeneities in hazards and opportunities, with patches characterized by higher concentration of resources, but also patches with high visibility (high predator risk), due to the reduction of canopy cover. Predators do not only influence prey by killing them, but create a landscape of fear that influence activity times, foraging tactics, and microhabitat selection of prey (Schmitz et al. 1997, Cowlshaw 1997). The giving up density (“GUD”) experimental approach has been long used to study spatial or temporal differences in the perception of predatory risk (Newman et al. 1988, Bowers 1990), frequently measured with artificial food patches (e.g., (Whitham 1977, Brown 1988). The giving up density corresponds to the resource density in a patch at which an animal stops to forage, because further time spent in the same patch will add more costs (energetic costs, risk of predation, missed opportunity cost of not engaging in alternative activities) than benefits (Brown 1988, Brown et al. 1992).

The increased landscape fragmentation caused by fire, can radically change the connectivity for long periods of time (Parkins et al. 2018) especially for small mammals as they perceive barriers to movement at finer spatial scales (Banks et al. 2005). Several studies have investigated the influence of fire and fuel management treatments on small mammal abundance (e.g., (Fisher and Wilkinson 2005, Converse et al. 2006, Amacher et al. 2008, Lawes et al. 2015, Hutchen et al. 2017). However, research focused on how disturbances affect animal behavior is scarce and the response is not always clear on burned patches (Reed 1982).

In this study we address the impact of burned forest areas on foraging of small mammals, on the Pinaleño Mountains of southeastern Arizona. In summer 2017, the Frye Fire burned 20,000 ha, ranged in elevation from 1,219 to above 3,000 m. It impacted the upper elevation spruce-fir forest as well as the lower elevation mixed-conifer forest, creating a mosaic landscape of different burn severity patches. We predict that 1) the small mammals perceives a higher predation risk in areas of high burned severity, corresponding to a higher giving up density, 2) not all species respond to

the mosaic of burned severity in the same way and arboreal mammals are more affected by differential burned severity of the vegetation. The results provide insights into the multivariate nature of the foraging process and the diversity of factors upon which foraging decisions are made. Through the use of giving up densities, it will be possible to understand how the post-fire landscape affects foraging behavior in small mammals including differential use of burned patches.

## ***Material and method***

### **Study site**

The study area is located above 2750 m in the Pinaleño Mountains, Graham County, Arizona, USA. We selected 4 areas (Grant Hill, Soldier Trail, Bible Camp, and near Mt. Graham International Observatory) in a mosaic of burn severity and where the federally endangered Mt Graham red squirrel (*Tamiasciurus fremonti grahamensis*, MGRS - (Hope et al. 2016) is present. The vegetation is dominated by Engelmann spruce (*Picea engelmannii*) and common name *Abies lasiocarpa* at highest elevations, with Douglas-fir *Pseudotsuga menziesii* and Southwestern white pine *Pinus strobiformis* occurring more frequently as elevation decreases (Hutton et al. 2003).

We studied the effects of burn severity on small mammals from May to July for two consecutive years (2018 and 2019) after the Frye Fire. The Frye Fire burned 20,000 ha in summer 2017 and ranged in elevation from 1,219 to above 3,000 m, impacting the remaining spruce-fir forest as well as the mixed-conifer forest. The Frye Fire created a mosaic landscape of different burn severity patches (McGuire and Youberg 2019).

### **Study design**

We identified 15 patches in each of the four study areas and each patch was classified in one of 3 distinct burn severity (non-burn, partial burn, complete burn). A patch is an area with a 10 m radius defined as completely burned when all trees are dead and burned, non-burned when all trees are alive and not affected by fire, and partially burned when trees are partially affected by the fire (burned trunk or burned needles), but most trees are still alive. To identify the patches, we generated for each study area 50 random points at least 50 m apart in Arc GIS. We overlapped this point with the aerial image of the area post fire, and subdivided the 50 random points in non-burn, complete burn, and partial burned areas. We randomly selected 5 points for each burn severity type

within the experimental area and ground u for burned severity (non-burn, partial burn and complete burn).

### **Foraging experiment**

We determined how the different burn severities affected the perception of predation risk in small mammals, using the giving up density (GUD) (Newman et al. 1988, Bowers 1990) in the 15 patches of each study area. We used one plastic tray (58x41x16 cm) placed in the center of the patch (2 l capacity each, 5 trays in each patch type, and 15 trays each study area) filled with 2 l of play sand mixed with 50 g of black oil sunflower seeds. Trays also contain a lattice like mesh to make the search for seeds more difficult. The seed trays were set out in the field for 3 consecutive days in summer 2018 and 2019. For 2019 two repetitions were completed in each area. We considered the first day as a pre-baiting session, to let animals become familiar with the artificial food and tray, whereas we consider the second and third day to determine the giving up density (GUD). We sifted the trays once a day before sunset, and the sunflower seeds that remained in the tray were collected and replaced with other 50 g of seeds. Each time the sifted seeds were weighed to determine the giving up density (GUD), that indicates when the benefit obtained from foraging is balanced by the summed energetic costs, the risk of predation, and the missed opportunity cost of not engaging in alternative activities (Brown 1988).

We used a camera trap in video mode (Bedoya-Perez et al. 2013) to enable identification of species using the trays. From each video, we recorded the species visiting the tray, the day, and the time. Cameras were placed at 40 cm above the ground facing the tray and set up to record 15 s videos, with 45 seconds-interval between consecutive videos. Cameras were active 24 h per day, and the batteries were checked every day.

### **Vegetation analysis**

To investigate microhabitat features that could affect the foraging behavior of small mammals in addition to burn severity, we established a 10 m radius plot around the tray at each patch location. In each plot, we measured the diameter at breast height (DBH; cm) of all woody plants (shrub DBH < 10 cm, tree DBH > 10 cm; Doumas and Koprowski 2013) and recorded the species. We recorded the number of dead standing trees (tree mortality) within the plot. At 5m and 10m intervals from the center of the plot, we measured canopy density in each of the four cardinal directions, using a spherical densiometer (Strickler 1959) and averaged the measures for each plot.

We measured the length and the diameter at both ends of any downed logs (diameter > 20 cm) in the plot, and calculated the total volume. To estimate the grass and small tree cover in each plot, we first recorded the percentage of each component (grass cover and shrub cover) in the 4 quadrants and subsequently we average the values. Small tree cover was considered as any vegetation at least 40 cm tall (including ferns and small trees).

### **Statistical analysis**

We performed all statistical analyses with R (R Development Core Team, Auckland, New Zealand). Before proceeding with the analysis, we averaged the grams of seeds retrieved in the tray (GUD) of the two consecutive nights of the experiments to avoid pseudo replication. We applied a two-step analysis, where we first modelled the presence/absence of any small mammals at the trays, and in a second step we analyzed the GUD.

We investigated the presence/absence of any small mammals at the trays, (we considered no seeds eaten as absence, value=0, whereas if any seeds were eaten, we considered as presence, value=1), using a generalized linear model with binomial distribution and logit link, with the explanatory variables year (2018 and 2019), patch type (complete partial, and non-burn), and total volume of logs, whereas area has been treated as random effect. Model assumptions were verified by plotting residuals versus fitted values. Next, we subset the data, considering only the trays where animals have eaten. We fitted a generalized linear model with Gaussian distribution and identity link, where the explanatory variable and random variables are the same as the previous model.

We used principal component analysis to create two variables to describe the vegetation characteristics of the three different burned severity areas. The initial variables included were canopy cover, grass cover, brush cover, number of tree species, total volume of logs, DBH, and percentage of living trees.

To determine which microhabitat characteristics influenced GUD in the 3 different burn severity patches, we fitted a linear model for each burn severity. The variables that we used for partial and non-burned patches are total volume of logs (m<sup>3</sup>), percentage of grass cover, percentage of brush cover and percentage of canopy cover, whereas for the completely burned areas we did not include canopy cover (due to the trees missing caused by high intensity fire).

We also assessed if the number of species present at each tray differed among the 3 burn severity patches, using ANOVA and Tukey's test to compare the patches. Normality was verified by plotting residuals versus fitted values, while heterogeneity of variance was tested using the Levene Test. We qualitatively analyzed species composition, as percentage of each species in each patch type, as well as the use of the three patches by each species, as percentage of their presence in the three types of burned severity.

## **Results**

In 2018, 65% of the trays (39/60) were visited by animals, whereas in 2019 animals were detected in all but one tray (59/60). The presence of animals at the trays was higher in 2019 than in 2018, but was not affected by burned severity or total volume of logs (Table 1.1). GUD, instead, differed between burned severity patches and total volume of logs, but not between years (Table 1.2). In fact, more grams of seeds were found in completely burned patches than in partially or non-burned patches and in area with lower volume of logs (Fig. 1.1).

The PCA transformation of the vegetation characteristics at burned severity patches, explained 78% of the variation in the first 3 PCs. The vegetation characteristic of completely burned patches is clearly different from the other two patch types, whereas non-burned and partially burned present some overlap. However, non-burned areas correspond to higher value of PC1 (Fig. 1.2).

Table 1.4 shows the results of linear models to determine the effect of vegetation characteristics on GUD. In the non-burned patches, GUD was negatively related to small trees, while positively related with canopy cover. In the partially burned patches, GUD is positively associated with canopy cover and grass cover. In the completely burned patches GUD is negatively influenced by the total volume of logs.

We detected the following species: Abert's squirrel (*Sciurus aberti*), cliff chipmunk (*Tamias dorsalis*), Mt Graham red squirrel (*Tamiasciurus fremonti grahamensis*), mouse (*Peromyscus sp.*), Mexican woodrat (*Neotoma mexicana*), rock squirrel (*Otospermophilus variegatus*), long-tailed vole (*Microtus longicaudus*), gray fox (*Urocyon cinereoargenteus*), black bear (*Ursus americanus*), bird (species unknown), striped skunk (*Mephitis mephitis*) (Table 1.3). We did not consider gray fox, black bear, bird and skunk for further analysis because the focus of this paper is centered on foraging behavior of small mammals, and these animals were not foraging on the tray's food.

The different burn severity patches were used by a different number of species (Figure 1.3), with a mean of 1.72 (sd 1.03) for non-burned areas, 1.36 (sd 0.59) for partial burned areas, and 1.22 (sd 0.48) for complete burned areas ( $F(2,105) = 4.36, p = 0.01$ ). In particular, completely burn patches are different from non-burned patches ( $p = 0.01$ ), whereas no differences occurred between the other pairs (NB-PB and PB-CB,  $p > 0.05$ ). We observed a different species composition in the 3 degrees of burned areas, although dominated by chipmunks and mice in all 3 patch types. Woodrat and Mt Graham red squirrel used primarily non burned areas, whereas voles and Abert's squirrels were present only in non-burned areas (Figure 1.4 and 1.5).

### ***Discussion***

Varying levels of burn severity influence small mammal foraging behavior. In completely burned patches, small mammals stopped foraging in trays earlier than in partially- and non-burned patches, leaving more seeds in them indicative of a greater perception of predation risk. Vegetation characteristics of different burn severities influenced the perception of predation risk (Potash et al. 2019) and consequently the costs and benefits of foraging in each patch-type (completely burned, partial burned and non-burn). In this study, we also found that fire affected the collective foraging behavior of small mammal communities but did not impact all species the same, causing larger impact on specialists.

Immediately after a fire, populations can decline due to mortality (Whelan 2002, Engstrom 2010), but total small mammal biomass increased in the two years after a fire (Converse et al. 2006). Indeed, small mammals' composition and abundance vary as a function of time since the fire (Briani et al. 2004), and depend upon the successional stages as well as the possibility of recolonization from nearby unburned habitats (Diffendorfer et al. 2012). From our data, the rodent populations in the study areas seemed to rebound 2 years after the fire. In contrast with the presence/absence of mammals in patches, GUD is instead affected by difference in level of burn severity and volume of logs, but not by year. Risk of predation is generally perceived to be higher in absence of cover, such as shrub cover, grass cover, canopy cover, or logs (Bowers et al. 1993, Doherty et al. 2015, Persons and Eason 2017). Completely burned patches are characterized by absence of canopy cover, whereas the other types are characterized by a higher canopy cover, number of tree species, alive trees, larger trees. As a result, GUD in completely burned patches increases (foraging decreases) over non-burned patches.

Predators create a landscape of fear that influences activity times, foraging tactics, and microhabitat selection of prey (Lima 1985, Schmitz et al. 1997). Perceived risk of predation, and foraging behavior, may be influenced by different elements when considering microhabitats in different burn severity patches. In non-burned areas and partial burned areas, tree canopy cover has an important influence on GUD. However, the relation between seeds eaten and canopy cover has an unexpected finding as canopy cover increased, GUD increased. Horizontal cover provides concealment from avian predators (Wywiałowski 1987), but vegetation can also reduce the visual detectability of predators by prey (Embar et al. 2011, Camp et al. 2013). Another possible explanation of this phenomena is the presence of birds of prey that are adapted to hunt below the canopy of mature trees, such as *Accipiter* sp. (ex. Cooper's hawk, sharp-shinned hawk), Mexican spotted owl (*Strix occidentalis lucida*), or great-horned owl (*Bubo virginianus*). With the canopy cover above the predators, prey are no longer directly protected. Instead, logs, or cover offered by lower vegetation can provide immediate refuge from predation (Doherty et al. 2015) by birds of prey, as well as terrestrial predators such grey foxes (*Urocyon cinereoargenteus*) and bobcats (*Lynx rufus*). In fact, in non-burned areas, an increase of small tree cover and volume of logs corresponds to a decrease of GUD, hence higher removal-rates of seeds in the trays. A similar pattern can be found in completely burned patches where log volume significantly affected GUD, with more seeds removed from trays when a larger volume of logs was present.

The positive relation between canopy cover and GUD, but negative relationship between cover offered by horizontal cover (logs, small tree cover) and GUD aligns with the explanation provided by Potash et al. (2019), who demonstrated that prey can perceive different predation risks as a consequence of interactions between multiple environmental cues in heterogeneous landscapes (Laundré et al. 2001, Potash et al. 2019). This heterogeneity is created by a different distribution of predators in the landscape, creating spatial variation in a prey's fear (Brown and Kotler 2004), and the interaction between vegetation cover along horizontal and vertical axes.

While fire did affect the foraging behavior of small mammals, the effects varied among species. Lower number of species used the trays in completely burned severity patches than in non-burned patches. Fire does influence small mammal populations; however, the level of effect is not uniform and appears to be associated with specific habitat requirements of individual species (Griffiths and Brook 2014) and the home range size of the animal. In this context, we expect that generalist

species are less impacted, whereas habitat specialists are more negatively affected (Waters and Zabel 1995, Roberts et al. 2015). We observed the use of all types of burn severity patches by the generalist *Tamias dorsalis* and *Peromyscus*, whereas voles and Abert's squirrels are present only in non-burned areas, and Mt Graham red squirrel used mostly non burned areas, rarely visiting trays in other patch types. Previous studies have shown a negative response of Mt Graham red squirrel to fire, with an increase home range size and maximum distance traveled (Koprowski et al. 2008, Merrick et al. 2021). After the Frye Fire surviving animals were forced to travel within and among isolated patches of live trees for cone harvesting and in search of new territories, leaving them more susceptible to predation (Merrick et al. 2021). In other studies, mice do not always modify their behavior as consequence of disturbances or habitat types. For example, the white-footed mouse (*Peromyscus leucopus*) did not change their use patterns in response to fuel reduction treatments (Greenberg et al. 2006), or deer mice (*Peromyscus maniculatus*) did not change the quantity of foraging activity between habitats characterized by different shrub density (Connolly and Orrock 2018).

To conclude, our study showed various effects of recent fire on foraging behavior of small mammals. Completely burned patches are perceived riskier by communities of small mammals than patches with no or lower burn severity and were used by fewer species. Moreover, the vegetation variables that influenced GUD differed among the 3 types of burn severity, showing a complicated interaction between horizontal (logs, grass, small tree cover) and vertical vegetation cover in relation to burn severity (Potash et al. 2019). We also underline how the impact of fire can be greater for specialist, such as tree squirrels, than for generalist species.

Results from this and other studies suggest that fire influence behavioral response, therefore potentially affecting animal fitness (Herzog et al. 2014, Álvarez-Ruiz et al. 2021, Lees et al. 2022). Wildfires threaten animals globally (Schoennagel et al. 2017, Ward et al. 2020, Ancillotto et al. 2021) and future increases in fire frequency and severity in southwest USA (Mueller et al. 2020) will increase loss of forest areas and potentially exacerbate the impact of predators on small mammals. Clarifying the perceived predation risk of small mammals across different patches of burn severities, as well as the interaction between burn severities and microhabitat within these patches, can help managers to plan actions to reduce the negative impacts of wildfires (Doherty et al. 2015). Burned patches are perceived more dangerous by small mammals, however microhabitat

features such as logs and shrubs, helped to mitigate the landscape of fear perceived by animals. In this scenario, animal behavior should be considered when implementing fire control, for example brush removal, to prevent large wildfire. Clearing the under canopy can prevent wildfires, but in the event of a wildlife can exacerbate the impact on small mammal behavior.

### ***Acknowledgment***

We thank the agency partner Arizona Game and Fish Department and the University of Arizona School of Natural Resources and the Environment. We would like to thank the Mt. Graham Red Squirrel Research Program graduate and undergraduate research assistants for valuable help in the field. This research was supported by grants to JLK from the University of Arizona, Arizona Game and Fish Department (grants no. I18005 and I16002), and T & E Inc. Grants for Conservation Biology. All field work was conducted under University of Arizona Institutional Animal Care and Use Committee protocol # 16-169, Arizona Game and Fish Department scientific collecting permit # SP651773 for 2019, SP403044 for 2020, SP407072 for 2021, U.S. Fish and Wildlife Service permit # TE041875-2 and adhered to the American Society of Mammologist's guidelines for the use of wild mammals in research (Sikes & Gannon, 2011). This manuscript was improved by comments from R. W. Mannan, L. Wauters, and R. Steidl.

## References

- Álvarez-Ruiz, L., J. Belliure, and J. G. Pausas. 2021. Fire-driven behavioral response to smoke in a Mediterranean lizard. *Behavioral Ecology* 32:662–667.
- Amacher, A. J., R. H. Barrett, J. J. Moghaddas, and S. L. Stephens. 2008. Preliminary effects of fire and mechanical fuel treatments on the abundance of small mammals in the mixed-conifer forest of the Sierra Nevada. *Forest Ecology and Management* 255:3193–3202.
- Ancillotto, L., G. Fichera, E. Pidinchredda, M. Veith, A. Kiefer, M. Mucedda, and D. Russo. 2021. Wildfires, heatwaves and human disturbance threaten insular endemic bats. *Biodiversity and Conservation* 30:4401–4416.
- Arthur, A. D., R. P. Pech, and C. R. Dickman. 2004. Habitat structure mediates the non-lethal effects of predation on enclosed populations of house mice. *Journal of Animal Ecology* 73:867–877.
- Bailey, L. D., and M. van de Pol. 2016. Tackling extremes: challenges for ecological and evolutionary research on extreme climatic events. *Journal of Animal Ecology* 85:85–96.
- Banks, S. C., D. B. Lindenmayer, S. J. Ward, and A. C. Taylor. 2005. The effects of habitat fragmentation via forestry plantation establishment on spatial genotypic structure in the small marsupial carnivore, *Antechinus agilis*. *Molecular Ecology* 14:1667–1680.
- Bedoya-Perez, M. A., A. J. R. Carthey, V. S. A. Mella, C. McArthur, and P. B. Banks. 2013. A practical guide to avoid giving up on giving-up densities. *Behavioral Ecology and Sociobiology* 67:1541–1553.
- Boone, S. R., A. M. Brehm, and A. Mortelliti. 2022. Seed predation and dispersal by small mammals in a landscape of fear: effects of personality, predation risk and land-use change. *Oikos* 2022.
- Bowers, M. A. 1990. Exploitation of seed aggregates by Merriam's kangaroo rat: harvesting rates and predatory risk. *Ecology* 71:2334–2344.
- Bowers, M. A., J. L. Jefferson, and M. G. Kuebler. 1993. Variation in giving-up densities of foraging chipmunks (*Tamias striatus*) and squirrels (*Sciurus carolinensis*). *Oikos* 66:229–236.
- Briani, D. C., A. R. T. Palma, E. M. Vieira, and R. P. B. Henriques. 2004. Post-fire succession of small mammals in the Cerrado of central Brazil. *Biodiversity and Conservation* 13:1023–1037.
- Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology* 22:37–47.
- Brown, J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. *Ecology Letters* 7:999–1014.
- Brown, J. S., R. A. Morgan, and B. D. Dow. 1992. Patch use under predation risk: II. A test with fox squirrels, *Sciurus niger*. *Annales Zoologici Fennici* 29:311–318.
- Camargo, A. C. L., R. O. L. Barrio, N. F. de Camargo, A. F. Mendonça, J. F. Ribeiro, C. M. F. Rodrigues, and E. M. Vieira. 2018. Fire affects the occurrence of small mammals at distinct spatial scales in a neotropical savanna. *European Journal of Wildlife Research* 64:63.
- Camp, M. J., J. L. Rachlow, B. A. Woods, T. R. Johnson, and L. A. Shipley. 2013. Examining functional components of cover: the relationship between concealment and visibility in shrub-steppe habitat. *Ecosphere* 4:1-14.

- Converse, S. J., G. C. White, K. L. Farris, and S. Zack. 2006. Small mammals and forest fuel reduction: national-scale responses to fire and fire surrogates. *Ecological Applications* 16:1717–1729.
- Cowlishaw, G. 1997. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour* 53:667–686.
- De Souza Lima Figueiredo, M., and F. A. D. S. Fernandez. 2004. Contrasting effects of fire on populations of two small rodent species in fragments of Atlantic Forest in Brazil. *Journal of Tropical Ecology; Cambridge* 20:225–228.
- Dennison, P. E., S. C. Brewer, J. D. Arnold, and M. A. Moritz. 2014. Large wildfire trends in the western United States, 1984–2011. *Geophysical Research Letters* 41:2928–2933.
- Diffendorfer, J., G. M. Fleming, S. Tremor, W. Spencer, and J. L. Beyers. 2012. The role of fire severity, distance from fire perimeter and vegetation on post-fire recovery of small-mammal communities in chaparral. *International Journal of Wildland Fire* 21:436.
- Doherty, T. S., R. A. Davis, and E. J. B. van Etten. 2015. A game of cat-and-mouse: microhabitat influences rodent foraging in recently burnt but not long unburnt shrublands. *Journal of Mammalogy* 96:324–331.
- Embar, K., B. P. Kotler, and S. Mukherjee. 2011. Risk management in optimal foragers: the effect of sightlines and predator type on patch use, time allocation, and vigilance in gerbils. *Oikos* 120:1657–1666.
- Engstrom, T. R. 2010. First-order fire effects on animals: review and recommendations. *Fire Ecology* Vol. 6:115–130.
- Fisher, J. T., and L. Wilkinson. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Review* 35:51–81.
- Forsman, A. 2015. Rethinking phenotypic plasticity and its consequences for individuals, populations and species. *Heredity* 115:276–284.
- Gerber, L. R., and R. Hilborn. 2001. Catastrophic events and recovery from low densities in populations of otariids: implications for risk of extinction. *Mammal Review* 31:131–150.
- Griffiths, A. D., and B. W. Brook. 2014. Effect of fire on small mammals: a systematic review. *International Journal of Wildland Fire* 23:1034–1043.
- Haim, A., I. Izhaki, and A. Golan. 1996. Rodent species diversity in pine forests recovering from fire. *Israel Journal of Ecology and Evolution* 42:353–359.
- Herzog, N. M., C. H. Parker, E. R. Keefe, J. Coxworth, A. Barrett, and K. Hawkes. 2014. Fire and home range expansion: A behavioral response to burning among savanna dwelling vervet monkeys (*Chlorocebus aethiops*). *American Journal of Physical Anthropology* 154:554–560.
- Hope, A. G., J. L. Malaney, K. C. Bell, F. Salazar-Miralles, A. S. Chavez, B. R. Barber, and J. A. Cook. 2016. Revision of widespread red squirrels (genus: *Tamiasciurus*) highlights the complexity of speciation within North American forests. *Molecular Phylogenetics and Evolution* 100:170–182.
- Horn, K. J., B. R. McMillan, and S. B. St. Clair. 2012. Expansive fire in Mojave Desert shrubland reduces abundance and species diversity of small mammals. *Journal of Arid Environments* 77:54–58.
- Hutchen, J., L. A. Volkmann, K. E. Hodges, J. Hutchen, L. A. Volkmann, and K. E. Hodges. 2017. Experimental designs for studying small-mammal responses to fire in North American conifer forests. *International Journal of Wildland Fire* 26:523–531.

- Hutton, K. A., J. L. Koprowski, V. L. Greer, M. I. Alanen, C. A. Schauffert, and P. J. Young. 2003. Use of mixed-conifer and spruce-fir forests by an introduced population of Abert's squirrels (*Sciurus aberti*). *The Southwestern Naturalist* 48:257–260.
- Jolly, W. M., M. A. Cochrane, P. H. Freeborn, Z. A. Holden, T. J. Brown, G. J. Williamson, and D. M. J. S. Bowman. 2015. Climate-induced variations in global wildfire danger from 1979 to 2013. *Nature Communications* 6:1–11.
- Koprowski, J. L., K. M. Leonard, C. A. Zugmeyer, and J. L. Jolley. 2006. Direct effects of fire on endangered Mount Graham red squirrels. *The Southwestern Naturalist* 51:59–63.
- Kreisel, K. J., and S. J. Stein. 1999. Bird use of burned and unburned coniferous forests during winter. *The Wilson Bulletin* 111:243–250.
- Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology* 79:1401–1409.
- Lawes, M. J., B. P. Murphy, A. Fisher, J. C. Z. Woinarski, A. C. Edwards, and J. Russell-Smith. 2015. Small mammals decline with increasing fire extent in northern Australia: evidence from long-term monitoring in Kakadu National Park. *International Journal of Wildland Fire* 24:712.
- Lees, D. M., D. J. Watchorn, D. A. Driscoll, T. S. Doherty, D. M. Lees, D. J. Watchorn, D. A. Driscoll, and T. S. Doherty. 2022. Microhabitat selection by small mammals in response to fire. *Australian Journal of Zoology* 69:67–79.
- Lima, S. L. 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. *Oecologia* 66:60–67.
- Lindenmayer, D. B., W. Blanchard, C. MacGregor, P. Barton, S. C. Banks, M. Crane, D. Michael, S. Okada, L. Berry, D. Florance, and M. Gill. 2016. Temporal trends in mammal responses to fire reveals the complex effects of fire regime attributes. *Ecological Applications* 26:557–573.
- Littell, J. S., D. L. Peterson, K. L. Riley, Y. Liu, and C. H. Luce. 2016. A review of the relationships between drought and forest fire in the United States. *Global Change Biology* 22:2353–2369.
- McGuire, L. A., and A. M. Youberg. 2019. Impacts of successive wildfire on soil hydraulic properties: Implications for debris flow hazards and system resilience. *Earth Surface Processes and Landforms* 44:2236–2250.
- McKenzie, D., and J. S. Littell. 2017. Climate change and the eco-hydrology of fire: Will area burned increase in a warming western USA? *Ecological Applications* 27:26–36.
- Merrick, M. J., M. Morandini, V. L. Greer, and J. L. Koprowski. 2021. Endemic population response to increasingly severe fire: a cascade of endangerment for the Mt. Graham red squirrel. *BioScience* 71:161–173.
- Mueller, S. E., A. E. Thode, E. Q. Margolis, L. L. Yocom, J. D. Young, and J. M. Iniguez. 2020. Climate relationships with increasing wildfire in the southwestern US from 1984 to 2015. *Forest Ecology and Management* 460:117861.
- Newman, J. A., G. M. Recer, S. M. Zwicker, and T. Caraco. 1988. Effects of predation hazard on foraging “constraints”: patch-use strategies in grey squirrels. *Oikos* 53:93–97.
- Parkins, K., A. York, and J. Di Stefano. 2018. Edge effects in fire-prone landscapes: Ecological importance and implications for fauna. *Ecology and Evolution* 8:5937–5948.
- Persons, W. E., and P. Eason. 2017. Human activity and habitat type affect perceived predation risk in urban white-footed mice (*Peromyscus leucopus*). *Ethology* 123:348–356.

- Potash, A. D., L. M. Conner, and R. A. McCleery. 2019. Vertical and horizontal vegetation cover synergistically shape prey behaviour. *Animal Behaviour* 152:39–44.
- Raynor, E. J., A. Joern, and J. M. Briggs. 2015. Bison foraging responds to fire frequency in nutritionally heterogeneous grassland. *Ecology* 96:1586–1597.
- Reed, T. M. 1982. Interspecific territoriality in the chaffinch and great tit on islands and the mainland of Scotland: Playback and removal experiments. *Animal Behaviour* 30:171–181.
- Roberts, S. L., D. A. Kelt, J. W. van Wagendonk, A. K. Miles, and M. D. Meyer. 2015. Effects of fire on small mammal communities in frequent-fire forests in California. *Journal of Mammalogy* 96:107–119.
- Schmitz, O. J., A. P. Beckerman, and K. M. O'Brien. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78:1388–1399.
- Schoennagel, T., J. K. Balch, H. Brenkert-Smith, P. E. Dennison, B. J. Harvey, M. A. Krawchuk, N. Mietkiewicz, P. Morgan, M. A. Moritz, R. Rasker, M. G. Turner, and C. Whitlock. 2017. Adapt to more wildfire in western North American forests as climate changes. *Proceedings of the National Academy of Sciences* 114:4582–4590.
- Smucker, K. M., R. L. Hutto, and B. M. Steele. 2005. Changes in bird abundance after wildfire: importance of fire severity and time since fire. *Ecological Applications* 15:1535–1549.
- Spencer, R.-J., and M. B. Thompson. 2005. Experimental analysis of the impact of foxes on freshwater turtle populations. *Conservation Biology* 19:845–854.
- Stott, P. 2016. How climate change affects extreme weather events. *Science* 352:1517–1518.
- Strickler, G. S. 1959. Use of the densiometer to estimate density of forest canopy on permanent sample plots:5.
- Sutherland, E. F., and C. R. Dickman. 1999. Mechanisms of recovery after fire by rodents in the Australian environment: a review. *Wildlife Research* 26:405.
- Ward, M., A. I. T. Tulloch, J. Q. Radford, B. A. Williams, A. E. Reside, S. L. Macdonald, H. J. Mayfield, M. Maron, H. P. Possingham, S. J. Vine, J. L. O'Connor, E. J. Massingham, A. C. Greenville, J. C. Z. Woinarski, S. T. Garnett, M. Lintermans, B. C. Scheele, J. Carwardine, D. G. Nimmo, D. B. Lindenmayer, R. M. Kooyman, J. S. Simmonds, L. J. Souter, and J. E. M. Watson. 2020. Impact of 2019–2020 mega-fires on Australian fauna habitat. *Nature Ecology & Evolution* 4:1321–1326.
- Waters, J. R., and C. J. Zabel. 1995. Northern flying squirrel densities in fir forests of northeastern California. *The Journal of Wildlife Management* 59:858.
- Whelan, R. J. 2002. Managing fire regimes for conservation and property protection: an Australian response. *Conservation Biology* 16:1659–1661.
- Whitham, T. G. 1977. Coevolution of foraging in *Bombus* and nectar dispensing in *Chilopsis*: a last dreg theory. *Science* 197:593–596.
- Wywiałowski, A. P. 1987. Habitat structure and predators: choices and consequences for rodent habitat specialists and generalists. *Oecologia* 72:39–45.

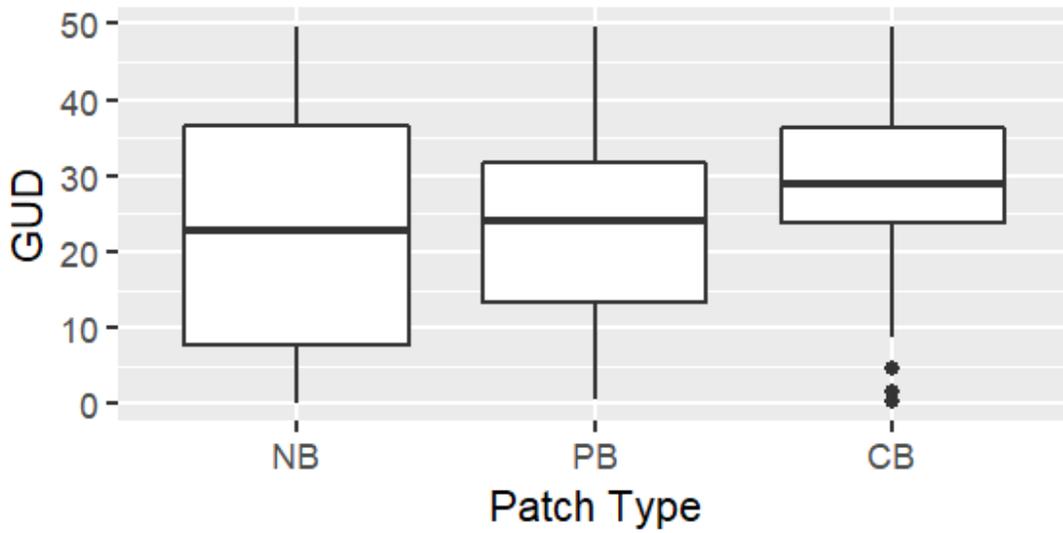


Figure 1.1: Grams of sunflower seeds collected from the trays (therefore non-eaten by animals = high GUD) in the 3 burn severity patches (CB=completely burned, PB= partially burned, NB=non-burned) on the Pinaleno Mountains, Graham County, Arizona, USA, in summer 2018 and 2019.

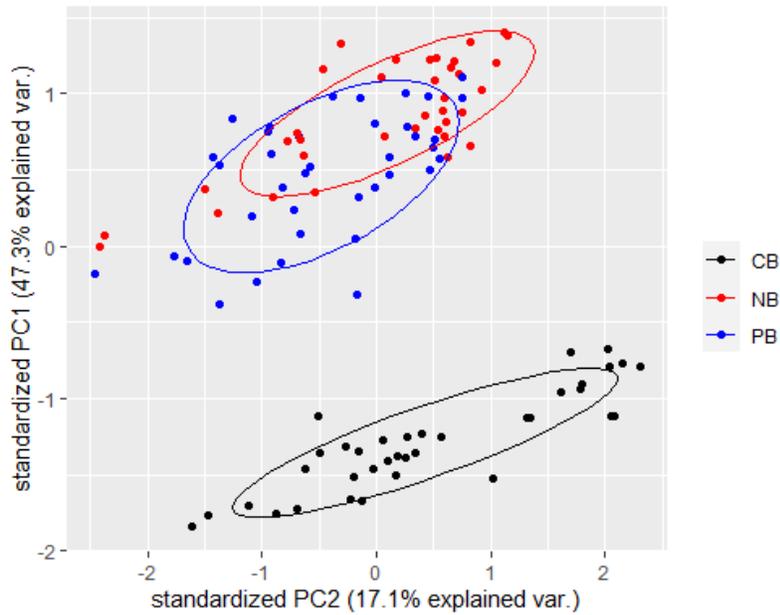


Figure 1.2: The PCA transformation of the vegetation characteristics, collected on the Pinaleño Mountains, Graham County, Arizona, USA, in summer 2018 and 2019. The PCA transformation of the vegetation characteristics at burned severity patches, explained 78% of the variation in the first 3 PCs. The first PC emphasized the change from more open areas of dead or dying trees to healthy small and large trees, with higher canopy cover. The second PC emphasized the change from numerous logs and less grass cover to less volume of logs and higher grass cover.

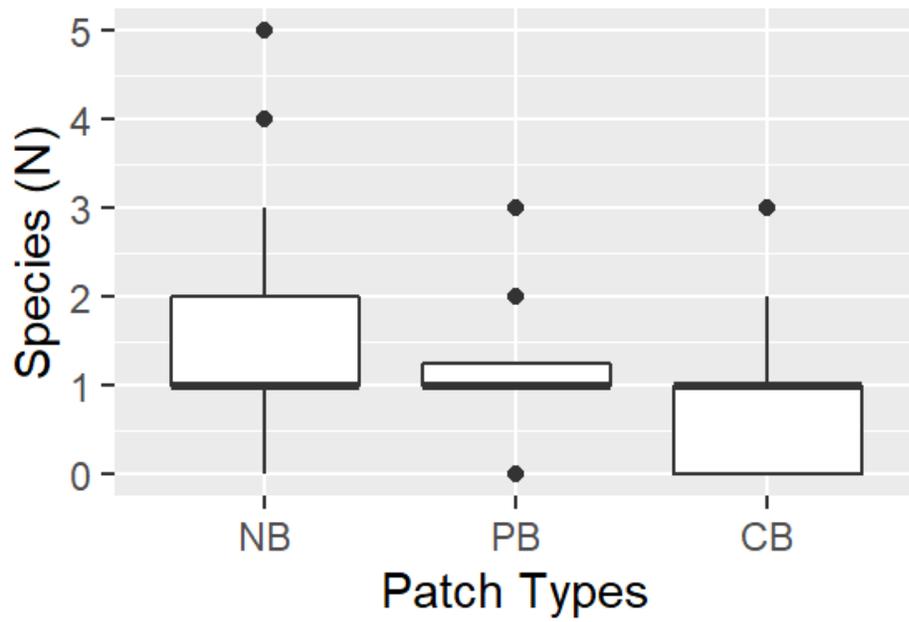


Figure 1.3: Box plot of the number of species of vertebrates detected in each tray per burn severity (CB=completely burned, PB= partially burned, NB=non-burned) on the Pinaleno Mountains, Graham County, Arizona, USA, in summer 2018 and 2019.

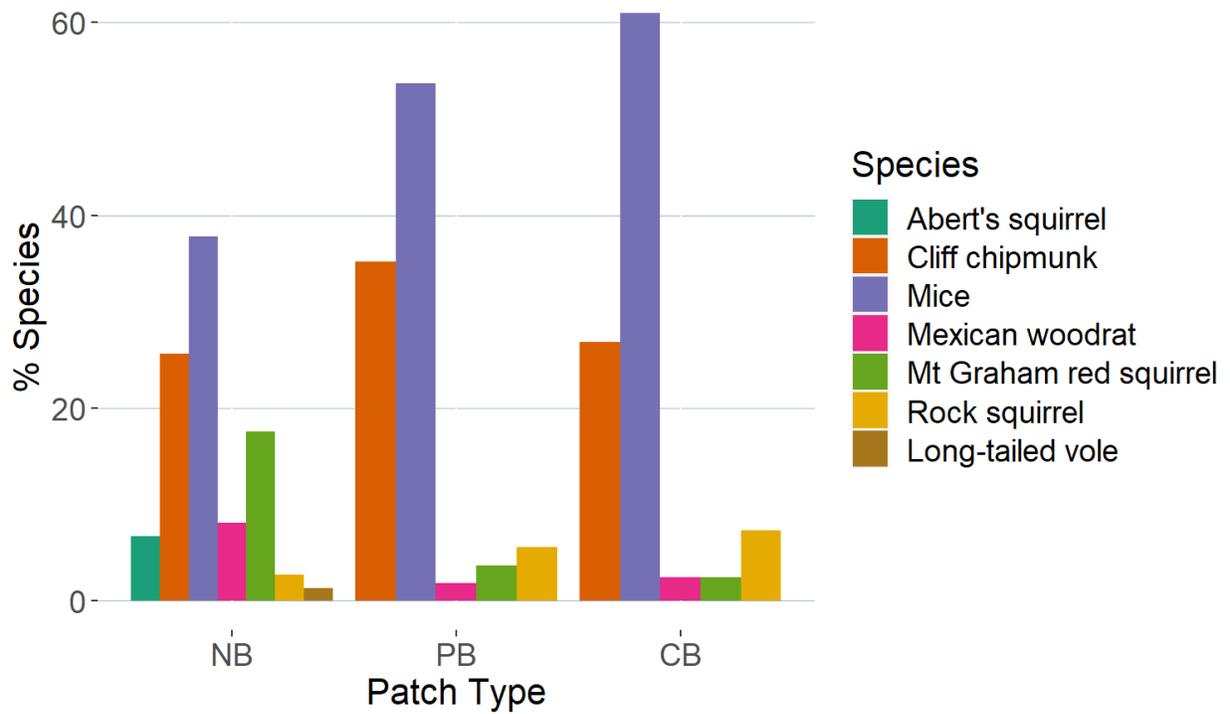


Figure 1.4: Species composition in each patch type, characterized by different burn severity (NB= non burned, PB= partial burned, CB= complete burned) on the Pinaleno Mountains, Graham County, Arizona, USA, in summer 2018 and 2019.

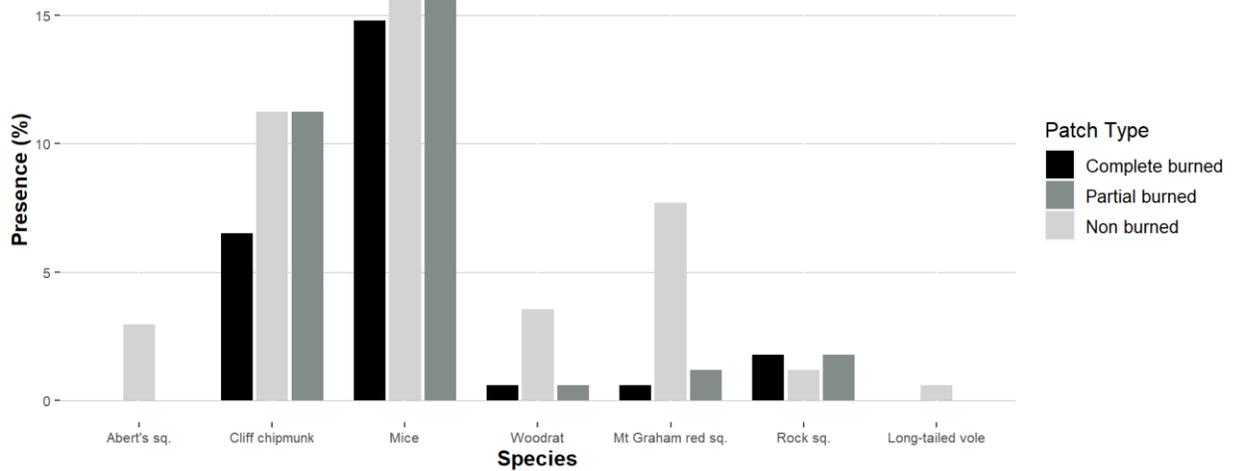


Figure 1.5: Percentage of presence of each species (Abert's squirrel - *Sciurus aberti*, cliff chipmunk - *Tamias dorsalis*, Mt Graham red squirrel - *Tamiasciurus fremonti grahamensis*, mouse - *Peromyscus sp.*, Mexican woodrat - *Neotoma mexicana*, rock squirrel - *Otospermophilus variegatus*, long-tailed vole - *Microtus longicaudus*) at the 3 different burn severity patches (Complete, partial and non-burned) on the Pinaleño Mountains, Graham County, Arizona, USA, in summer 2018 and 2019.

Table 1.1: Results of generalized linear mixed model (Binomial distribution, logit link), examining the effect of burn severity, year, and total volume of logs on the GUD (grams of seeds left at the tray) on the Pinaleño Mountains, Graham County, Arizona, USA, in summer 2018 and 2019. Area was entered as a random effect in the model.

<b>Fixed effects</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>Z value</b>	<b>P value</b>
Intercept	0.581	0.633	0.918	0.335
Year (2019)	4.376	1.053	4.153	< 0.0001
Non burned patches	-0.057	0.676	-0.085	0.933
Partial burned patches	0.461	0.692	0.666	0.505
Tot. logs volume	0.097	0.460	0.211	0.833

Table 1.2: Results of linear mixed model (Gaussian distribution, identity link), examining the effect of burn severity, year, and total volume of logs on the GUD (grams of seeds left at the tray) on the Pinaleno Mountains, Graham County, Arizona, USA, in summer 2018 and 2019. Area was entered as a random effect in the model.

<b>Fixed effects</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>T value</b>	<b>P value</b>
Intercept	31.44	4.37	7.180	0.0006
Patch Type Non Burned	-7.038	2.34	-2.997	0.003
Patch Type Partially Burned	-5.367	2.30	-2.325	0.021
Year 2019	-2.902	2.22	-1.307	0.193
Total Volume of Logs (m <sup>3</sup> )	-0.924	1.02	-0.901	0.369

Table 1.3: Results of linear mixed models, examining the effect of vegetation characteristics on the GUD (grams of seeds left at the tray) in different burned severity patches on the Pinaleno Mountains, Graham County, Arizona, USA, in summer 2018 and 2019. Area was entered as a random effect in the model.

Variable	NB			PB			CB		
	Estimate	T	p	Estimate	T	p	Estimate	T	p
<b>Intercept</b>	17.149 ± 5.10	3.362	0.004	22.419 ± 2.80	7.995	0.004	28.517 ± 2.65	10.749	0.002
<b>Tot. Volume logs (m<sup>3</sup>)</b>	-5.423 ± 2.66	- 2.038	<b>0.048</b>	2.915 ± 1.60	1.818	0.075	-6.675 ± 1.73	-3.853	< <b>0.001</b>
<b>% Grass Cover</b>	0.345 ± 1.91	0.181	0.859	3.812 ± 2.18	1.746	0.087	-2.010 ± 1.75	-1.145	0.259
<b>% Small Tree Cover</b>	-5.796 ± 2.07	- 2.798	<b>0.014</b>	-0.0423 ± 2.00	-0.021	0.983	-0.633 ± 1.99	0.318	0.752
<b>% Canopy Cover</b>	10.093 ± 4.45	2.267	<b>0.033</b>	9.080 ±2.75	3.296	<b>0.002</b>			

Table 1.4: Number of trays where each species has been detected during the experiment (60 trays for 3 rounds) and percentage of each species detected over the total amount of trays during the entire experiment (180 trays) on the Pinaleño Mountains, Graham County, Arizona, USA, in summer 2018 and 2019.

<b>Species</b>	<b>N. detection</b>	<b>Percentage</b>
<i>Peromyscus sp.</i> - Mouse	82	45.55%
<i>Tamias dorsalis</i> – Cliff chipmunk	49	27.22%
<i>Tamiasciurus fremonti grahamensis</i> - Mt Graham red squirrel	16	8.88%
<i>Mephitis mephitis</i> – Striped skunk	10	5.55%
<i>Otospermophilus variegatus</i> - Rock squirrel	8	4.44%
<i>Neotoma mexicana</i> – Mexican woodrat	8	4.44%
<i>Ursus americanus</i> - Black bear	6	3.33%
<i>Sciurus aberti</i> - Abert’s squirrel	5	2.77%
Bird sp.	4	2.22%
<i>Urocyon cinereoargenteus</i> - Gray fox	1	0.55%
<i>Microtus longicaudus leucophaeus</i> – Long-tailed vole	1	0.55%
No species detected	30	16.66%
NA (problems with camera, but seeds eaten)	25	13.88%

## Appendix B: Using a substitute species to inform translocation of an endangered territorial mammal

Marina Morandini<sup>1</sup>, John L. Koprowski<sup>2</sup>

1 School of Natural Resources and the Environment, University of Arizona, Tucson, AZ

2 Haub School of Environment and Natural Resources, University of Wyoming, Laramie, WY

### ***Abstract***

Substitute species can inform management strategies without exposing endangered species unnecessarily. Further, experimental approaches may help to identify the causes of translocation failures, leading to improve the chances of success. We used a surrogate subspecies, *Tamiasciurus fremonti fremonti* to test different translocation techniques to inform potential management actions on the endangered Mt. Graham red squirrel (*Tamiasciurus fremonti grahamensis*). We fitted VHF radio collars to 54 animals, and we monitored their survival and movements until individuals settled on a new territory. We considered the effect of season, translocation technique (soft or hard release), and body mass on survival, distance moved after release, and time to settlement of translocated animals. Survival probability averaged 0.48 after 60 days from the translocation event and was not affected by season or translocation technique. Predation was the 54% cause of mortality. Distance moved and number of days to settlement varied with season, where winter was characterized by shorter distances (average of 364 m in winter versus 1752 m in fall) and fewer days (6 in winter versus 23 in fall). These data emphasize the potential of substitute species to provide valuable information on possible outcomes of management strategies for closely related endangered species.

**Keywords:** substitute species, translocation, endangered species, management techniques, squirrels

## ***Introduction***

Managing endangered species to ensure their long-term persistence is a central theme in modern conservation science (Wiens and Hobbs 2015, Scheele et al. 2018). Endangered species are broadly characterized by small population sizes (IUCN 2021), which can lead to genetic problems such as inbreeding depression, loss of genetic variation, and accumulation of deleterious mutations (Hedrick and Kalinowski 2000, Díez-del-Molino et al. 2018), and elevated risk of extinction due to stochastic events (Hylander and Ehrlén 2013). The intrinsic value of species, as well as the services and the economic benefits that biodiversity provide to humans, are key reasons to consider conservation actions to slow or reverse biodiversity losses (Pearson 2016).

Translocation—the intentional movement of animals for conservation purposes—is a technique used since the beginning of 1900’s for reintroductions (Seddon et al. 2007), and from 1990’s also as a technique to mitigate the loss and depletion of endangered species (Blumstein and Fernández-Juricic 2010, Drake and Temple 2012, Resende et al. 2020). However, numerous examples worldwide have shown failures for translocation programs across a wide variety of species (Drake and Temple 2012, Nafus et al. 2017). Multiple factors contribute to the outcomes of translocations, and often differ among species (Bubac et al. 2019). Individual characteristics (e.g. personality, physical condition, age, sex), source populations (e.g. genotype, captive vs wild born), post-release environments (e.g. predation, habitat), seasonality, and translocation techniques (e.g. handling procedures, soft vs. hard release) can all lead to varying outcomes (Letty et al. 2007). Common problems with translocations include high mortality, low breeding success, and wandering behavior associated with translocated individuals (Letty et al. 2007).

An experimental approach may help identify and mitigate factors that influence the outcome of translocations, which could reduce translocations failures (Bubac et al. 2019). However, such an approach may not be feasible for endangered taxa that, ethically, should not be used for experimentation in the wild (National Research Council, 1995, Gannon & Sikes, 2007). In this context, using ecologically and genetically similar species (i.e., substitute species) to test management strategies is a valuable tool to avoid disturbance of species already facing numerous challenges (Caro et al. 2005, Murphy et al. 2011). A substitute species is defined as “species or populations studied with the assumption that they show how populations of conservation concern might respond to environmental disturbance” (Caro et al. 2005). For this reason, the criteria used

to choose an appropriate surrogate species is critical to obtain the most reliable information to support conservation efforts (Caro and O’Doherty 1999, Caro et al. 2005, Murphy et al. 2011).

The endangered Mt. Graham red squirrel (*Tamiasciurus fremonti grahamensis*, (Hope et al. 2016) declined to 35 animals after the extreme decrease in population size resulting from a wildfire in 2017 (Merrick et al. 2021). Given the critical status of this population, active conservation efforts that include translocation to new areas or augmentation of the population from *ex situ* bred stock should be considered. Because these actions involve translocating squirrels between areas, proper translocation techniques must be developed and evaluated. Using a surrogate species to illuminate how an endangered species may respond to conservation translocation techniques is a logical management strategy. Fremont’s red squirrel, (*T. f. fremonti*, Hope et al. 2016) is genetically similar to the Mt. Graham red squirrel (Fitak et al. 2013). Thus, this subspecies could be a substitute species candidate to test different translocation techniques to inform management actions for the endangered Mt. Graham red squirrel.

Although assessing the outcomes of substitute species may better inform conservation decisions for other imperiled taxa, these strategies have not been thoroughly evaluated in a conservation context. In this study, we use a substitute species to examine the potential effects of seasonality, translocation technique, and body mass on the survival, post-release dispersal distances, and time to settlement of translocated animals. In particular: 1) we think body mass at the time of release, translocation type, and season will influence the survival of animals after translocation. We predict higher survival for larger animals released in fall with soft release techniques. Higher body mass indicates more fat reserves, constituting energy reservoir, (Humphries and Boutin 1996, Wauters et al. 2007) which may be important during the period when animals search for a new area to settle. Soft release allows animals to acclimate to the area prior to release (Wanless et al. 2002). Fall is characterized by the availability of a large quantity of conifer cones, the principal food source of red squirrels (Lamontagne and Boutin 2007, Fletcher et al. 2010). 2) We predict that in winter with soft release techniques, animals will settle closer to the release site and spend less time before settling in a new site. Winter is characterized by limited food availability (Smith 1968; Hurly and Lourie 1997). In winter, intraspecific competition is also lower because most of the juveniles who did not establish a new midden likely experienced mortality, decreasing population density (Larsen and Boutin 1994). Therefore, we expect higher site fidelity in translocated animals during winter when competition is low and animals have more time to explore the surroundings without

encountering conspecifics. Soft release, instead, allows animals to learn their new environment (Wanless et al. 2002, Parker et al. 2012), therefore, to mitigate their homing response after removal of the holding pen.

## ***Methods and study area***

### **Study species**

We selected *Tamiasciurus fremonti fremonti* as a substitute species because it is the closest genetically and ecologically subspecies to the Mt. Graham red squirrel that is not endangered (Fitak et al. 2013).

The Mt. Graham red squirrel is endemic to the Pinaleño Mountains of southeastern Arizona (Hoffmeister 1956). This population is separated by desert and grasslands approximately 110 km from populations of the nearest related subspecies *T. fremonti fremonti*, located in the White Mountains. This separation occurred approximately 11,000 y ago at the end of the Wisconsin glaciation (Spicer, 1985). Both subspecies inhabit similar forests with comparable habitat characteristics, elevations and weather conditions (Young et al. 2002, Leonard and Koprowski 2009).

Red squirrels are diurnal mammals and are active year around. Red squirrels typically have a single reproductive season focused in late spring or early summer (Smith, 1968; Koprowski, Alanen, & Lynch, 2005). In western North America, red squirrels are territorial and vigorously defend the center of their territory and their larderhoard (midden) from conspecifics (Smith, 1968; Gurnell, 1984; Koprowski, King, & Merrick, 2008). Squirrels store conifer cones when available in their midden and in pits in the ground. Middens are necessary for survival as they provide cool, moist conditions that prevent cones from drying and opening (Merrick et al. 2021), thus furnishing a reliable food supply over winter (Smith 1968, Hurly and Lourie 1997). For this reason, acquisition of a territory after natal dispersal is critical to survival and reproduction of male and female red squirrels (Rusch and Reeder 1978, Larsen and Boutin 1994). Forest structure around middens is important in creating a microclimate necessary for cone preservation in addition to providing nesting sites, cover and escape routes from predators, and access to foraging sites (Smith 1968).

## **Study area**

We studied squirrels in two study sites in the Apache-Sitgreaves National Forest in the White Mountains (Arizona, USA). The first study site was near Big Lake (UTM coordinates: 12S 647118.39216871 3750447.4959222), while the second site was near Hannagan Meadow (12S 655714.23295814 3723357.028484). Both sites had similar elevation, between 2650 - 2750 m and mixed conifer forest type. Common species were Douglas fir (*Pseudotsuga menziesii*), blue spruce (*Picea pungens*), corkbark fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), ponderosa pine (*Pinus ponderosa*), southwestern white pine (*P. strobiformis*), and aspen (*Populus tremuloides*) (Young et al. 2002). Sites are 32 km apart.

## **Trapping and release strategies of the animals**

We experimentally translocated squirrels during the fall of 2018, 2019, and 2020, and during the winter of 2018/2019 and 2019/2020. In fall, we started translocations in August until October, and we monitored the animals until the first snow (October for 2018, November for 2019). In winter, we translocated animals starting in December, until the beginning of March and we check the translocated animals until the end of April.

We used Big Lake in fall and Hannagan Meadow in winter due to accessibility. Although it is possible season might be confounded with location, both sites have stable red squirrel populations and the same vegetation type and structure suggesting this is unlikely.

We trapped squirrels with wire-mesh box live traps (Tomahawk Live Trap, Tomahawk WI: Model # 201) baited with peanuts and peanut butter. We transferred animals to a cloth handling cone (Koprowski 2002) and marked each animal with a unique numbered ear tag (Monel 1005-1, National Band and Tag) and coloured ear disks (1 cm Model 1842, National Band and Tag), for individual identification. We weighed each animal with a Pesola spring balance to the nearest 5g and recorded reproductive condition. Handling time was never more than 5 min to reduce stress. Before translocating an individual, each was equipped with a radio collar (SOM 2190, Wildlife Materials International, 5-7g which is less than 5% of the individual's body mass).

During the first fall in 2018, we translocated two animals 900 m from the point of capture, and both returned to their territory within a few hours. For all other translocations, we used a distance > 3000 m. All animals were translocated to areas inhabited by other red squirrels due to difficulty

of finding areas that had no established squirrels yet met the environmental requirements for settlement.

We implemented the hard release technique by trapping animals and transferring each in nest boxes to the new area (34 cm H, 18 cm W, 23 cm L). Nest boxes were provisioned with nesting material (hay), peanuts, and peanut butter with entrance holes closed to minimize visual cues known to facilitate homing (Bakker 2006). We retained squirrels at their release site in their closed nest boxes during the first night at a height of 2 m.

For soft releases, we transferred individuals inside a nest box to an enclosure (152 cm H, 90cm W, 90 cm L). We provided the enclosure with approximately 400 locally collected spruce cones and a feeder with peanuts, peanuts butter, and rodent chow as supplemental feeding. We kept the squirrels in the enclosure for 5 days. After five days, we opened the enclosure and let the animals leave when they chose to do so. Sample size for soft release (n=12) is smaller than hard release (n=42) because we were able to obtain the required permit and IACUC approval only in late fall 2019.

We supplemented food different of animals translocated in winter (peanuts, peanuts butter, and rodent chow) at the release site and at different telemetry locations, using a feeder until April. We initially provided 500 g of peanuts, 500 g of rodent chow and 4 tablespoons of peanuts butter and checked the feeder every two weeks and we refilled when necessary.

### **Telemetry**

We used digital receivers (Communication Specialists Inc. R-1000) and yagi 3-element directional antennas (Wildlife Materials Inc., Murphysboro IL, USA) to track each squirrel's movements from capture to settlement, locating all individuals a minimum of once per day during the first 5 days after translocation. Subsequently, squirrels were tracked at least once per week until settlement, death, or they were missing from the study area. When locating individuals, we were also collected behavioral information.

We classified animals as settled when they exhibited territorial behaviour, including the rattle vocalizations or caching of cones (Larsen and Boutin 1994), or if they remained in a 100-m radius for at least 3 consecutive days. The first day that individuals exhibited territorial vocalization or cone caching was considered the day of settlement; when staying within the same area for at least 3 days, we considered the 3<sup>rd</sup> day as the settlement day. When possible, we trapped animals after

settlement to characterize change in body mass. We defined animals as missing if their signals disappeared during the season (we checked for animals consistently through all seasons) and were never detected subsequently.

We defined 3 types of mortality: unknown predator, avian predator, unknown cause. We identified avian-caused mortalities by the presence of plucked fur, a clipped tail, gut piles, and other miscellaneous parts such as ears; raptor feces or “white wash” was also often located nearby (Goldstein et al. 2018). When we found only a radio-collar, we defined mortality as predation from an unknown predator. When the signal was constantly from a tree with no additional movement but it was not possible to reach the cavity, we defined the mortality as unknown cause. When we were able to recover the body of the animal, we sent the corpse to the Arizona Veterinary Diagnostic Lab, Tucson, Arizona for a detailed post-mortem analysis.

### **Statistical analysis**

We used Proportional Hazard Regression (Cox 1972) to estimate survival for all translocated animals and for post-settlement survival. This approach models event rates (failures) as a log-linear function of predictor variables. In our case, we used body mass (continuous variable), season and type of release (both categorical predictors). Regression coefficients give the relative effect of each covariate on the survivor function (Tabachnick and Fidell 2001).

We used generalized linear models (GLMs, Hadfield 2010) to examine the effect of season (fall or winter), type of release, and body mass on two response variables: time to settlement (d) and distance to settlement (m). Time to settlement was modelled using a Poisson error distribution with log-link, distance of settlement was modelled using a Gaussian error distribution with identity link. We used generalized mixed models (with Gaussian distribution, identity link, and individual treated as a random effect) to determine if season and translocation influenced body mass of squirrels.

### **Results**

In total, we translocated then monitored 54 individual red squirrels (Table 2.1) during 3 fall and 2 winter seasons (2018-2020).

### **Fate of translocated animals**

For the 54 animals translocated, 22 (40.7%) settled, 16 (29.7%) died, 4 (7.4%) returned to their original territory, and 12 (22.2%) disappeared with unknown fates. Excluding animals with unknown fates, of the 42 animals translocated, 52% settled in a new territory, 38% died prior to settling in a new territory, and 10% returned to the original territory. After settlement, 6 of 22 animals were depredated, 4 in winter and 2 in fall (between 17 and 32 days after settlement). The fate of translocated squirrels was similar for both sexes and both seasons (Fig. 2.1).

### **Mortality**

In total, we confirmed 22 mortalities (40%), 15 in winter and 7 in fall. In particular, 12 (54%) died due to predation (6 by raptor and 6 by unknown predator) and 10 (46%) from unknown causes. Among the unknown causes, we had one animal with the signal in a burned area, with the collar under the snow (but impossible to recover), and 5 animals with constant signal coming from a nest, suggesting that the animals died in the nest. In fact, we were able to recover two intact squirrels from the nest where they died, one from a cavity and one from a drey. We sent these two animals, plus a squirrel found dead at the base of a tree (with intact body and no apparent signs of predation), plus one found with signs of predation to a veterinary hospital for a post-mortem examination. For all these animals, the pathologist considered fat stores as adequate, excluding starvation as the cause of death. Except for the animal with signs of predation, which had an ear and few fingers of the front paws missing, no signs of organ damage, or wounds were recorded.

### **Survival and change in body mass after translocation**

Survival probability decreased steadily after translocation and stabilized at about 0.47, 40 days after translocation (Fig. 2.2). Survival did not differ between season or translocation type; however, we observed an effect of body mass on the hazard risk, where an increase of body mass corresponded to a slight decrease in survival (Hazard ratio = 0.97, CI = 0.95-0.99,  $p = 0.039$ ).

We were able to document changes in body mass for 6 of 11 (54%) animals that settled in winter and 4 of 11 (36%) in fall. Translocation resulted in a decrease in body weight ( $\beta = -5.69$ ; SE = 2.36;  $t = -2.4$ ;  $p = 0.02$ ), whereas season had no effect ( $\beta = 2.47$ ; SE = 2.36;  $t = 1.04$ ,  $p = 0.31$ ). On average, we observed a loss of body mass following translocation both in winter and in fall (Fig 2.3).

### **Days before settlement and distance to settlement**

The number of days before settlement and settlement distance were lower in winter than in fall (Fig. 2.4, Table 2.2). Body mass and type of release did not affect the number of days before settlement or settlement distance (Table 2.2). Intensive radio-tracking during the first week post release showed that for 20 of 48 documented individuals (41%), the translocated squirrel was chased away from the release site by a resident local animal. However, in winter only 7 of 25 (28%) were chased away, whereas in fall 13 of 24 were chased away (54%).

## ***Discussion***

We considered season, translocation technique, and body mass on survival, distance moved, and time to settlement of translocated animals. As we predicted, during winter animals showed higher site fidelity than in fall. Moreover, the distance and number of days before settlement were reduced in winter, likely due to limited food availability. Translocation techniques (soft vs. hard) did not influence days and distance to settlement site. Contrary to our prediction, season and type of release did not affect animal survival. Survival was slightly lower for animals with higher biomass, although the effect was quite small.

### **Mortality after translocation: the cost of wandering in a “forced dispersal”**

Translocation forces animals to effectively experience dispersal. During dispersal, we observe three phases: (1) Initiation, when an individual leaves its home area; (2) Wandering, when the dispersing individual searches for new areas before settling; and (3) Settlement, when the individual settles in an area (Penteriani and Delgado 2009). Likewise, translocated animals leave the release site and wander in unfamiliar areas until they select a new place to establish. In those terms, translocation can be viewed as a “forced dispersal” (Kemink and Kesler 2013). The lack of familiarity with the environment likely increases predation risk during dispersal (Larsen and Boutin, 1994), and this was similarly observed during forced dispersal after translocation. The mortality rate of animals during the wandering phase in this study was 42% (excluding animals with unknown fates). In a forced dispersal, however, it is important to distinguish mortalities due to predation from causes connected with the translocation (for example stress). Predation mortality accounted for 31% (excluding missing animals), a similar value to the mortality rate of red squirrels prior to settlement [22% mortality for juvenile in the forests of the Athabasca Sand Hills region of Alberta - Canada (Larsen and Boutin 1994); 27% in the Yukon (Stuart-Smith and Boutin,

1995); 59-67% in Rochester, Alberta (Kemp and Keith, 1970 and Rusch and Reeder, 1978); and 23% for the subspecies, Mt Graham red squirrel - (Merrick and Koprowski 2017)].

The mortality rate in this study is also comparable to other translocated prey species. Translocated Eurasian red squirrels (*Sciurus vulgaris*) in Belgium had 50% (females) to 67% (males) mortality rates in the first months following release (Wauters et al. 1997), 50% for European rabbit (*Oryctolagus cuniculus* - Letty et al., 2000; Letty et al., 2002; Letty et al., 2003), 75% for Iberian hares (Sánchez-García et al. 2021). For each of these studies, the main cause of mortality was predation, which represents a widely documented cost associated with dispersal among mammal species (Bonte et al. 2012). In our study, predation accounted for at least 54% of deaths, mainly due to avian predators. Birds of prey caused 75% of deaths in juveniles and 65% in adults for the Mt Graham red squirrel in the Pinaleño Mountains for settled animals (Goldstein et al. 2018) as well as during dispersal (Merrick and Koprowski 2017).

Although the most common cause of mortality was predation, 10 translocated animals died from unknown causes. Through necropsy, we were able to exclude starvation for 3 of these. A tentative explanation for at least some of these unknown cases of mortality is stress, an inevitable component of translocation (Dickens et al. 2010). Translocation alters stress physiology and chronic stress is potentially a major factor in translocation failure (Dickens et al. 2009). Interestingly, 8 of these 10 animals died during winter translocation. Even if season is not a factor that explained animal survival, mortality inside the nest was more frequent during winter than fall.

### **Seasonal effects on dispersal: food availability as limiting factor in winter**

Seasonality in environmental factors as well as in life-history traits can represent an important factor for the success of translocations. In resource-limited systems, different seasons are often characterized by changes in food availability and/or distribution, which in turn can influence body mass, travel distance, and mortality (Bright and Morris 1994, Poole and Lawton 2009, Milligan et al. 2018). We did not observe a seasonal effect on survival; however, we report an influence of season on the number of days spent by translocated individuals to settle as well as on the distance between release and settlement site. In winter, animals settled faster and closer to the release site than in fall. Food distribution probably affects the movement of the animals. In fact, the cones cached in middens by the red squirrels during the fall are fundamental to sustain the animal during

winter. In the case of translocated animals during winter, the only reliable food source is the artificial food supply provided at the release site (Smith 1968; Hurly and Lourie 1997).

A second factor with potential to explain the difference between seasons on site fidelity of translocated red squirrels is intraspecific competition. In fact, habitat selection is not only affected by the suitability of the settlement site, but also by the density of conspecifics within that habitat (Fretwell and Lucas 1969). In territorial red squirrels, intraspecific competition in fall is high because juveniles disperse from their natal area and try to establish a new midden, or to take a resident's territory (Sullivan and Moses 1986, Berteaux and Boutin 2000, Dantzer et al. 2012, Lane et al. 2015). Since the behaviours associated with dispersal and competition to obtain a territory are costly, juvenile mortality between fall and the onset of winter will be high and population density will decrease (Larsen and Boutin 1994). Therefore, in winter, animals have more time to explore the surroundings without encountering territorial conspecifics. We observed a higher number of aggressive interactions during fall than winter, with local squirrels entering the nest box of translocated animals to chase from the translocation site. Hence, seasonal variation in the intensity of intraspecific competition seems an important factor in the settlement decisions after translocation.

#### **No difference between hard and soft release**

We used both soft and hard releases in the translocation of red squirrels. Soft release provides translocated animals the opportunity to acclimate to their release site (Eastridge and Clark 2001, Mitchell et al. 2011, Parker et al. 2012) and allows translocated animals time to learn about key aspects of their new environment, including novel stimuli (Wanless et al. 2002) and potential competitors (Parker et al. 2012). However, soft release techniques do not necessarily improve results (for example higher survival) over hard release. In our study, the type of translocation (hard/soft) did not affect survival, distance to settlement site, or number of days to settlement in red squirrels. The smaller sample of soft release animals relative to hard release animals, might have affected our results. However, results from other studies also reported mixed advantages of soft release. Soft release generally improved survival, reduced movement and increased site fidelity (Tetzlaff et al. 2019). However, multiple cases exist where no difference in outcomes have been documented between hard and soft releases, as for the case of brushtail possums (*Trichosurus*

*vulpecula* - Bannister et al. 2020), hare-wallaby (Hardman and Moro 2006), and translocated colonies of black-eared miner (Clarke et al. 2002).

The absence of benefit of soft release on site fidelity can be attributed to the pressure exerted by resident conspecifics. In fact, most translocated animals (41%) were chased away by residents in the first 3 days after release. During the fall, the pressure exerted by the red squirrels present in the release area was intensified, where resident animals were exploring the enclosure and were making territorial calls from the top of the enclosure directly towards the translocated animals within the enclosure. This solitary territorial species benefits from having stable neighbours (Siracusa et al. 2018a), at a point where animals avoid settlement in new empty middens even when they occupy poorer quality territories (Larsen and Boutin 1995). For this reason, translocating single animals can cause the disruption of social relationship with territorial neighbours, which could have an impact on survival and behavior of translocated animals (Shier and Swaisgood 2012).

#### **Qualitative observations: translocation and weigh loss**

We observed a loss of body mass following translocation both in winter and in fall. One individual lost 9.5% of body mass during only 5 days of wandering behavior (released at 280 grams and 5 days later recaptured with a weight of 255 g). Many explanations are possible for this phenomenon. Translocation might cause increased physiological stress in animals, which in turn can reduce their body mass (Dickens et al. 2009); or increase energetically costly behaviours, such as wandering (Penteriani and Delgado 2009). Therefore, individuals with a higher fat reserve can be better equipped to deal with low food intake during the wandering phase after translocation. In this phase animals also need to learn where to find food and shelter, and the quality of nest sites will influence energy consumption for thermoregulation, particularly when weather conditions are extreme. After an initial loss of weight, we also recorded an increase in body mass after one month post settlement.

Middens are a fundamental component of red squirrels' territory; they provide shelter, escape from predators and a reliable food supply during winter (Woods 1980). For this reason, we can consider that translocated animals that settled in a new midden, successfully completed the post-translocation period. For these new residents, we expect normal behavior as well as a survival rate similar to other resident animals in the area. We observed two females in lactation, after settling in a midden, as well as males in scrotal reproductive condition. During winter, some individuals settled in an area, using artificial food, stealing cones from other middens, and moved into an

existing midden only later in the season. In fall, we observed squirrels using old middens, or creating a new midden by initiating caching of cones in a new area.

### **Implication for conservation management: can we use translocation on the endangered Mt Graham red squirrel?**

The lesson learned from this study using a substitute species showed that translocation as a conservation strategy could result in a low survival rate of the squirrels translocated. Our findings showed that the winter is the best season for translocating squirrels if retention at the release site is a priority. However, while in the fall the most common cause of death was predation, in winter animals mostly died of unknown causes (potentially stress). The identification of the cause of death during winter could provide the possibility to mitigate this cause and increase survival.

An important factor to be considered when planning on the translocation of the Mt. Graham red squirrel is the intra- and interspecific competition (Richardson and Ewen 2016). If the release site is not occupied by any other tree squirrel, the quality of the habitat would be the condition to select such site and we can expect higher retention, and/or shorter movements before settlement. However, if the translocation happened in multiple years, it is important to consider the distribution of resident conspecifics to address the translocation outcome (Sullivan et al. 2012). Moreover, multiple translocation events in the same site might negatively impact those individuals that have already settled because of a sudden increase of abundance of the local population. For a solitary and territorial species such as the Mt Graham red squirrel, the translocation of squirrels with their stable neighbors might benefit translocation (Shier and Swaisgood 2012). In fact, red squirrels during natal dispersal often choose territory sites close to familiar neighbors (Berteaux and Boutin 2000, Lane et al. 2015) and the presence of familiar neighbors reduces rates of territorial rattle calls and increases time spent in the nest (Siracusa et al. 2018b).

Specifically on Mt. Graham, the presence of Abert's squirrel (*Sciurus aberti*), non-territorial tree squirrel spread across the entire mountain, could be a limiting factor for the success of the translocation. In fact, this species went extinct in this mountain range but was later reintroduced in the 1950s. Abert's squirrels indirectly compete with Mt Graham red squirrels for food resources (Derbridge and Koprowski 2018); hence, the presence of this competitor could change the availability of food for the red squirrel and limit the density of the new translocated population.

Finally, another variable that could affect the success of the translocation is the age of the individuals translocated (Letty et al. 2007). In this study we translocated only adult individuals. However, squirrels naturally disperse when they leave their natal territory to settle on their own, where they usually spend the rest of their life. Therefore, there might be the possibility of a higher retention of juveniles at the release site due to reduced homing response and a predisposition to settle in a new area. We highlight the need of further research before this conservation strategy could be applied on the endangered Mt Graham red squirrel.

### **Lessons from using substitute species**

Our results emphasize the potential of substitute species to provide valuable information on possible outcomes of management strategies for closely related endangered species. In fact, our methodology was useful to develop and improve management strategies, including translocation, to achieve an increase in the likelihood of success (Sarrazin and Barbault 1996). For example, substitute species can help to design individual marking, monitoring methods, and to test translocation techniques (Spencer 2000), as well as to compare soft vs hard release (Tennant and Germano 2017), and to refine the techniques to translocate and hand-rearing chicks (Deguchi et al. 2012). Substitute species also aid in the identification of key problems that can arise during phases of management plans and that may affect the related target species (Fischer & Lindenmayer, 2000). Hence, the outcomes of these trials will assist with different and better management strategies, as illustrated by the translocation of mountain lions in Florida (Belden and Hagedorn 1993).

Finally, our study shows that substitute species allow us to test management strategies, obtain an adequate sample size for statistical inference, and to test multiple scenarios, without risking the endangered species. In our case, the estimated population size of the endangered species when we planned this study (fall 2017) was only 35 individuals (Merrick et al. 2021), therefore it would be impossible to test any management strategies directly on the remaining animals, without the multiple risks associated with any type of manipulation. Despite the potential offered by substitute species, not many studies used a non-endangered relative species as a substitute for an actual target species (Harrington et al. 2013). Here, we have demonstrated, using a substitute species to obtain essential knowledge, how the translocation technique can be potentially detrimental when applied to an endangered species. Such results assist in delivering the appropriate methods and testing new

approaches using the substitute species. We therefore conclude the value of a substitute species for testing management strategies before applying to an endangered species and suggest that such applications should be considered early in the process.

## *Acknowledgments*

We thank the agency partner Arizona Game and Fish Department and the University of Arizona School of Natural Resources and the Environment. We would like to thank the Mt. Graham Red Squirrel Research Program graduate and undergraduate research assistants for valuable help in the field. This research was supported by grants to JLK from the University of Arizona, Arizona Game and Fish Department (grants no. I18005 and I16002), and T & E Inc. Grants for Conservation Biology. All field work was conducted under University of Arizona Institutional Animal Care and Use Committee protocol # 16-169, Arizona Game and Fish Department scientific collecting permit # SP651773 for 2019, SP403044 for 2020, SP407072 for 2021, U.S. Fish and Wildlife Service permit # TE041875-2 and adhered to the American Society of Mammologist's guidelines for the use of wild mammals in research (Sikes & Gannon, 2011). This manuscript was improved by comments from R. W. Mannan, L. Wauters, R. Steidl, and M.V. Mazzamuto.

## References

- Bakker, V. J. 2006. Microhabitat features influence the movements of red squirrels (*Tamiasciurus hudsonicus*) on unfamiliar ground. *Journal of Mammalogy* 87:124–130.
- Bannister, H. L., R. Brandle, S. Delean, D. C. Paton, and K. E. Moseby. 2020. Supportive release techniques provide no reintroduction benefit when efficacy and uptake is low. *Oryx* 54:206–214.
- Belden, R. C., and B. W. Hagedorn. 1993. Feasibility of translocating panthers into Northern Florida. *The Journal of Wildlife Management* 57:388–397.
- Berteaux, D., and S. Boutin. 2000. Breeding dispersal in female North American red squirrels. *Ecology* 81:1311–1326.
- Blumstein, D. T., and E. Fernández-Juricic. 2010. A primer of conservation behavior. Sinauer Associates, Sunderland, Mass.
- Bonte, D., H. V. Dyck, J. M. Bullock, A. Coulon, M. Delgado, M. Gibbs, V. Lehouck, E. Matthysen, K. Mustin, M. Saastamoinen, N. Schtickzelle, V. M. Stevens, S. Vandewoestijne, M. Baguette, K. Barton, T. G. Benton, A. Chaput-Bardy, J. Clobert, C. Dytham, T. Hovestadt, C. M. Meier, S. C. F. Palmer, C. Turlure, and J. M. J. Travis. 2012. Costs of dispersal. *Biological Reviews* 87:290–312.
- Bright, P. W., and P. A. Morris. 1994. Animal translocation for conservation: performance of dormice in relation to release methods, origin and season. *Journal of Applied Ecology* 31:699–708.
- Bubac, C. M., A. C. Johnson, J. A. Fox, and C. I. Cullingham. 2019. Conservation translocations and post-release monitoring: Identifying trends in failures, biases, and challenges from around the world. *Biological Conservation* 238:108239.
- Caro, T., J. Eadie, and A. Sih. 2005. Use of substitute species in conservation biology. *Conservation Biology* 19:1821–1826.
- Caro, T., and G. O’Doherty. 1999. On the Use of surrogate species in conservation biology. *Conservation Biology* 13:805–814.
- Clarke, R. H., R. L. Boulton, and M. F. Clarke. 2002. Translocation of the socially complex Black-eared Miner *Manorina melanotis*: a trial using hard and soft release techniques. *Pacific Conservation Biology* 8:223–234.
- Cox, D. R. 1972. Regression models and life-tables. *Journal of the Royal Statistical Society: Series B* 34:187–202.
- Dantzer, B., S. Boutin, M. M. Humphries, and A. G. McAdam. 2012. Behavioral responses of territorial red squirrels to natural and experimental variation in population density. *Behavioral Ecology and Sociobiology* 66:865–878.
- Deguchi, T., J. Jacobs, T. Harada, L. Perriman, Y. Watanabe, F. Sato, N. Nakamura, K. Ozaki, and G. Balogh. 2012. Translocation and hand-rearing techniques for establishing a colony of threatened albatross. *Bird Conservation International* 22:66–81.
- Dickens, M. J., D. J. Delehanty, and L. Michael Romero. 2010. Stress: An inevitable component of animal translocation. *Biological Conservation* 143:1329–1341.
- Dickens, M. J., D. J. Delehanty, and L. M. Romero. 2009. Stress and translocation: alterations in the stress physiology of translocated birds. *Proceedings of the Royal Society B: Biological Sciences* 276:2051–2056.

- Díez-del-Molino, D., F. Sánchez-Barreiro, I. Barnes, M. T. P. Gilbert, and L. Dalén. 2018. Quantifying temporal genomic erosion in endangered species. *Trends in Ecology & Evolution* 33:176–185.
- Drake, D., and S. A. Temple. 2012. Captive propagation and translocation. Pages 293–306 *The wildlife techniques manual*. Silvy, N.J. Johns Hopkins University Press., Baltimore.
- Eastridge, R., and J. D. Clark. 2001. Evaluation of 2 soft-release techniques to reintroduce black bears. *Wildlife Society Bulletin (1973-2006)* 29:1163–1174.
- Fitak, R. R., J. L. Koprowski, and M. Culver. 2013. Severe reduction in genetic variation in a montane isolate: the endangered Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*). *Conservation Genetics* 14:1233–1241.
- Fletcher, Q. E., S. Boutin, J. E. Lane, J. M. LaMontagne, A. G. McAdam, C. J. Krebs, and M. M. Humphries. 2010. The functional response of a hoarding seed predator to mast seeding. *Ecology* 91:2673–2683.
- Fretwell, S. D., and H. J. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:45–52.
- Gannon, W. L., and R. S. Sikes. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy*. 88:15.
- Goldstein, E. A., M. J. Merrick, and J. L. Koprowski. 2018. Low survival, high predation pressure present conservation challenges for an endangered endemic forest mammal. *Biological Conservation* 221:67–77.
- Gurnell, J. 1984. Home range, territoriality, caching behaviour and food supply of the red squirrel (*Tamiasciurus hudsonicus fremonti*) in a subalpine lodgepole pine forest. *Animal Behaviour* 32:1119–1131.
- Hadfield, J. D. 2010. MCMC Methods for multi-response generalized linear mixed models: The MCMCglmm R Package. *Journal of Statistical Software* 33:1–22.
- Hardman, B., and D. Moro. 2006. Optimising reintroduction success by delayed dispersal: Is the release protocol important for hare-wallabies? *Biological Conservation* 128:403–411.
- Harrington, L. A., A. Moehrenschrager, M. Gelling, R. P. D. Atkinson, J. Hughes, and D. W. Macdonald. 2013. Conflicting and complementary ethics of animal welfare considerations in reintroductions. *Conservation Biology* 27:486–500.
- Hedrick, P. W., and S. T. Kalinowski. 2000. Inbreeding depression in conservation biology. *Annual Review of Ecology and Systematics* 31:139–162.
- Hoffmeister, D. F. 1956. Mammals of the Graham (Pinaleno) Mountains, Arizona. *The American Midland Naturalist* 55:257–288.
- Hope, A. G., J. L. Malaney, K. C. Bell, F. Salazar-Miralles, A. S. Chavez, B. R. Barber, and J. A. Cook. 2016. Revision of widespread red squirrels (genus: *Tamiasciurus*) highlights the complexity of speciation within North American forests. *Molecular Phylogenetics and Evolution* 100:170–182.
- Humphries, M. M., and S. Boutin. 1996. Reproductive demands and mass gains: a paradox in female red squirrels (*Tamiasciurus hudsonicus*). *Journal of Animal Ecology* 65:332–338.
- Hurly, T. A., and S. A. Lourie. 1997. Scatterhoarding and larderhoarding by red squirrels: size, dispersion, and allocation of hoards. *Journal of Mammalogy* 78:529–537.
- Hylander, K., and J. Ehrlén. 2013. The mechanisms causing extinction debts. *Trends in Ecology & Evolution* 28:341–346.
- Kemink, K. M., and D. C. Kesler. 2013. Using movement ecology to inform translocation efforts: a case study with an endangered lekking bird species. *Animal Conservation* 16:449–457.

- Koprowski, J. L., M. I. Alanen, and A. M. Lynch. 2005. Nowhere to run and nowhere to hide: Response of endemic Mt. Graham red squirrels to catastrophic forest damage. *Biological Conservation* 126:491–498.
- Koprowski, J. L., S. King, and M. Merrick. 2008. Expanded home ranges in a peripheral population: space use by endangered Mt. Graham red squirrels. *Endangered Species Research* 4:227–232.
- Lamontagne, J. M., and S. Boutin. 2007. Local-scale synchrony and variability in mast seed production patterns of *Picea glauca*. *Journal of Ecology* 95:991–1000.
- Lane, J. E., A. G. McAdam, A. Charmantier, M. M. Humphries, D. W. Coltman, Q. Fletcher, J. C. Gorrell, and S. Boutin. 2015. Post-weaning parental care increases fitness but is not heritable in North American red squirrels. *Journal of Evolutionary Biology* 28:1203–1212.
- Larsen, K. W., and S. Boutin. 1994. Movements, Survival, and Settlement of Red Squirrel (*Tamiasciurus Hudsonicus*) Offspring. *Ecology* 75:214–223.
- Larsen, K. W., and S. Boutin. 1995. Exploring territory quality in the North American red squirrel through removal experiments. *Canadian Journal of Zoology* 73:1115–1122.
- Leonard, K. M., and J. L. Koprowski. 2009. A Comparison of habitat use and demography of red squirrels at the southern edge of their range. *The American Midland Naturalist* 162:125–138.
- Letty, J., J. Aubineau, S. Marchandeu, and J. Clobert. 2003. Effect of translocation on survival in wild rabbit (*Oryctolagus cuniculus*). *Mammalian Biology* 68:250–255.
- Letty, J., S. Marchandeu, and J. Aubineau. 2007. Problems encountered by individuals in animal translocations: Lessons from field studies. *Écoscience* 14:420–431.
- Letty, J., S. Marchandeu, J. Clobert, and J. Aubineau. 2000. Improving translocation success: an experimental study of anti-stress treatment and release method for wild rabbits. *Animal Conservation forum* 3:211–219.
- Letty, J. ((Université P. 6 (France) L. d'Ecologie)), S. Marchandeu, F. Reitz, J. Clobert, and F. Sarrazin. 2002. Survival and movements of translocated wild rabbits (*Oryctolagus cuniculus*). *Game and Wildlife Science (France)*.
- Merrick, M. J., and J. L. Koprowski. 2017. Altered natal dispersal at the range periphery: The role of behavior, resources, and maternal condition. *Ecology and Evolution* 7:58–72.
- Merrick, M. J., M. Morandini, V. L. Greer, and J. L. Koprowski. 2021. Endemic population response to increasingly severe fire: A cascade of endangerment for the Mt. Graham red squirrel. *BioScience* 71:161–173.
- Milligan, S., L. Brown, D. Hobson, P. Frame, and G. Stenhouse. 2018. Factors affecting the success of grizzly bear translocations. *The Journal of Wildlife Management* 82:519–530.
- Mitchell, A. M., T. I. Wellicome, D. Brodie, and K. M. Cheng. 2011. Captive-reared burrowing owls show higher site-affinity, survival, and reproductive performance when reintroduced using a soft-release. *Biological Conservation* 144:1382–1391.
- Murphy, D. D., P. S. Weiland, and K. W. Cummins. 2011. A critical assessment of the use of surrogate species in conservation planning in the Sacramento-San Joaquin Delta, California (U.S.A.). *Conservation Biology* 25:873–878.
- National Research Council. 1995. *Science and the Endangered Species Act*. National Academies Press.
- Parker, K. A., M. J. Anderson, P. F. Jenkins, and D. H. Brunton. 2012. The effects of translocation-induced isolation and fragmentation on the cultural evolution of bird song. *Ecology Letters* 15:778–785.

- Pearson, R. G. 2016. Reasons to conserve N\nature. *Trends in ecology & evolution* 31:366–371.
- Penteriani, V., and M. M. Delgado. 2009. Thoughts on natal dispersal. *Journal of Raptor Research* 43:90–98.
- Poole, A., and C. Lawton. 2009. The translocation and post release settlement of red squirrels *Sciurus vulgaris* to a previously uninhabited woodland. *Biodiversity and Conservation* 18:3205–3218.
- Resende, P. S., A. B. Viana–Junior, R. J. Young, and C. S. de Azevedo. 2020. A global review of animal translocation programs. *Animal Biodiversity and Conservation* 43:221–232.
- Rusch, D. A., and W. G. Reeder. 1978. Population Ecology of Alberta Red Squirrels. *Ecology* 59:400–420.
- Sánchez-García, C., J. A. Pérez, J. A. Armenteros, V. R. Gaudioso, and E. J. Tizado. 2021. Survival, spatial behaviour and resting place selection of translocated Iberian hares *Lepus granatensis* in Northwestern Spain. *European Journal of Wildlife Research* 67:22.
- Sarrazin, F., and R. Barbault. 1996. Reintroduction: challenges and lessons for basic ecology. Cambridge University Press:5.
- Scheele, B. C., S. Legge, D. P. Armstrong, P. Copley, N. Robinson, D. Southwell, M. J. Westgate, and D. B. Lindenmayer. 2018. How to improve threatened species management: An Australian perspective. *Journal of Environmental Management* 223:668–675.
- Shier, D. M., and R. R. Swaisgood. 2012. Fitness costs of neighborhood disruption in translocations of a solitary mammal. *Conservation Biology* 26:116–123.
- Siracusa, E., D. R. Wilson, E. K. Studd, S. Boutin, M. M. Humphries, B. Dantzer, J. E. Lane, and A. G. McAdam. 2018a. Red squirrels mitigate costs of territory defence through social plasticity. [bioRxiv:453993](https://doi.org/10.1101/453993).
- Smith, M. C. 1968. Red Squirrel responses to spruce cone failure in Interior Alaska. *The Journal of Wildlife Management* 32:305–317.
- Spencer, W. D. 2000. Recovery research for the endangered Pacific pocket mouse: An Overview of Collaborative Studies. Page 19.
- Sullivan, T. P., and R. A. Moses. 1986. Red squirrel populations in natural and managed stands of lodgepole pine. *The Journal of Wildlife Management* 50:595–601.
- Tennant, E. N., and D. J. Germano. 2017. Survival of translocated Heermann’s kangaroo rats (*Dipodomys heermanni*) in the San Joaquin Desert of California using hard and soft release methods. *Western Wildlife* 4:1-11.
- Tetzlaff, S. J., J. H. Sperry, and B. A. DeGregorio. 2019. Effects of antipredator training, environmental enrichment, and soft release on wildlife translocations: A review and meta-analysis. *Biological Conservation* 236:324–331.
- Wanless, R. M., J. Cunningham, P. A. R. Hockey, J. Wanless, R. W. White, and R. Wiseman. 2002. The success of a soft-release reintroduction of the flightless Aldabra rail (*Dryolimnas [cuvieri] aldabranus*) on Aldabra Atoll, Seychelles. *Biological Conservation* 107:203–210.
- Wauters, A. L., M. Vermeulen, S. Van Dongen, S. Bertolino, A. Molinari, G. Tosi, and E. Matthysen. 2007. Effects of spatio-temporal variation in food supply on red squirrel *Sciurus vulgaris* body size and body mass and its consequences for some fitness components. *Ecography* 30:51–65.
- Wauters, L. A., L. Somers, and André A. Dhondt. 1997. Settlement behaviour and population dynamics of reintroduced red squirrels *Sciurus vulgaris* in a park in Antwerp, Belgium. *Biological Conservation* 82:101–107.

- Wiens, J. A., and R. J. Hobbs. 2015. Integrating conservation and restoration in a changing world. *BioScience* 65:302–312.
- Woods, S. 1980. *The Squirrels of Canada*. Canadian Museum of Nature.
- Young, P. J., V. L. Greer, and S. K. Six. 2002. Characteristics of bolus nests of red squirrels in the Pinaleno and White Mountains of Arizona. *The Southwestern Naturalist* 47:267–275.

Figure 2.1: Number of red squirrels *Tamiasciurus fremonti fremonti* per different fate by sex and season (winter and fall), after translocation in the White Mountains (Arizona, USA), from 2018 to 2020. The different fate has been identified as dead, establish (settled in a new area, different from the original home range), missing (when the animals was not trackable by telemetry and not possible to locate again), home (animals able to homing after being translocated).

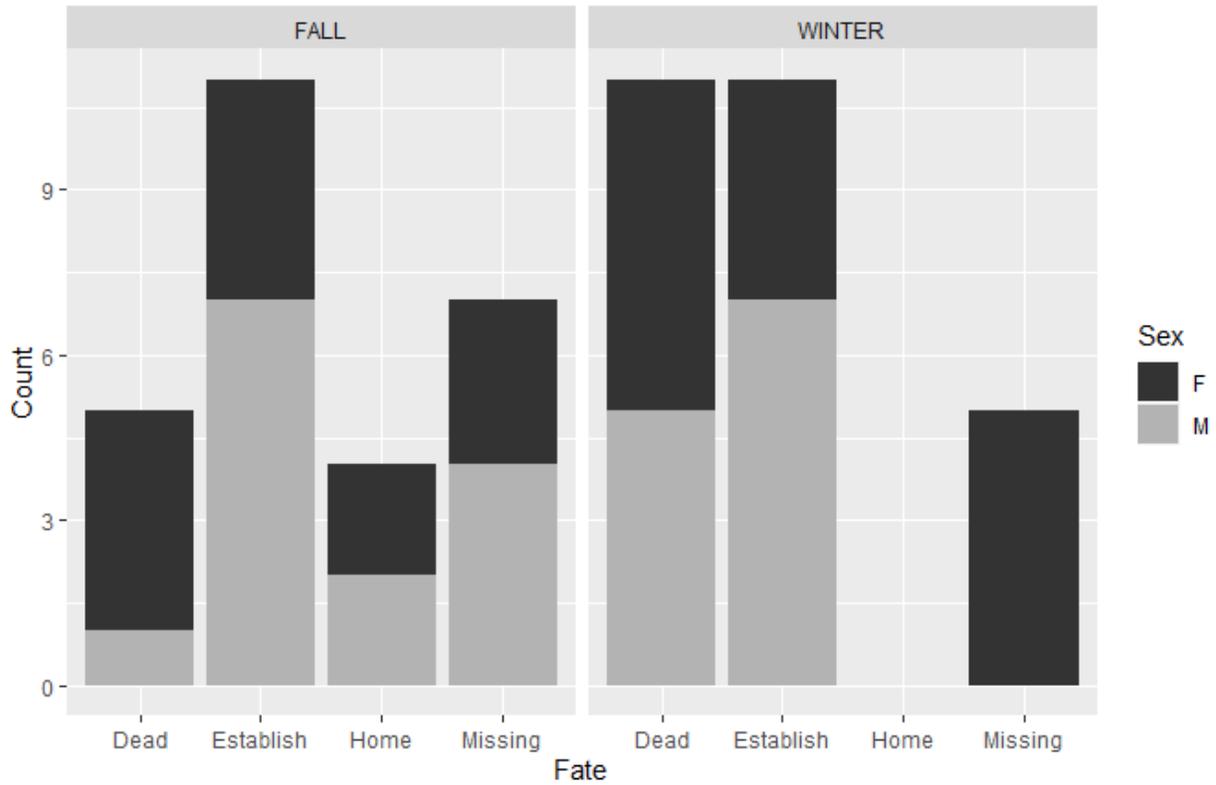


Figure 2.2: Cox Model survival curve of red squirrels *Tamiasciurus fremonti fremonti* after translocation, from the first day of release until 60 days after the release (usually corresponding also to the end of the field season) in the White Mountains (Arizona, USA), from 2018 to 2020. The x-axis is time in days after translocation and the y-axis is survival probability, starting as 1 the day of the animal release and decreasing until just below 0.5 after 40 days.

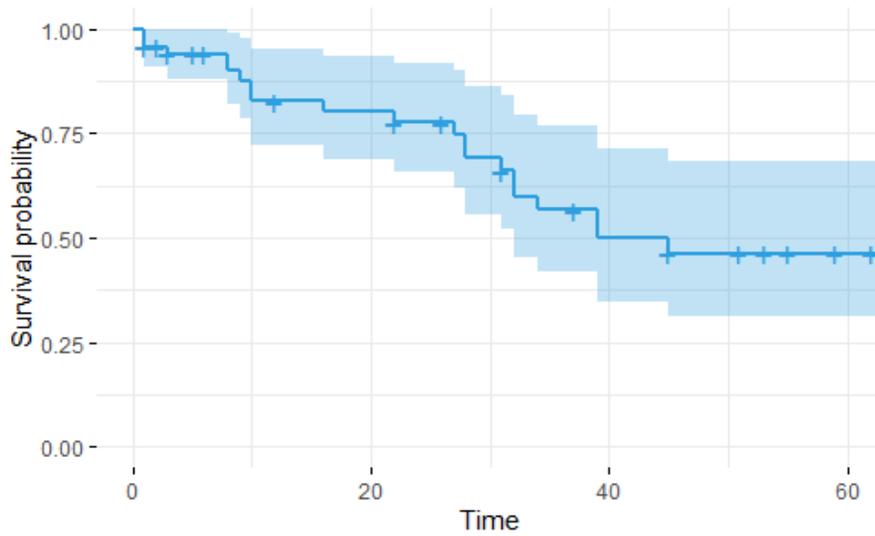


Figure 2.3: Variation in body mass of translocated red squirrels *Tamiasciurus fremonti fremonti* (N=10), expressed as percentage of body mass change after translocation in respect to the weight at release in the White Mountains (Arizona, USA), from 2018 to 2020. In red the variation in body mass of non-translocated animals (N=9), expressed as percentage of body mass change between two trapping sections in respect to the weight of the first trapping event (as a control group).

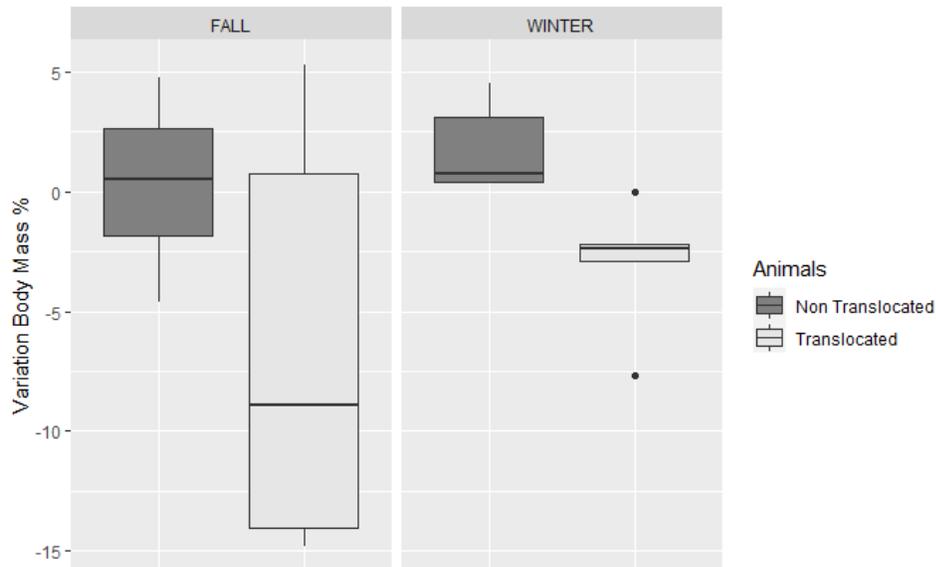
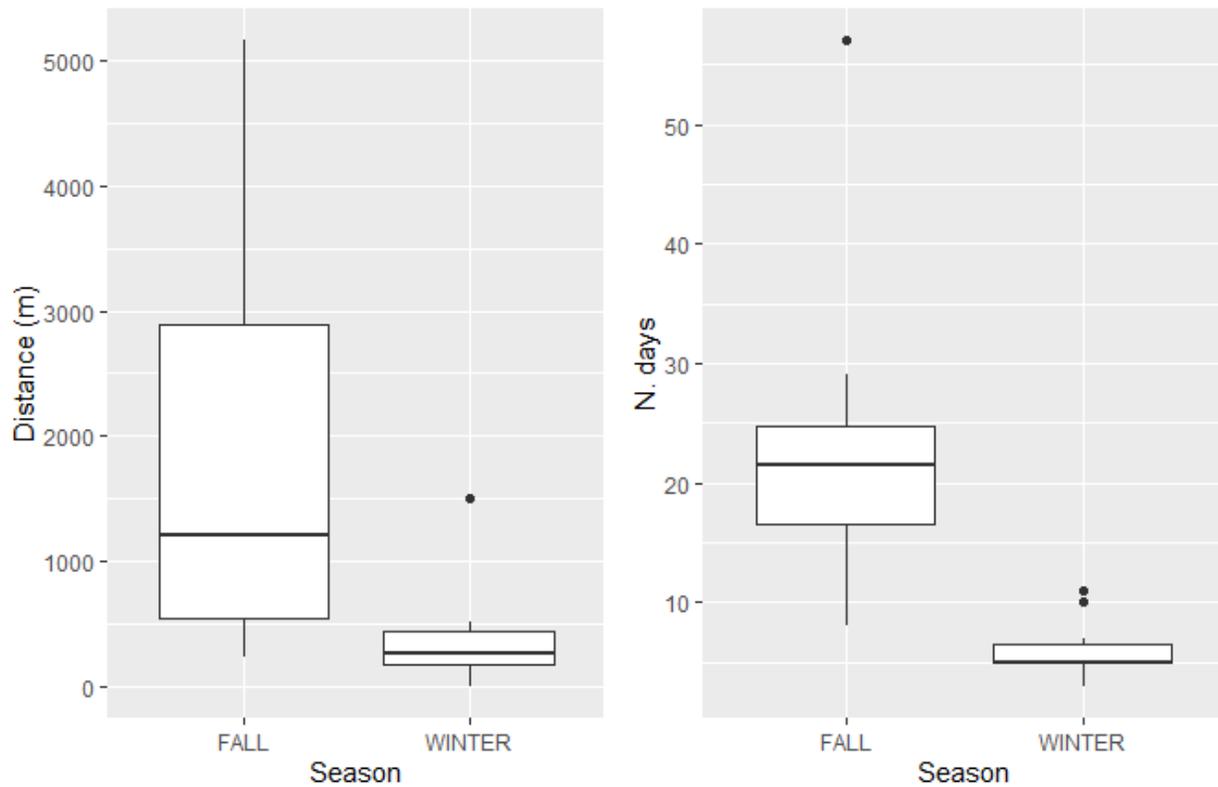


Figure 2.4: Plot of mean, sd, minimum and maximum distance of settlement site to release site (Fall: mean 1752, sd 1472, maximum 5162, minimum 233. Winter: mean 364, sd 421, maximum 1494, minimum 0 - one squirrel stayed at the release site), and number of days passed before squirrel (*Tamiasciurus fremonti fremonti*) settled (Fall: mean 23, sd 13.6, maximum 57, minimum 8. Winter: mean 6, sd 2.45, maximum 11, minimum 3) in the White Mountains (Arizona, USA), from 2018 to 2020.



<i>SEASON</i>	<i>HARD</i>	<i>SOFT</i>	<i>TOTAL</i>
<i>FALL</i>	21 (11 males, 10 females)	6 (3 males, 3 females)	27
<i>WINTER</i>	21 (9 males, 12 females)	6 (3 males, 3 females)	27
<i>TOTAL</i>	42	12	<b>54</b>

Table 2.1: Total number of red squirrels, *Tamiasciurus fremonti fremonti* translocated in the White Mountains (Arizona, USA) from 2018 to 2020, by sex, season (fall and winter), and translocation type (soft and hard).

***DAYS BEFORE SETTLEMENT***

	<b>Estimate</b>	<b>Std. error</b>	<b>Z value</b>	<b>P value</b>
<i>Intercept</i>	2.841	0.833	3.41	0.0006
<i>Season-Winter</i>	-1.326	0.141	-9.34	2 e-16
<i>Type-Soft</i>	-0.111	0.15	-0.73	0.46
<i>Body Mass</i>	0.001	0.003	0.383	0.70

***DISTANCE TO SETTLEMENT SITE***

	<b>Estimate</b>	<b>Std. error</b>	<b>t value</b>	<b>P value</b>
<i>Intercept</i>	4153.84	3605.34	1.15	0.26
<i>Season-Winter</i>	-1.849.54	527.48	-3.58	0.002
<i>Type-Soft</i>	-446.63	602.89	-0.74	0.47
<i>Body Mass</i>	-7.14	13.69	-0.52	0.61

Table 2.2: Estimate regression parameters, standard errors, z values and P values for the generalized linear to examine the effect of season (fall or winter), type of release, and body mass on two response variables: time to settlement (d) and distance to settlement (m) from release site, in the White Mountains (Arizona, USA), from 2018 to 2020.

## Appendix C: Post-translocation movements and the important of conspecific distribution to settlement site selection in a territorial species

Marina Morandini<sup>1</sup>, Javan Bauder<sup>2</sup>, John L. Koprowski<sup>3</sup>

<sup>1</sup> School of Natural Resources and the Environment, University of Arizona, Tucson, AZ, USA

<sup>2</sup> U.S. Geological Survey, Arizona Cooperative Fish and Wildlife Research Unit, University of Arizona, Tucson, AZ, USA

<sup>3</sup> Haub School of Environment and Natural Resources, University of Wyoming, Laramie, WY, USA

### ***Abstract***

Animal translocations are frequently used in conservation programs to assist the recovery of endangered species. Despite its wide use and importance, translocation programs often fail across a wide variety of species as an indirect consequence of extensive post-release movements. Therefore, understanding the factors contributing to extreme post-release movements is crucial for improving translocation efficacy. We examined post-release movement phases and habitat selection of translocated red squirrels (*Tamiasciurus fremonti fremonti*) and how those phases differed between post-release behavioral states. We conducted our study in the White Mts of Arizona and translocated 27 squirrels and monitored their post-release movements using radio telemetry. Post-release movements of translocated red squirrels represent at least two different behavioral phases characterized by differences in movement patterns and the scale of selection for environmental features. During the first phase (hereafter “exploratory phase”), squirrels made long rapid movements and selected areas with taller trees and valley bottoms basing their landscape evaluation at relatively broad spatial scales (i.e., 500-600 m). In contrast, during the second behavioral phase (hereafter ‘settlement phase’), squirrels seemed to behave like resident squirrels by displaying shorter movements within a smaller area, caching food, and defending their middens. Squirrels still selected settlement sites within primarily forested areas in valley bottoms but the scale of response was much lower than during the initial phase. Importantly, translocated squirrels also selected areas with fewer resident conspecifics. Our results highlight the importance of

considering the role of conspecifics, as well as environmental features, also in translocations of solitary species.

## ***Introduction***

Animal translocations —the intentional movement of animals for conservation purposes— have been used since 1900's for reintroductions (Seddon et al. 2007), and from 1990's they have been utilised also as a technique to assist the recovery of endangered species (Blumstein and Fernández-Juricic 2010, Drake and Temple 2012, Resende et al. 2020). Despite its wide use and importance, translocation programs can fail across a wide variety of species (Griffith et al. 1989, Drake and Temple 2012a, Nafus et al. 2017) and these failures are often an indirect consequence of extensive post-release movements (Harrington et al. 2013, Berger-Tal et al. 2020). Such movements have been documented across taxa (Thalmann et al. 2015, Woodford et al. 2013) and are energetically costly while exposing individuals to numerous hazards including increased predation risk, road mortality, and anthropogenic mortality (Jones and Witham 1990, Eastridge and Clark 2001, Yott et al. 2011). Consequently, translocated individuals often have relatively low survival (Letty et al. 2000, Moehrensclager and Macdonald 2003, Stamps and Swaisgood 2007, Ewen et al. 2012), which may jeopardize translocation success. Additionally, translocated individuals may have negative (e.g., aggressive) intraspecific interactions with resident conspecifics which may further exacerbate post-release movement and mortality risk (Linklater and Swaisgood 2008). Understanding the factors contributing to extreme post-release movements is therefore crucial for improving translocation efficacy.

Translocated animals face a unique situation of encountering a completely novel environment and must explore their surroundings to gain knowledge to survive (Frair et al. 2007). These exploratory movements are generally characterized by long and linear movements (Berger-Ta and Saltz 2014). Exploratory, post-release movements may reflect initial disorientation, due to lack of familiarity landmarks for navigation, or attempts to identify suitable resources (Reinert and Rupert 1999, Moehrensclager and Macdonald 2003, Roe et al. 2010, Kesler et al. 2012). These movements may also represent attempts to return to an individual's former home range (homing-behavior; Miller and Ballard 1982, Dickens et al. 2009, Tsoar et al. 2011, Hinderle et al. 2015). As translocated individuals become more familiar with their environment, we expect individuals to shift their movements from exploratory to more localized reflecting the spatial distribution of resources (Eliassen et al. 2007, Berger-Ta and Saltz 2014). In this second phase, animals will show fidelity to areas they perceive as valuable, or as safe from predators, and where they can concentrate on the exploitation of resources (MacArthur and Pianka 1966, Bar-David et al. 2009).

This process of post-translocation behavioral transition has been called post-release behavioral modification (PRBM) from Berger-Tal and Saltz (2014). Therefore, movement after translocation can be classified in two groups: exploration and exploitation (McNicol et al. 2020, Cohen et al. 2022), or, for territorial animals, exploration and settlement.

Post release behavioral modification has implications for understanding post-release habitat selection (Picardi et al. 2022) as different behavioral states may correspond to different resource priorities and scales at which individuals respond to landscape features. For example, if animals during the exploratory phase are primarily focused on locating resource patches or landmarks for navigation, we might expect to see minimal use of resources otherwise used in their original home range. Other studies have observed differences in habitat used patterns between different behavioral states in non-translocated individuals (Zeller et al. 2014, Picardi et al. 2022). For example, reduced selection strength is often observed with dispersing juveniles (Elliot et al. 2014) that may be undertaking similar exploratory movements during dispersal. Therefore, we must consider the different behavioral phases when modeling habitat selection in post-translocated animals (Picardi et al. 2022), although few translocation studies have considered behavioral phase when modeling post-translocation habitat selection (Milligan et al. 2018, Picardi et al. 2022).

The presence of conspecifics can play an important role in guiding individual habitat selection, providing social cues through the interactions or observations of others in the environment (Seppänen et al. 2007, Wagner and Danchin 2010). The presence of conspecifics can attract a disperser, acting as a cue for good habitat quality (Serrano and Tella 2003, Parejo et al. 2007, Martin et al. 2008, Harrison et al. 2009), or, alternatively, can cause intraspecific competition and restrict settlement (Dolev et al. 2002). Understanding the role of intra-specific interactions in habitat selection by translocated individuals is important, particularly for territorial species where the presence of resident conspecifics may limit habitat availability. This is particularly true when repeated translocations are attempted in the same area as increased animal abundance may lead to increased competition and reduction of available habitat (Stamps 2001, Stamps and Krishnan 2005). Therefore, both social structure and landscape characteristics must be considered in translocation project design and implementation.

Increasingly, scientists have used post-release monitoring of translocated individuals to adaptively inform translocation protocols (Coates et al. 2006, Bodinof et al. 2012, Kemink and Kesler 2013).

For example, translocations has been evaluated to implement conservation efforts to protect the federally endangered Mt. Graham red squirrel (*Tamiasciurus fremonti grahamensis*, Hope et al. 2016, Morandini and Koprowski 2022), whose entire population declined to 35 animals after a 2017 wildfire (Merrick et al. 2021). Given the critical status of this population, active conservation efforts including translocation to new areas or population augmentation from *ex situ* captive-bred populations have been considered. However, it is often preferable to develop management protocols for imperiled species using closely related and more abundant surrogate species (Caro et al. 2005, Murphy et al. 2011, Morandini and Koprowski 2022). We therefore studied post-release movement and use of landscape features employing a surrogate species Fremont's red squirrel (*T. f. fremonti*, Hope et al. 2016) to inform management actions for the endangered Mt. Graham red squirrel. Our study addresses the following objectives: 1) we characterized post-release movements as exploratory or settlement movements using a combination of movement metrics and behavioral observations; 2) we tested for selection of landscape features during exploratory phase movements; 3) we evaluated the selection of settlement locations as a function of landscape features and the abundance of conspecific resident squirrels; 4) we compared landscape features at settlement sites to those at each squirrel's original point-of-capture, to test if animals were selecting features similar to their original midden.

## ***Materials and methods***

### **Study species**

The study species for this project is *Tamiasciurus fremonti fremonti* (Hope et al. 2016). Red squirrels (*Tamiasciurus*) are arboreal diurnal mammals with year-round activity and a single annual reproductive season during late spring or early summer (Smith 1968, Koprowski 2005). Red squirrels are territorial and vigorously defend their territory and their larderhoard of conifer cones (i.e., midden) from conspecifics (Smith 1968, Gurnell 1984, Koprowski et al. 2008). Middens are necessary for squirrel survival as they provide cool, moist conditions that prevent cones from drying and opening (Merrick et al. 2021), thus furnishing a reliable food supply over winter (Smith 1968, Hurly and Lourie 1997). For this reason, acquisition of a territory after natal dispersal is critical to survival and reproduction of male and female red squirrels (Rusch and Reeder 1978, Larsen and Boutin 1994). Furthermore, forest structure around middens is important

in creating a microclimate necessary for cone preservation in addition to providing nesting sites, cover and escape routes from predators, and access to foraging sites (Smith, 1968).

### **Study area**

We studied red squirrels near Big Lake (NAD83 UTM coordinates: 12S 647118, 3750447) in the Apache-Sitgreaves National Forest in the White Mountains of east-central Arizona, USA. Dominant tree species were Douglas-fir (*Pseudotsuga menziesii*), blue spruce (*Picea pungens*), corkbark fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), ponderosa pine (*Pinus ponderosa*), southwestern white pine (*P. strobiformis*), and aspen (*Populus tremuloides*) (Young et al. 2002). Spruce was primarily found on northerly aspects or at the base of cooler, wetter valleys.

### **Trapping and release strategies**

We translocated squirrels during three years (2018, 2019, 2020) from August to October. We trapped squirrels with wire-mesh box live traps (Tomahawk Live Trap, Tomahawk WI: Model # 201) baited with peanuts and peanut butter. We transferred animals into a cloth handling cone (Koprowski 2002) and marked each with unique numbered ear tag (Model 1005-1, National Band and Tag Company, Newport, KY) and colored ear disks (1 cm Model 1842, National Band and Tag Company, Newport, KY), for individual identification. We weighed each animal with a Pesola (Pesola, Schindellegi, Switzerland) spring balance to the nearest 5 g and recorded reproductive condition. Handling time was never more than 5 min to reduce stress. Immediately prior to release, we equipped each animal with a 5-7 g radio collar (SOM 2190, Wildlife Materials International, Murphysboro, IL) ensuring that all collars were < 3% of the individual's body mass.

We translocated the first two squirrels in 2018 approximately 900 m from their capture points. However, each animal returned to its territory in only few hours, so we translocated all subsequent animals > 3000 m from their capture point, and we did not include these first two animals in subsequent analysis. All translocated animals were released in areas inhabited by conspecifics, because we were not able to detect any areas with squirrel habitat and also unoccupied by the species. Animals were transported in wooden nest boxes without access to visual cues. We released 21 animals using a hard release method where we released the animal immediately at its release point and 6 animals using a soft release method where we place the animals in an enclosure (152 cm H, 90 cm W, 90 cm L) for 5 d. The enclosure contained a nest box, approximately 400 locally

collected spruce cones, water, a feeder with peanuts, peanuts butter, and rodent chow, and some branches. However, we found no differences in movement patterns or survival between release methods (Morandini and Koprowski 2022), so we pooled data across all squirrels for subsequent analyses.

### **Telemetry**

We used R-1000 digital receivers (Communication Specialists Inc., Orange, CA) and 3-element yagi directional antennas (Wildlife Materials Inc., Murphysboro IL, USA) to track each squirrel's movements from release point to settlement, locating all individuals  $\geq 1$  time per day during the first 5 d after translocation. Subsequently, squirrels were tracked at least one time per week until settlement, death, disappearance from the study area, or the first snow (late October through late November). We recorded behavioral observation whenever we located an individual and defined animals as settled when they exhibited territorial behavior, including the rattle vocalizations or caching of cones (Larsen & Boutin, 1994), or if they remained in a 100-m radius for at least 3 consecutive days. The first day that individuals exhibited territorial vocalization or cone caching was considered the day of settlement. We classified all locations prior to settlement as exploratory locations. We defined animals as missing if their signals disappeared and were not subsequently detected.

### **Measuring landscape features**

We evaluated selection of landscape features by translocated squirrels by comparing landscape features at the locations where each squirrel settled after translocation (hereafter settlement points) to landscape features at each squirrel's original (i.e., pre-translocation) midden and at random points throughout our study area. We defined our study area by buffering all telemetry points by 1 km (the most frequent daily distance traveled by red squirrel after translocation) and excluding open water. We generated 5000 random points throughout our study area which we used to measure available landscape features.

We measured the mean values of each covariate of landscape features within 14 radii circular buffers centered on each squirrel location (at 70 m and increments of 30 m until 300m, 400 m, 500m, 600m, 900m, 1200m). We calculated mean percent canopy cover and tree height using 30-m pixel Landfire rasters (Landfire, 2016). We used 9-m digital elevation models (U.S. Geological Survey 2022) to calculate slope using ArcMap (v. 10.8.1, ESRI 2020). We were also interested in

identifying northerly and northeasterly aspects, which we expected to be cooler, moister, and more likely to support spruce (*Picea* spp.) that are preferred food sources for red squirrels (Smith and Mannan 1994). We therefore quantified aspect using the topographic radiation aspect index (TRASP, Roberts and Cooper 1989) which quantifies the deviation from north-northeast and south-southwest on a scale from 0 to 1, respectively. We calculated TRASP in ArcMap using the extension of Evans et al. (2014). Finally, we calculated topographic position index (TPI) to quantify the relative topographic position (ridge top vs. valley bottom) of a point as the difference between the point's elevation and the mean elevation within that point's buffer using R (R Development Core Team 2021). All subsequent analyses were also conducted within R.

Because Fremont's squirrels are highly territorial (Gurnell 1984, Koprowski et al. 2008), and therefore likely to influence the settlement process, we collected information about the spatial distribution of middens in our study area during September 2021. We assumed that the spatial distribution of inhabited middens in our study area remained constant between 2018 and 2021 because middens persist for many years and vacant middens are quickly reoccupied by resident squirrels such that middens remain constantly occupied over time (Sanderson and Koprowski 2009). We recorded the UTM coordinates of all middens within 130 m of our translocated squirrels' settlement points and original middens. We used 130-m buffers because previous research indicates that red squirrels perceive neighboring conspecifics at this scale (Smith 1978, Siracusa et al. 2017). We also measured middens in 130 m buffers around 43 random points within forested areas throughout our study area. To ensure that our random points were well dispersed throughout our study area, we first created a grid of 800-m grid cells across our study area and then randomly selected a point within each grid cell. If the first random point was inaccessible or not within forest (i.e., potential red squirrel habitat), we selected a second random point within that grid cell. We restricted our random points to forests because we were specifically interested in the effects of conspecific red squirrels on settlement location, rather than landscape features (e.g., forest cover), in this particular analysis. Furthermore, we had no *a priori* reason to expect squirrels to settle in non-forested areas. We used these midden locations to calculate midden density within 70, 100, and 130 m buffers and the mean distance from each midden to settlement or random point.

### **Analysis of movement**

We calculated the distance of each telemetry points from the release site (i.e., displacement), distance between successive telemetry locations (m), movement speed (m/h), and relative turning angles (-180–180°). Because we often obtained multiple telemetry locations per day immediately following release with subsequently less frequent locations over time, we summed the distance between successive locations across locations collected during the same day and calculated the average movement speed and turn angle for that day. We tested for effects of sex, settlement (yes or no), and number of days since release on these four-movement metrics using generalized linear mixed models (GLMM) with Gaussian error distributions and identity link function. We included in the model also the number of telemetry points obtained per day (one if there was only one location on a given day) to control for temporal variation in tracking and estimated random intercepts across individuals. We log transformed distance and speed. We fit models for distance moved and speed using the lme4 package (function *lmer*; lme4 package - Bates et al 2015) and the glmmTMB package (function *glmmTMB*; glmmTMB package - Brooks et al. 2017) for turn angle. We visually evaluated each model for residual normality and homogeneity of variance.

### **Habitat selection for landscape features during exploratory movements**

We evaluated how individuals selected landscape features during exploratory movements. Because we often were unable to locate squirrels daily, we did not estimate step-selection functions (Johnson et al. 2004, Thurfjell et al. 2014); but rather estimated point-selection functions (PSF, Zeller et al. 2012) implemented conceptually as step-selection functions (Bauder et al. 2018). Specifically, we measured an individual's feature use at time  $t$  and paired that value with a measure of feature availability for that individual at time  $t - 1$ . We measured the availability of landscape features relative to exploratory telemetry locations based on a squirrel's inter-location movement potential. To calculate the potential movement, we first fit generalized Pareto distributions (GPD), which accommodate highly right-skewed data, to our observed distributions of distances between consecutive locations (Zeller et al. 2014, Bauder et al. 2018). We estimated separate GPD using locations <24 h apart (i.e., locations collected during the same day) and locations  $\geq 24$  h apart after standardizing the latter to meters moved per 24-h. We only used steps originating from exploratory locations. Finally, we used these GPD to calculate GPD-weighted averages of available landscape features and used either the <24-h or  $\geq 24$ -h GPD depending on the duration between consecutive

locations. We used data from all individuals translocated until their settlement, death, or disappearance, for a total of 535 observations of 27 animals.

We determined the optimal scale (i.e., radius of a circular uniform buffer) for each landscape covariate using a pseudo-optimization approach (McGarigal et al. 2016). We first applied a circular uniform buffer as a moving window across our original covariate rasters so that each pixel value represented the average covariate value within that buffer. We then used these smoothed rasters to measure use and availability as described above. We fit our PSF using Cox proportional hazard regression model with the *coxph* function of the survival package (Therneau 2021). This allowed us to pair each used point with its unique measure of availability. We attempted to model random slopes with individual as the random effect but these models did not converge with more than one covariate (c.f., Zeller et al. 2016). We therefore calculated robust standard errors using individual animal as the cluster to account for the non-independence of locations from the same individual (Hardin and Hilbe 2002, Fortin et al. 2005). To account for sampling individuals multiple times per day during the early phases of telemetry, we weighted used and available points so that the sum of weights for points from the same day equaled one. We selected the optimal scale for each covariate across a range of spatial scales (70-300 at 30 m increments and 400, 500, 600, 900, 1200, and 1500 m). We identified the optimal scale as the scale with the lowest Akaike Information Criterion adjusted for small sample sizes (AICc; Burnham and Anderson 2002). We then created our final candidate model set with each covariate represented at its optimal scale. Canopy cover and tree height were strongly correlated at their optimal scales, so we retained tree height because it had more empirical support. We compared all the models using AICc.

### **Habitat selection during settlement**

We evaluated selection for settlement locations by comparing landscape features at settlement points to those at random points selected across our study area. We again determined the optimal scale (i.e., buffer size) for each covariate using a pseudo-optimization approach (McGarigal et al. 2016) and binomial generalized linear models (GLM) with logit links. We identified the optimal scale as the scale with the lowest AICc. We used buffer sizes ranging from 70-300 m at 30-m increments for all GIS-based covariates and scales of 70, 100, and 130 m for midden density and mean midden distance. We considered our GLMs comparing settlement points to our 5000 random points as resource selection functions characterizing relative probability or intensity of use (Avgar

et al. 2017, Northrup et al. 2021). We therefore assigned large weights (5000) to each available point because binomial GLMs with highly weighted available points are equivalent to an inhomogeneous Poisson point process model that facilitates the interpretation of resource selection function coefficients as relative selection strength and provides better estimates of relative intensity of use (Warton and Shepherd 2010, Fithian and Hastie 2013, Fieberg et al. 2021). Finally, we used a principal components analysis (PCA) to condense variation from our five GIS-based covariates at their optimal scales into single components, to explain differences in vegetative and topographic features between settlement and random points given our limited sample size of settlement points.

We developed 8 candidate models to test for differences in environmental features between settlement and our 5000 random points using all combinations of the first three principal components characterizing vegetation and landscape characteristics. We also included an intercept-only model as a null model. We also used binomial GLMs to test for differences in environmental features between settlement and 43 random points using a combination of PC1 + PC3 (resulted most explanatory from the previous analysis), midden density, and average midden distance, without attributing any weights for available points. For each analysis, we drew inference from models with  $\Delta AICc \leq 2$ .

Finally, we used a series of paired t-tests or paired Wilcoxon rank tests (for non-normally distributed data) to test for differences in environmental features (i.e., informative principal components and midden density and distance) between each squirrel's original midden at which it was captured and the squirrel's settlement midden following translocation. We also evaluated the same parameter between each squirrel's original midden and release site to make sure the site selection has been appropriate.

## ***Results***

We translocated 27 Fremont's squirrels (14 males, 13 females) during our study (n = 10, 11, and 6 in 2018, 2019, and 2020, respectively). Of these 27 squirrels, 7 (25.9%) disappeared, 12 (44.4%) settled, 3 (11.1%) returned to original territory and 5 (18.6%) died.

### **Analysis of movement metrics**

Eleven squirrels were determined to have settled during our study. Their post-release movements were characterized by long, rapid movements away from their release site with some individuals returning to their release site before resuming long, rapid movements in a different direction (e.g., Squirrels 5002 and 5098 in Figure 3.1). These exploratory movements contrasted with shorter movements in a more confined area in the settlement phase (Figure 3.1, 3.3). Squirrels that were lost (killed or disappeared) before settling displayed similar long-distance movements characteristic of exploratory movements (Supplemental Material Figure 3.8). Individuals during the dispersal phase primarily used the ground and logs for traveling, while they use mostly ponderosa pine, Douglas-fir and spruce for resting and foraging (Figure 3.2). Daily distance moved was lower during the settlement phase than during the exploration phase (Table 3.1). Specifically, daily distance moved during the settlement phase averaged 83.6 m (sd 101) and 1524 m (sd. 1403) during the exploration phase where we observed a maximum of 6830 m moved in 24 h. Daily distance also decreased with the increase of number of days after release, while there was no effect of sex (Table 3.1). Speed showed similar results to daily average: lower during the settlement phase than during the exploration phase, decreased with the increase of number of days after release, and no effect of sex (Table 3.1). There was no significant effect of any of our covariates on mean relative turning angles (Table 3.1).

### **Habitat selection for landscape features during exploratory movements**

The optimal scale (i.e., buffer radius) for canopy cover and tree height was 500 m, 600 m for TPI, 190 m for TRASP, and 1200 m for slope (Figure 3.4; supplemental material Table 3.6). During exploratory movements squirrels used areas with taller trees, valley bottoms and lower slopes (Table 3.2, model selection in supplemental material Table 3.7).

### **Habitat selection during settlement**

The optimal scale (i.e., buffer radius) for canopy cover, TPI and TRASP was 100 m, 70 m for tree height, and 300 m for slope (Figure 3.5; Supplemental material Table 3.8). The optimal scale for average middens distance and number of middens was 100 m (Figure 3.5; Supplemental material Table 3.8).

The vegetation and landscape characteristics were possible to summarize them in 3 principal components: the first one strongly positively influenced by forested areas (canopy cover and tree

height), the second PC was indicative of steep, northeasterly aspects, while the third PC was indicative of valley bottoms (Figure 3.6, Table 3.3). These three components each explained 40%, 23%, and 20% of the variance, respectively, and together explained a total of 83% of the variance in our GIS-based covariates (Table 3.3).

During settlement, animals select site with more canopy cover, tree height, located in valleys and with lower slope and location facing north (Table 3.4, model selection in supporting material Table 3.9). However, if density of red squirrel residents has been considered, animals not only select for areas with more canopy cover, tree height, and located in valleys, but they also select for areas with lower density of squirrels (Table 3.5, Model selection in supplementing material Table 3.10).

Squirrels settled at sites where there was lower density of squirrel residents in a 100 m buffer (reflected in fewer middens) compared to the midden at their original capture site ( $t = 2.36$ ,  $df = 11$ ,  $p\text{-value} = 0.0381$ , Figure 3.7). In contrast, there were no differences in the means of any vegetation and landscape measures (PC1, PC3, and midden density) between the original capture sites and translocation release sites (Figure 3.7).

## ***Discussion***

Post-release movements of translocated Fremont's squirrels in our study seemed to represent two different behavioral phases characterized by differences in movement patterns and the scale of selection for environmental features. During the first phase, squirrels made long rapid movements and selected areas with taller trees and valley bottoms at relatively broad spatial scales (i.e., 500-600 m). In contrast, during the second behavioral phase (hereafter settlement phase), squirrels seemed to act like residents, displaying shorter movements within a smaller area, caching food, and defending their middens. Squirrels still used primarily forested areas in valley bottoms and fewer conspecific middens, but the scale of response was much lower than during the initial phase. Different behavioral phases have been observed in multiple species after translocation. Translocated pine martens, *Martes martes*, exhibit an "exploration" phase followed by a "settlement" phase, as a result of initial searching of the new environment for denning and foraging habitat (McNicol et al. 2020). Translocated female greater sage-grouse, *Centrocercus urophasianus*, also display an initial phase characterized by rapid, linear movements and a second phase, the restricted state, characterized by shorter, less directional movements (Picardi et al.

2022). A decrease in movements and space used with time after release has been also been observed in translocated turkeys (*Meleagris gallopavo* - Cohen et al. 2022).

Translocated red squirrels moved much larger distances than resident red squirrels observed in other studies. Translocated red squirrels moved a mean of 1600 m daily during the exploration phase, and one individual moved over 6000 m in only 24 h. These distances are not only much larger than their home ranges (0.05 ha - Leonard and Koprowski 2009), but even much larger than the distance that squirrels move during natal dispersal. Mt Graham red squirrels, the closest subspecies, dispersed at average distance of 679.8, SD 1067.7 from the natal area (Merrick and Koprowski 2016), whereas other species of red squirrel in North America dispersed an average of 92.4 m, SD 123.3 (Kerr et al., 2007). Larger post-release movements of translocated individuals are common in wildlife translocation studies (Hester et al. 2008, Nussear et al. 2012, Scillitani et al. 2012). The driving forces behind this long-distance dispersal remain unclear but could include attempts to return to their original home range (Miller and Ballard 1982, Dickens et al. 2009, Tsoar et al. 2011, Hinderle et al. 2015) as well as variation in individual personality, stress responses, and disorientation (Stamps and Swaisgood 2007). For example, two squirrels in our study were translocated 900 m and returned to their original capture site within 24 h. Another squirrel that was translocated 3500 m returned to its original capture site after 5 days. Translocated animals may therefore use extensive post-release movements in an attempt to locate environmental cues (Stamps and Swaisgood 2007, Dickens et al. 2009) that can help navigate to their original territory. It was interesting to notice that several animals came back to their original release area, as if they had to re-evaluate the environment. In a previous study this behavior has been explained as a tradeoff between using the information they have to go back home and proceeding up to a distance normally covered in spontaneous exploratory trips (Bovet, 1984).

Many researchers define the first phase after translocation as exploratory movement (McNicol et al. 2020, Moehrenschrager & MacDonald 2003; Rittenhouse et al. 2007; Roe et al. 2010). However, we would argue that movements immediately after translocation constitutes only a locomotion behavior and not an exploratory behavior. Locomotion behavior is defined as the movement from one location to another, while exploration behavior is a complex cognitive process, involving sensory processes, investigation and responding to novel stimuli, and information-gathering (Kelley 1993). These two terms have been frequently confused: during

spatial exploration animals use locomotion, however this behavior may not necessarily reflect true exploration (Kelley 1993). Although translocated animals move into a completely new space, reflecting the definition of “reaction to a new situation” (Réale et al. 2007), they do not have any choice to approach or avoid this new situation. For this reason, we believe the initial behavior likely consists of a response to acute stress event (translocation), followed by exploration to acquire knowledge of the environment, and finally establishment. This pattern has been recognized in swift foxes (*Vulpes velox*), where after release they undergo to an initial “acclimation phase”, moving erratically and quickly, far from the release site. During the establishment phase, distances from the release site did not change significantly but daily movements were more wide-ranging than resident swift foxes. In the final settlement phase, movements of translocated foxes reflected those of resident individuals (Moehrensclager and Macdonald 2003). We were not able to identify three phases, probably due to a lack of telemetry points through time. The long movements made by squirrels, and the availability of VHF collars, put some constraints on the availability to relocate the animals daily for long periods of time, therefore we focused mostly on following their movement in the first 5 days.

Translocated red squirrels showed similar patterns of use for landscape features during both behavioral phases, yet the scale of selection differed markedly. Using valley bottoms (low TPI) could reflect attempts to minimize energetic costs, especially during initial post-release movements. Utilizing areas with taller trees during their movements could provide cover from areal predators (Wieniawski 1987) and offer increased arboreal vantage points to view the landscape. In fact, we frequently observed squirrels using tall trees (especially ponderosa or larger Douglas-fir) to rest and presumably view their surroundings. Animals can perceive the presence of faraway landscape elements such as patches of habitat (Zollner 2000). This perceptual range is approximately 120 m for chipmunks (*Tamias*), 300 m for eastern gray squirrels (*Sciurus carolinensis*), and 400 m for fox squirrels (*S. niger*; Zollner 2000). Red squirrels (*Tamiasciurus hudsonicus*) have a perceptual range of about 400 m (Goheen et al. 2003) with a few individuals able to cross a field up to 954 m (Goheen et al. 2003). The perceptual range of red squirrels can also explain the larger scale animals use during the first phase after translocation (500/600 m) than during settlement (70/100 m). Red squirrels traveling in novel landscape face numerous challenges, such as risk of predation, risk of conspecific attack, and energetic costs. Moving in a

straight line could be a way to minimize such challenges (Bakker and Van Vuren 2004) as well as quickly evaluate the landscape features for potential resources and plan subsequent moves.

Red squirrels are highly territorial animals, and our results suggest that translocated red squirrels select areas with lower densities of resident conspecifics. Red squirrels benefit from having stable neighbors (Siracusa et al. 2018), at a point where animals avoid settlement in new empty middens even when they occupy poorer quality territories (Larsen and Boutin 1995). While dispersing, red squirrel must weigh the benefit and cost of establishing a new territory around other individuals. Therefore, a driver of settlement choices in translocated red squirrels could be density-dependent dispersal (Shier and Swaisgood 2012). The importance of neighbors has been documented also in the translocation of the solitary species Stephens' kangaroo rats (*Dipodomys stephensi*), where animals translocated in group had a higher survival and traveled shorter distances than animals translocated alone (Shier and Swaisgood 2012). Red squirrels experience high intraspecific competition during fall, when our translocations occurred, due to natal dispersal of juveniles and their attempts to establish new middens or to take a resident's territory (Sullivan and Moses 1986, Berteaux and Boutin 2000, Dantzer et al. 2012). This situation can create a harsh environment and impact the survival and behavior of translocated animals (Shier and Swaisgood 2012). Other landscape features were also important in influencing settlement site selection, specifically tree height and topography. Selecting settlement sites in areas with tall trees could reflect the potential for larger trees to produce enough cones that can be cached by the squirrels to survive over winter, a key function of a midden.

Animals settled in areas with similar vegetation and topographic characteristics as their original capture locations, but selected areas with fewer resident conspecifics than their original capture location. During natal dispersal, juveniles select areas in a heterogeneous landscape with attributes similar to those encountered early in life (Davis and Stamps 2004, Larue et al. 2018). This phenomena, called Natal Habitat Preference Induction (NHPI), has been recognized in a wide variety of taxa (Davis and Stamps 2004, Larue et al. 2018), including in juvenile Mt Graham red squirrel in a montane conifer forest similar to our study area (Merrick and Koprowski 2016). We assumed that, if NHPI minimizes the time for a juvenile disperser to acquire a territory and concurrently minimize the energetic and predation risks associated with dispersal (Stamps et al. 2009), then we would expect also for a translocated squirrel to be advantageous for the same

reasons to settle in sites similar to their original capture location. However, our results seem inconclusive with respect to the Natal Habitat Preference Induction (NHPI) hypothesis in influencing translocated red squirrel post-release behavior. The fact that animals selected areas with fewer resident conspecifics than their original capture location, can reflect the advantages of reduced intraspecific competition more generally rather than NHPI. Midden densities were similar at translocated squirrels' original capture site and their release site which may also explain why animals did not settle at their release site. However, our limited sample sizes and lack of high-resolution data on vegetation structure and composition (c.f., Merrick and Koprowski 2016) limit our ability to draw inference from these results.

### **Management implications and conclusion**

Translocated animals may exhibit a variety of post-release behaviors with consequences for translocation success. The importance of understanding dispersal behavior in reintroduction biology is well recognized to improve conservation translocations (Armstrong and Seddon 2008). Our study illustrates how translocated Fremont's squirrels engage in a period of rapid and extensive post-release movement prior to settling within a new territory and that landscape features and the presence of conspecifics influence this process. These results have important implications for future efforts that might involve translocation of the endangered Mt. Graham red squirrel. For example, the selection for forested areas during exploratory movements suggests that releasing squirrels in areas of sufficient forest cover may be important in facilitating their movements in search of new settlement sites and highlights the need for additional research determine suitable landscape-level thresholds in forest cover. This research need is particularly important given widespread fires in Mt. Graham red squirrel habitat. Furthermore, our finding that translocated squirrels select areas with fewer conspecifics highlights the importance of considering the role of conspecifics, as well as environmental features, in translocations of territorial species (Richardson and Ewen 2016). For a territorial species with small population sizes, like Mt. Graham red squirrels, translocations of new individuals may also have an impact on resident individuals by increasing local abundance. We encourage managers conducting translocations to consider the distribution of resident conspecifics and changes over time if the translocation will happen in multiple years (Sullivan et al. 2012). Finally, our results highlight the need for translocation studies of territorial species to consider the presence and abundance of resident conspecifics when studying translocation success.

## *Acknowledgments*

We thank the agency partner Arizona Game and Fish Department and the University of Arizona School of Natural Resources and the Environment. We would like to thank the Mt. Graham Red Squirrel Research Program graduate and undergraduate research assistants for valuable help in the field. This research was supported by grants to JLK from the University of Arizona, Arizona Game and Fish Department (grants no. I18005 and I16002), and T & E Inc. Grants for Conservation Biology. All field work was conducted under University of Arizona Institutional Animal Care and Use Committee protocol # 16-169, Arizona Game and Fish Department scientific collecting permit # SP651773 for 2019, SP403044 for 2020, SP407072 for 2021, U.S. Fish and Wildlife Service permit # TE041875-2 and adhered to the American Society of Mammalogist's guidelines for the use of wild mammals in research (Sikes & Gannon, 2011). This manuscript was improved by comments from R. W. Mannan, L. Wauters, and R. Steidl.

## References

- Armstrong, D. P., and P. J. Seddon. 2008. Directions in reintroduction biology. *Trends in Ecology & Evolution* 23:20–25.
- Avgar, T., S. R. Lele, J. L. Keim, and M. S. Boyce. 2017. Relative selection strength: quantifying effect size in habitat- and step-selection inference. *Ecology and Evolution* 7:5322–5330.
- Bakker, V. J., and D. H. Van Vuren. 2004. Gap-crossing decisions by the red squirrel, a forest-dependent small mammal. *Conservation Biology* 18:689–697.
- Bar-David, S., I. Bar-David, P. C. Cross, S. J. Ryan, C. U. Knechtel, and W. M. Getz. 2009. Methods for assessing movement path recursion with application to African buffalo in South Africa. *Ecology* 90:2467–2479.
- Bates D, Mächler M, Bolker B, Walker S (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48.
- Bauder, J. M., D. R. Breining, M. R. Bolt, M. L. Legare, C. L. Jenkins, B. B. Rothermel, and K. McGarigal. 2018. Multi-level, multi-scale habitat selection by a wide-ranging, federally threatened snake. *Landscape Ecology* 33:743–763.
- Berger-Ta, O., and D. Saltz. 2014. Using the movement patterns of reintroduced animals to improve reintroduction success. *Current Zoology* 60:515–526.
- Berger-Tal, O., D. T. Blumstein, and R. R. Swaisgood. 2020. Conservation translocations: a review of common difficulties and promising directions. *Animal Conservation* 23:121–131.
- Berteaux, D., and S. Boutin. 2000. Breeding dispersal in female North American red squirrels. *Ecology* 81:1311–1326.
- Blumstein, D. T., and E. Fernández-Juricic. 2010. A primer of conservation behavior. Sinauer Associates, Sunderland, Mass.
- Bodinof, C. M., J. T. Briggler, R. E. Junge, J. Beringer, M. D. Wanner, C. D. Schuette, J. Ettl, R. A. Gitzen, and J. J. Millspaugh. 2012. Postrelease movements of captive-reared Ozark hellbenders (*Cryptobranchus alleganiensis bishopi*). *Herpetologica* 68:160–173.
- Boutin, S., and S. Schweiger. 1988. Manipulation of intruder pressure in red squirrels (*Tamiasciurus hudsonicus*): effects on territory size and acquisition. *Canadian Journal of Zoology* 66:2270–2274.
- Bovet, J. 1984. Strategies of homing behavior in red squirrel, *Tamiasciurus hudsonicus*. *Behavioral Ecology and Sociobiology* 16: 81-88
- Brooks, M.E., Kristensen K., van Benthem K.J., Magnusson A., Berg C.W., Nielsen A., Skaug H.J., Maechler M. and Bolker B.M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9:378-400.
- Burnham, K. P., D. R. Anderson, and K. P. Burnham. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer, New York.
- Caro, T., J. Eadie, and A. Sih. 2005. Use of substitute species in conservation biology. *Conservation Biology* 19:1821–1826.
- Coates, P. S., S. J. Stiver, and D. J. Delehanty. 2006. Using Sharp-tailed grouse movement patterns to guide release-site selection. *Wildlife Society Bulletin* 34:1376–1382.
- Cohen, B. S., B. Oleson, N. Fyffe, A. Smallwood, N. Bakner, S. Nelson, M. J. Chamberlain, and B. A. Collier. 2022. Movement, spatial ecology, and habitat selection of translocated Gould’s wild turkeys. *Wildlife Society Bulletin* 46:e1270.

- Dantzer, B., S. Boutin, M. M. Humphries, and A. G. McAdam. 2012. Behavioral responses of territorial red squirrels to natural and experimental variation in population density. *Behavioral Ecology and Sociobiology* 66:865–878.
- Davis, J. M., and J. A. Stamps. 2004. The effect of natal experience on habitat preferences. *Trends in Ecology & Evolution* 19:411–416.
- Dickens, M. J., D. J. Delehanty, and L. M. Romero. 2009. Stress and translocation: alterations in the stress physiology of translocated birds. *Proceedings of the Royal Society B: Biological Sciences* 276:2051–2056.
- Dolev, A., D. Saltz, S. Bar-David, and Y. Yom-Tov. 2002. Impact of repeated releases on space-use patterns of persian fallow deer. *The Journal of Wildlife Management* 66:737–746.
- Drake, C., and S. A. Temple. 2012a. Captive propagation and translocation. Pages 293–306 *The wildlife techniques manual: management*. Seventh edition. N. J. Silvy, editor. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Drake, D., and S. A. Temple. 2012b. Captive propagation and translocation. Pages 293–306 *The wildlife techniques manual*. Silvy, N.J. Johns Hopkins University Press., Baltimore.
- Eastridge, R., and J. D. Clark. 2001. Evaluation of 2 soft-release techniques to reintroduce black bears. *Wildlife Society Bulletin* 29:1163–1174.
- Eliassen, S., C. Jørgensen, M. Mangel, and J. Giske. 2007. Exploration or exploitation: life expectancy changes the value of learning in foraging strategies. *Oikos* 116:513–523.
- Elliot, N. B., S. A. Cushman, D. W. Macdonald, and A. J. Loveridge. 2014. The devil is in the dispersers: predictions of landscape connectivity change with demography. *Journal of Applied Ecology* 51:1169–1178.
- Ewen, J. G., D. P. Armstrong, R. Empson, S. Jack, T. Makan, K. McInnes, K. A. Parker, K. Richardson, and M. Alley. 2012. Parasite management in translocations: lessons from a threatened New Zealand bird. *Oryx* 46:446–456.
- Fieberg, J., J. Signer, B. Smith, and T. Avgar. 2021. A ‘How to’ guide for interpreting parameters in habitat-selection analyses. *Journal of Animal Ecology* 90:1027–1043.
- Fithian, W., and T. Hastie. 2013. Finite-sample equivalence in statistical models for presence-only data. *The Annals of Applied Statistics* 7:1917–1939.
- Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320–1330.
- Frair, J. L., E. H. Merrill, J. R. Allen, and M. S. Boyce. 2007. Know the enemy: experience affects elk translocation success in risky landscapes. *The Journal of Wildlife Management* 71:541–554.
- Goheen, J. R., R. K. Swihart, T. M. Gehring, and M. S. Miller. 2003. Forces structuring tree squirrel communities in landscapes fragmented by agriculture: species differences in perceptions of forest connectivity and carrying capacity. *Oikos* 102:95–103.
- Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. *Science* 245:477–480.
- Gurnell, J. 1984. Home range, territoriality, caching behaviour and food supply of the red squirrel (*Tamiasciurus hudsonicus fremonti*) in a subalpine lodgepole pine forest. *Animal Behaviour* 32:1119–1131.
- Hardin, J. W., and J. M. Hilbe. 2002. *Generalized estimating equations*. Chapman and Hall/CRC, New York.

- Harrington, L. A., A. Moehrensclager, M. Gelling, R. P. D. Atkinson, J. Hughes, and D. W. Macdonald. 2013. Conflicting and complementary ethics of animal welfare considerations in reintroductions. *Conservation Biology* 27:486–500.
- Harrison, M. L., D. J. Green, and P. G. Krannitz. 2009. Conspecifics influence the settlement decisions of male Brewer's sparrows at the northern edge of their range. *The Condor* 111:722–729.
- Hinderle, D., R. L. Lewison, A. D. Walde, D. Deutschman, and W. I. Boarman. 2015. The effects of homing and movement behaviors on translocation: desert tortoises in the western Mojave Desert. *The Journal of Wildlife Management* 79:137–147.
- Hope, A. G., J. L. Malaney, K. C. Bell, F. Salazar-Miralles, A. S. Chavez, B. R. Barber, and J. A. Cook. 2016. Revision of widespread red squirrels (genus: *Tamiasciurus*) highlights the complexity of speciation within North American forests. *Molecular Phylogenetics and Evolution* 100:170–182.
- Hurly, T. A., and S. A. Lourie. 1997. Scatterhoarding and larderhoarding by red squirrels: size, dispersion, and allocation of hoards. *Journal of Mammalogy* 78:529–537.
- Johnson, C. J., D. R. Seip, and M. S. Boyce. 2004. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. *Journal of Applied Ecology* 41:238–251.
- Jones, J. M., and J. H. Witham. 1990. Post-translocation survival and movements of metropolitan white-tailed deer. *Wildlife Society Bulletin* 18:434–441.
- Kelley, A. E. 1993. Chapter 19 - Locomotor activity and exploration. Pages 499–518 in F. van Haaren, editor. *Techniques in the Behavioral and Neural Sciences*. Elsevier.
- Kemink, K. M., and D. C. Kesler. 2013. Using movement ecology to inform translocation efforts: a case study with an endangered lekking bird species. *Animal Conservation* 16:449–457.
- Kesler, D. C., A. S. Cox, G. Albar, A. Gouni, J. Mejeur, and C. Plassé. 2012. Translocation of tuamotu kingfishers, postrelease exploratory behavior, and harvest effects on the donor population. *Pacific Science* 66:467–480.
- Koprowski, J. L. 2002. Handling tree squirrels with a safe and efficient restraint. *Wildlife Society Bulletin (1973-2006)* 30:101–103.
- Koprowski, J. L. 2005. Annual cycles in body mass and reproduction of endangered Mt. Graham red squirrels. *Journal of Mammalogy* 86:309–313.
- Koprowski, J. L., S. King, and M. Merrick. 2008. Expanded home ranges in a peripheral population: space use by endangered Mt. Graham red squirrels. *Endangered Species Research* 4:227–232.
- Larsen, K. W., and S. Boutin. 1994. Movements, survival, and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. *Ecology* 75:214–223.
- Larsen, K. W., and S. Boutin. 1995. Exploring territory quality in the North American red squirrel through removal experiments. *Canadian Journal of Zoology* 73:1115–1122.
- Larue, B., S. D. Côté, M.-H. St-Laurent, C. Dussault, and M. Leblond. 2018. Natal habitat preference induction in large mammals—Like mother, like child? *Ecology and Evolution* 8:12629–12640.
- Leonard, K. M., and J. L. Koprowski. 2009. A comparison of habitat use and demography of red squirrels at the southern edge of their range. *The American Midland Naturalist* 162:125–138.

- Letty, J., S. Marchandeu, J. Clobert, and J. Aubineau. 2000. Improving translocation success: an experimental study of anti-stress treatment and release method for wild rabbits. *Animal Conservation Forum* 3:211–219.
- Linklater, W. L., and R. R. Swaisgood. 2008. Reserve size, conspecific density, and translocation success for black rhinoceros. *The Journal of Wildlife Management* 72:1059–1068.
- MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. *The American Naturalist* 100:603–609.
- Martin, J., C. Calenge, P.-Y. Quenette, and D. Allainé. 2008. Importance of movement constraints in habitat selection studies. *Ecological Modelling* 213:257–262.
- McGarigal, K., H. Y. Wan, K. A. Zeller, B. C. Timm, and S. A. Cushman. 2016. Multi-scale habitat selection modeling: a review and outlook. *Landscape Ecology* 31:1161–1175.
- McNicol, C. M., D. Bavin, S. Bearhop, J. Bridges, E. Croose, R. Gill, C. E. D. Goodwin, J. Lewis, J. MacPherson, D. Padfield, H. Schofield, M. J. Silk, A. J. Tomlinson, and R. A. McDonald. 2020. Postrelease movement and habitat selection of translocated pine martens *Martes martes*. *Ecology and Evolution* 10:5106–5118.
- Merrick, M. J., and J. L. Koprowski. 2016. Evidence of natal habitat preference induction within one habitat type. *Proceedings of the Royal Society B: Biological Sciences* 283:20162106.
- Merrick, M. J., M. Morandini, V. L. Greer, and J. L. Koprowski. 2021. Endemic population response to increasingly severe fire: a cascade of endangerment for the Mt. Graham red squirrel. *BioScience* 71:161–173.
- Miller, S. D., and W. B. Ballard. 1982. Homing of transplanted Alaskan brown bears. *The Journal of Wildlife Management* 46:869–876.
- Milligan, S., L. Brown, D. Hobson, P. Frame, and G. Stenhouse. 2018. Factors affecting the success of grizzly bear translocations. *The Journal of Wildlife Management* 82:519–530.
- Moehrensclager, A., and D. W. Macdonald. 2003. Movement and survival parameters of translocated and resident swift foxes *Vulpes velox*. *Animal Conservation* 6:199–206.
- Morandini, M., and J. L. Koprowski. 2022. Substitute species to inform translocation techniques. Manuscript submitted for publication.
- Murphy, D. D., P. S. Weiland, and K. W. Cummins. 2011. A critical assessment of the use of surrogate species in conservation planning in the Sacramento-San Joaquin Delta, California (U.S.A.). *Conservation Biology* 25:873–878.
- Nafus, M. G., T. C. Esque, R. C. Averill-Murray, K. E. Nussear, and R. R. Swaisgood. 2017. Habitat drives dispersal and survival of translocated juvenile desert tortoises. *Journal of Applied Ecology* 54:430–438.
- Northrup, J. M., C. R. Anderson Jr., B. D. Gerber, and G. Wittemyer. 2021. Behavioral and demographic responses of Mule deer to energy development on winter range. *Wildlife Monographs* 208:1–37.
- Parejo, D., J. White, J. Clobert, A. Dreiss, and E. Danchin. 2007. Blue tits use fledgling quantity and quality as public information in breeding site choice. *Ecology* 88:2373–2382.
- Picardi, S., P. Coates, J. Kolar, S. O’Neil, S. Mathews, and D. Dahlgren. 2022. Behavioural state-dependent habitat selection and implications for animal translocations. *Journal of Applied Ecology* 59:624–635.
- Price, K., K. Broughton, S. Boutin, and A. R. E. Sinclair. 1986. Territory size and ownership in red squirrels: response to removals. *Canadian Journal of Zoology* 64:1144–1147.
- Réale, D., S. M. Reader, D. Sol, P. T. McDougall, and N. J. Dingemans. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews* 82:291–318.

- Reinert, H. K., and R. R. Rupert. 1999. Impacts of translocation on behavior and survival of timber rattlesnakes, *Crotalus horridus*. *Journal of Herpetology* 33:45–61.
- Resende, P. S., A. B. Viana–Junior, R. J. Young, and C. S. de Azevedo. 2020. A global review of animal translocation programs. *Animal Biodiversity and Conservation* 43:221–232.
- Richardson, K. M., and J. G. Ewen. 2016. Habitat selection in a reintroduced population: social effects differ between natal and post-release dispersal. *Animal Conservation* 19:413–421.
- Roe, J. H., M. R. Frank, S. E. Gibson, O. Attum, and B. A. Kingsbury. 2010. No place like home: an experimental comparison of reintroduction strategies using snakes. *Journal of Applied Ecology* 47:1253–1261.
- Rusch, D. A., and W. G. Reeder. 1978. Population ecology of Alberta red squirrels. *Ecology* 59:400–420.
- Sanderson, H.R. and Koprowski, J.L. 2009. The last refuge of the Mt. Graham red squirrel: ecology of endangerment. University of Arizona Press.
- Seppänen, J.-T., J. T. Forsman, M. Mönkkönen, and R. L. Thomson. 2007. Social Information Use is a process across time, space, and ecology, reaching heterospecifics. *Ecology* 88:1622–1633.
- Serrano, D., and J. L. Tella. 2003. Dispersal within a spatially structured population of lesser kestrels: the role of spatial isolation and conspecific attraction. *Journal of Animal Ecology* 72:400–410.
- Shier, D. M., and R. R. Swaisgood. 2012. Fitness costs of neighborhood disruption in translocations of a solitary mammal. *Conservation Biology* 26:116–123.
- Siracusa, E., M. Morandini, S. Boutin, M. M. Humphries, B. Dantzer, J. E. Lane, and A. G. McAdam. 2017. Red squirrel territorial vocalizations deter intrusions by conspecific rivals. *Behaviour* 154:1259–1273.
- Siracusa, E., D. R. Wilson, E. K. Studd, S. Boutin, M. M. Humphries, B. Dantzer, J. E. Lane, and A. G. McAdam. 2018. Red squirrels mitigate costs of territory defence through social plasticity. *bioRxiv*:453993.
- Smith, A. A., and R. W. Mannan. 1994. Distinguishing characteristics of Mount Graham red squirrel midden sites. *The Journal of Wildlife Management* 58:437–445.
- Smith, C. C. 1978. Structure and function of the vocalizations of tree squirrels (*Tamiasciurus*). *Journal of Mammalogy* 59:793–808.
- Smith, M. C. 1968. Red squirrel responses to spruce cone failure in interior Alaska. *The Journal of Wildlife Management* 32:305–317.
- Stamps, J. 2001. Habitat selection by dispersers: integrating proximate and ultimate approaches 230–242.
- Stamps, J. A., and R. R. Swaisgood. 2007. Someplace like home: experience, habitat selection and conservation biology. *Applied Animal Behaviour Science* 102:392–409.
- Stamps, J., and V. V. Krishnan. 2005. Nonintuitive cue use in habitat selection. *Ecology* 86:2860–2867.
- Stamps, J., B. Luttbeg, and V. V. Krishnan. 2009. Effects of survival on the attractiveness of cues to natal dispersers. *The American Naturalist* 173:41–46.
- Sullivan, T. P., and R. A. Moses. 1986. Red squirrel populations in natural and managed stands of lodgepole pine. *The Journal of Wildlife Management* 50:595–601.
- Sullivan, T. P., D. S. Sullivan, P. M. F. Lindgren, and D. B. Ransome. 2012. Silviculture and wildlife: snowshoe hare abundance across a successional sequence of natural and intensively managed forests. *International Scholarly Research Notices*, vol. 2012.

- Thalmann, S., S. Peck, P. Wise, J. Potts, J. Clarke, and J. Richley. 2015. Translocation of a top-order carnivore: tracking the initial survival, spatial movement, home-range establishment and habitat use of Tasmanian devils on Maria Island. *Australian Mammalogy* 38:68-79.
- Thurfjell, H., S. Ciuti, and M. S. Boyce. 2014. Applications of step-selection functions in ecology and conservation. *Movement Ecology* 2:4.
- Therneau T (2021). A package for survival analysis in R. R package version 3.2-13
- Tsoar, A., R. Nathan, Y. Bartan, A. Vyssotski, G. Dell’Omo, and N. Ulanovsky. 2011. Large-scale navigational map in a mammal. *Proceedings of the National Academy of Sciences* 108:E718–E724.
- Wagner, R. H., and É. Danchin. 2010. A taxonomy of biological information. *Oikos* 119:203–209.
- Warton, D. I., and L. C. Shepherd. 2010. Poisson point process models solve the “pseudo-absence problem” for presence-only data in ecology. *The Annals of Applied Statistics* 4:1383–1402.
- Yott, A., R. Rosatte, J. A. Schaefer, J. Hamr, and J. Fryxell. 2011. Movement and spread of a founding population of reintroduced elk (*Cervus elaphus*) in Ontario, Canada. *Restoration Ecology* 19:70–77.
- Young, P. J., V. L. Greer, and S. K. Six. 2002. Characteristics of bolus nests of red squirrels in the Pinaleno and White Mountains of Arizona. *The Southwestern Naturalist* 47:267–275.
- Zeller, K. A., K. McGarigal, P. Beier, S. A. Cushman, T. W. Vickers, and W. M. Boyce. 2014. Sensitivity of landscape resistance estimates based on point selection functions to scale and behavioral state: Pumas as a case study. *Landscape Ecology* 29:541–557.
- Zeller, K. A., K. McGarigal, S. A. Cushman, P. Beier, T. W. Vickers, and W. M. Boyce. 2016. Using step and path selection functions for estimating resistance to movement: pumas as a case study. *Landscape Ecology* 31:1319–1335.
- Zeller, K. A., K. McGarigal, and A. R. Whiteley. 2012. Estimating landscape resistance to movement: a review. *Landscape Ecology* 27:777–797.
- Zollner, P. A. 2000. Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. *Landscape Ecology* 15:523–533.

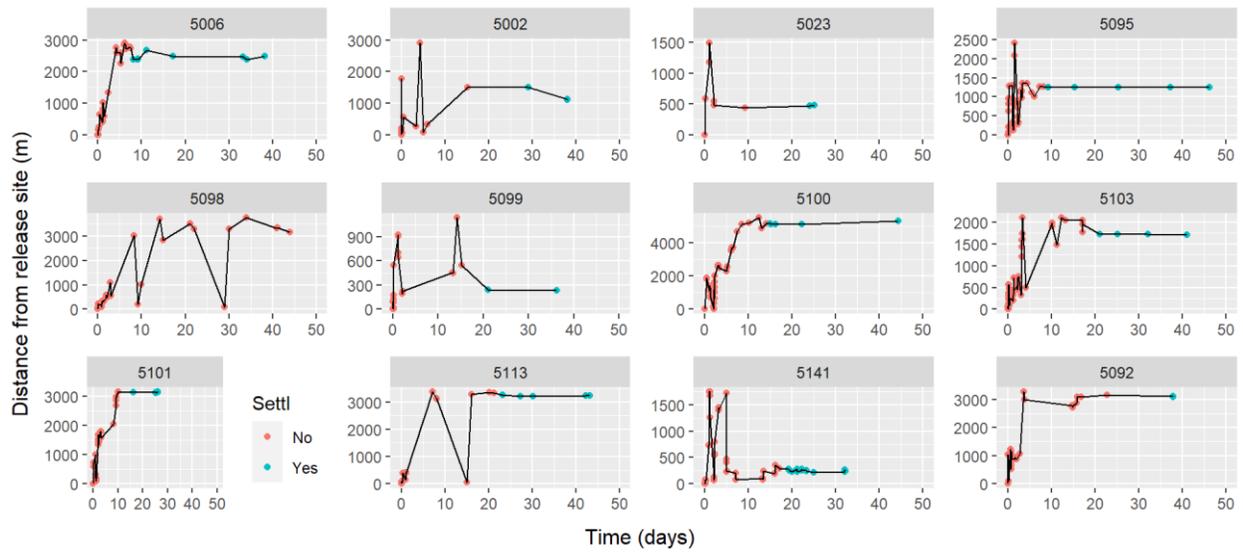


Figure 3.1: Distance (m) from the release point as a function of days post-release for translocated red squirrel (*Tamiasciurus fremonti fremonti*) in the White Mountains, Arizona, USA, from 2018 to 2020. The orange dots represent the telemetry points while the animals were dispersing after translocation, while the blue dots are the telemetry points when the animals settled.

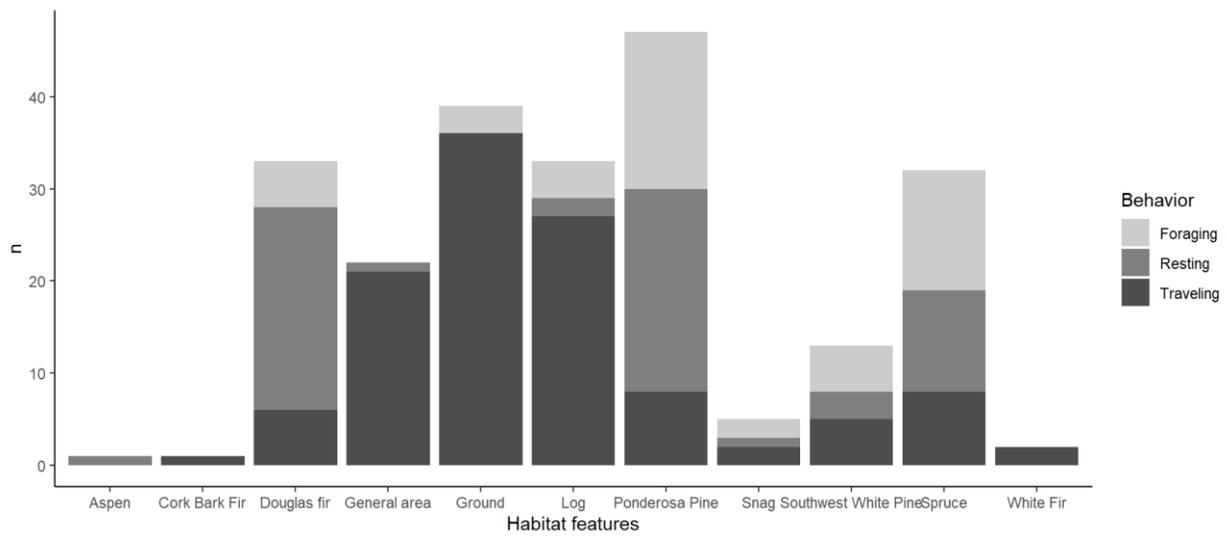


Figure 3.2: Use of habitat features during different behaviors (Foraging, resting, traveling) by translocated squirrels (*Tamiasciurus fremonti fremonti*) during dispersal after translocation in the White Mountains, Arizona, USA, from 2018 to 2020.

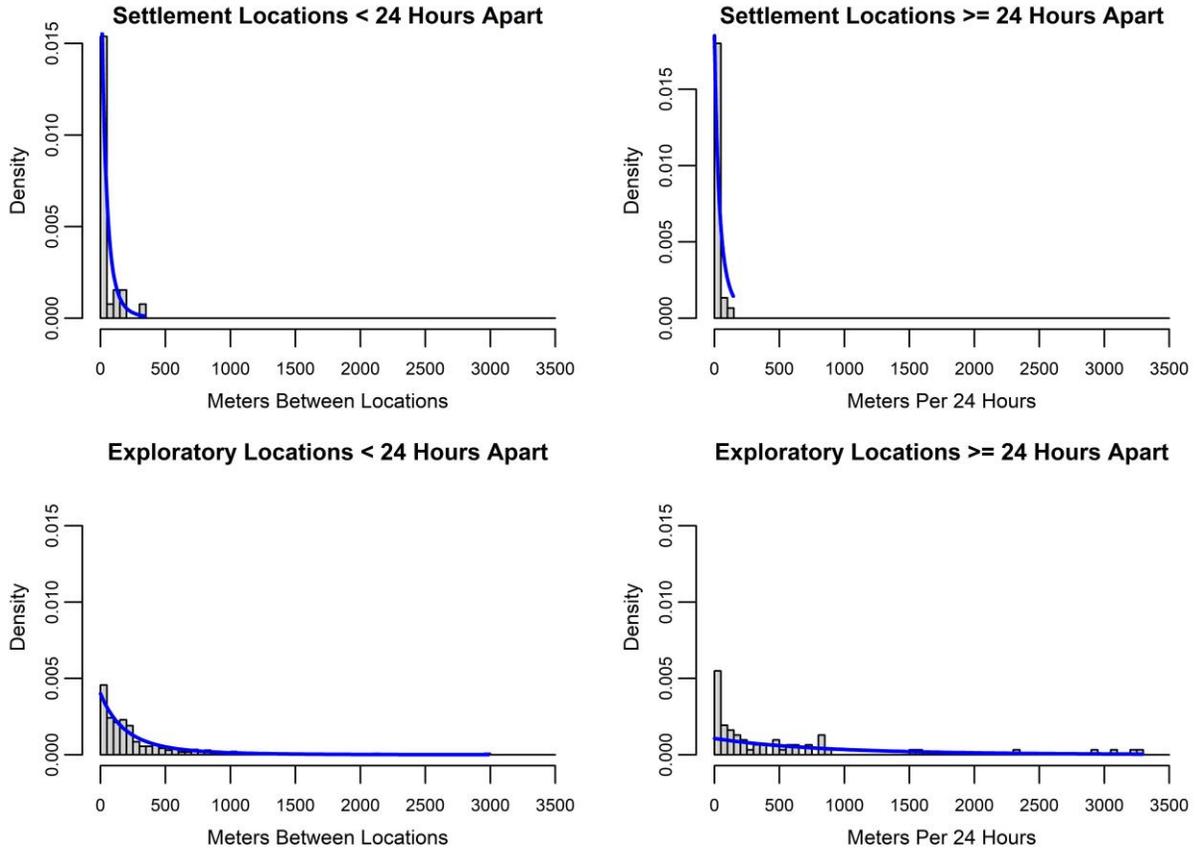


Figure 3.3: Distributions of distance moved (locations separated by  $< 24$  hours) or movement rates (locations separated by  $\geq 24$  hours) between telemetry locations during exploratory and settlement behavioral phases for translocated red squirrel (*Tamiasciurus fremonti fremonti*) in the White Mountains, Arizona, USA, from 2018 to 2020. Curves were estimated using generalized Pareto distributions.

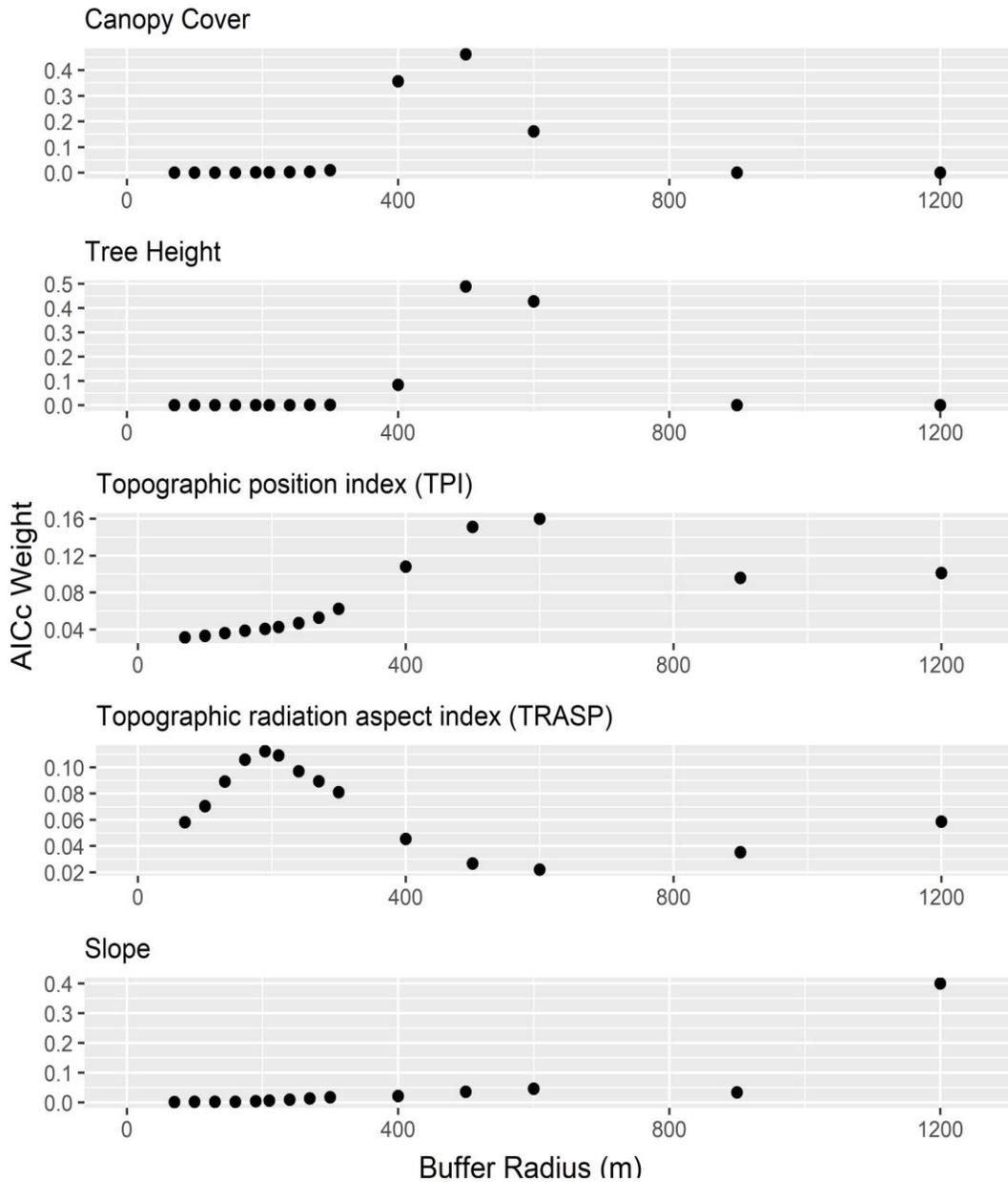


Figure 3.4: Model support (AICc weight) across spatial scales testing for selection of environmental features by translocated red squirrel (*Tamiasciurus fremonti fremonti*) in the White Mountains, Arizona, USA, from 2018 to 2020, during the exploratory phase of post-release dispersal.

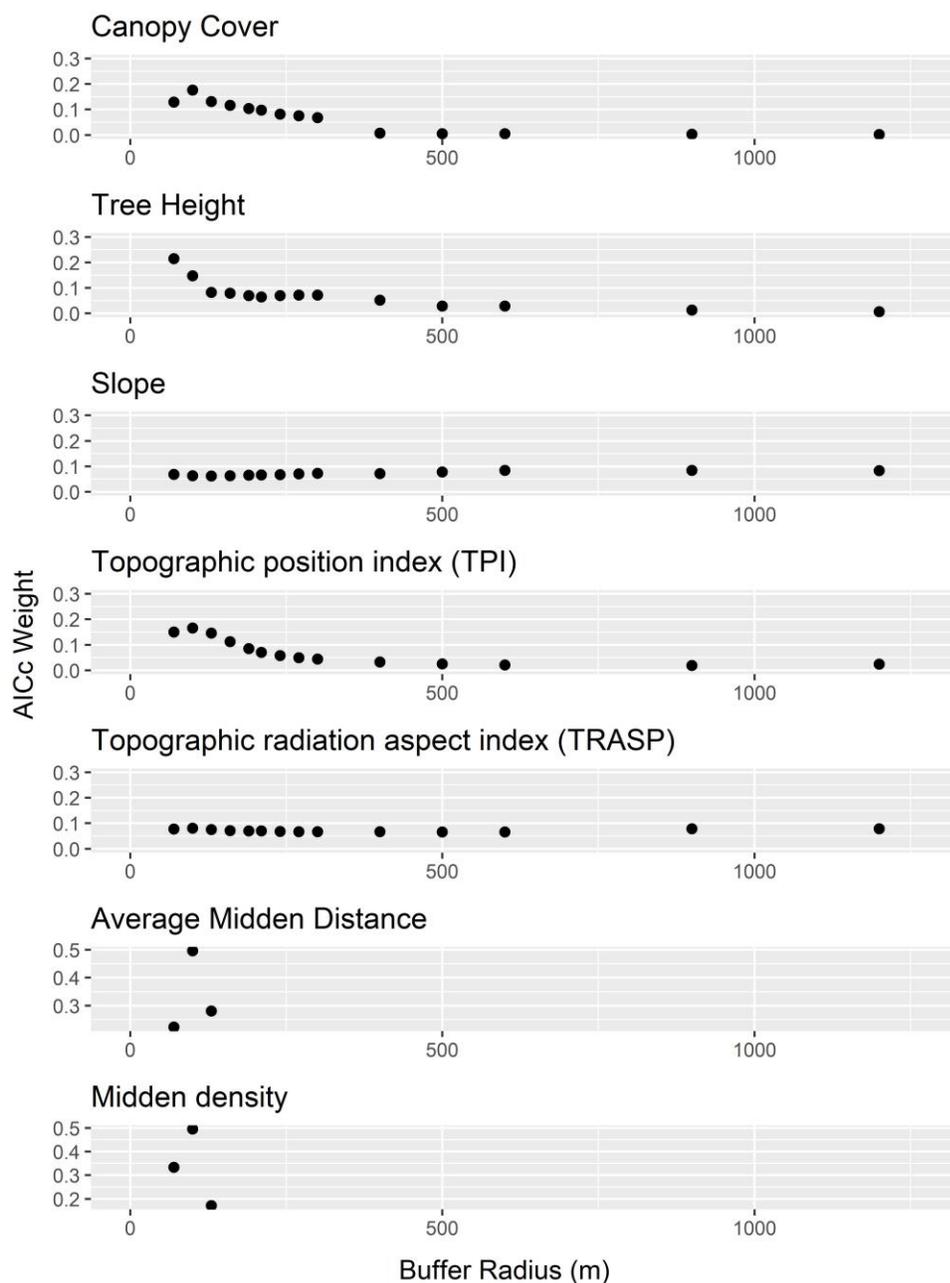


Figure 3.5: Model support (AICc weight) across spatial scales testing for differences in environmental covariates between red squirrel (*Tamiasciurus fremonti fremonti*) settlement locations (n = 12) and 5000 random available points in the White Mountains, Arizona, USA; and model support (AICc weight) across spatial scales testing for differences in mean distance among middens and midden density (middens /area of buffer) between red squirrel (*Tamiasciurus fremonti fremonti*) settlement locations (n = 12) and 43 ground-based random points from within forest habitat in the White Mountains, Arizona, USA, from 2018 to 2020.

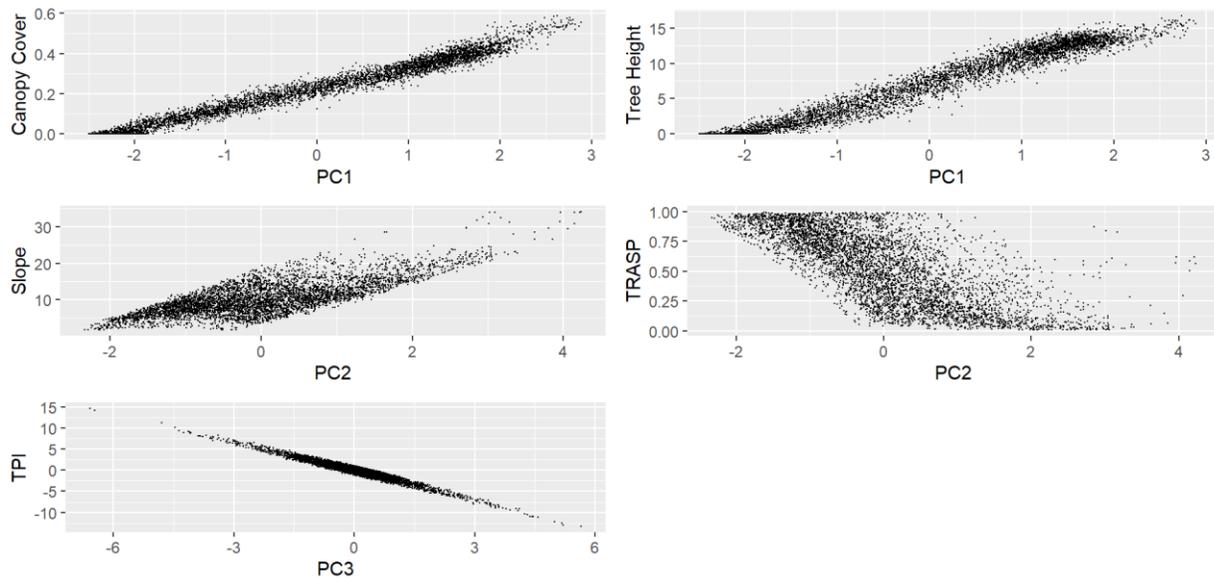


Figure 3.6: Plots of principal components analyses versus environmental features (with the best supported spatial scale) used in describing settlement point selection by translocated red squirrel (*Tamiasciurus fremonti fremonti*) in the White Mountains, Arizona, USA, from 2018 to 2020.

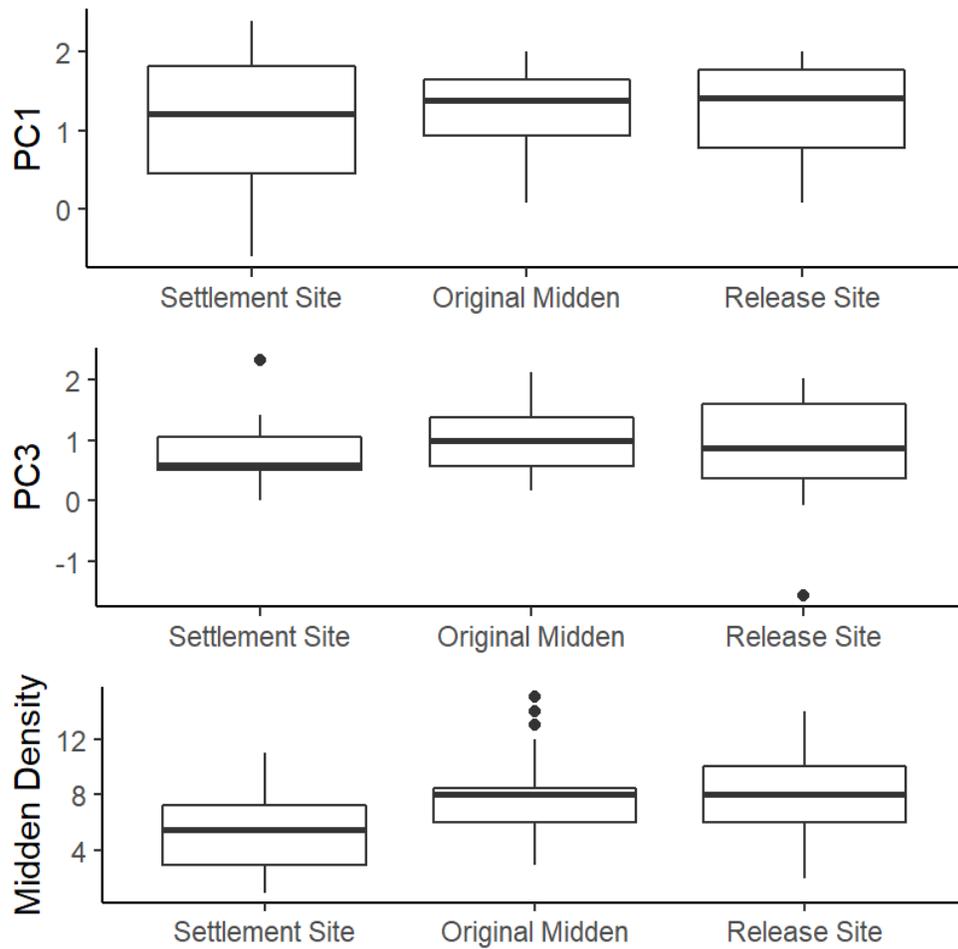


Figure 3.7: Boxplot of settlement site, original midden, and release site characteristics (PC1, PC3, and number of middens) used by red squirrel (*Tamiasciurus fremonti fremonti*) during different phases of translocation in the White Mountains, Arizona, USA, from 2018 to 2020.

Table 3.1 Results of generalized mixed models with gaussian distribution and identity link, to understand the effect of sex, days from the release event, settlement, and number of telemetry points respectively on daily distance (m/day), speed (m/h), and turning angle of translocated animals on the White Mountains, AZ, USA, from 2018 to 2020. Animal ID has been included as random effect for each model.

<b>DAILY DISTANCE</b>				
	<b>Estimate</b>	<b>SE</b>	<b>T</b>	<b>p</b>
Intercept	6.09	0.30	20.03	< 0.001
Sex - M	0.22	0.32	0.67	0.50
Days from release event	-0.03	0.01	-2.96	0.003
Settlement - Yes	-1.90	0.33	-5.62	< 0.001
Number of telemetry points	0.17	0.03	4.76	< 0.001
<b>SPEED</b>				
	<b>Estimate</b>	<b>SE</b>	<b>T</b>	<b>p</b>
Intercept	3.47	0.29	11.88	< 0.001
Sex - M	0.02	0.27	0.07	0.94
Days from release event	-0.04	0.01	-3.35	0.001
Settlement - Yes	-1.17	0.36	-3.20	0.001
Number of telemetry points	0.25	0.04	6.32	< 0.001
<b>TURNING ANGLE</b>				
	<b>Estimate</b>	<b>SE</b>	<b>T</b>	<b>p</b>
Intercept	97.33	7.63	12.74	< 0.001
Sex - M	7.66	6.50	1.17	0.24
Days from release event	0.32	0.35	0.91	0.36
Settlement - Yes	8.32	10.40	0.80	0.42
Number of telemetry points	-1.19	1.36	-0.87	0.38

Table 3.2: The two models selected with AICc to explain point selection by translocated red squirrel (*Tamiasciurus fremonti fremonti*) in the White Mountains, Arizona, USA. We measured availability using empirically derived generalized Pareto distribution (GPD) kernels centered on telemetry locations. PSF has been fitted using Cox proportional hazard regression model with the coxph function of the survival package.

		<i>Coefficient</i>	<i>CI</i>	<i>Robust se</i>	<i>Z</i>
<b>Model 1</b>	<b><i>TPI</i></b>	-0.059	[-0.096; -0.021]	0.019	-3.034
	<b><i>Tree Height</i></b>	0.959	[-0.63; 1.288]	0.168	5.684
<b>Model 2</b>	<b><i>TPI</i></b>	-0.062	[-0.103; -0.021]	0.021	-2.950
	<b><i>Tree Height</i></b>	0.918	[0.571; 1.265]	0.177	5.178
	<b><i>Slope</i></b>	-0.246	[-0.706; 0.246]	0.235	-1.049

Table 3.3: Results of principal components analyses describing variation in environmental features used in describing settlement point selection by translocated red squirrel (*Tamiasciurus fremonti fremonti*) in the White Mountains, Arizona, USA, between 2018 and 2020. Distance values represent the best supported spatial scale (i.e., buffer radius) for each covariate.

Covariate	Comp. 1	Comp. 2	Comp. 3	Comp. 4	Comp. 5
Canopy Cover (100 m)	0.694			0.102	0.710
Tree Height (70 m)	0.689			0.161	-0.703
Slope (300 m)	0.114	0.712		-0.690	
Topographic Position Index (100 m)	0.102	-0.159	-0.980		
Topographic Radiation Aspect Index (100 m)	0.140	-0.684	0.170	-0.695	

Table 3.4: The two models selected to explain settlement selection by translocated red squirrel (*Tamiasciurus fremonti fremonti*) in the White Mountains, Arizona, USA. The models are generalized linear model, with binomial family and logit link. The variables in the model are for the first model PC1 and PC3, while for the second model PC1, PC3, and PC2.

		<b>Coefficient</b>	<b>SE</b>	<b>Z</b>	<b>p</b>
<b>Model 1</b>	<b>Intercept</b>	-5.30	0.45	-30.73	<0.001
	<b>PC1</b>	0.75	0.29	2.57	0.01
	<b>PC3</b>	0.73	0.24	3.12	0.001
<b>Model 2</b>	<b>Intercept</b>	-15.33	0.49	-30.76	<0.001
	<b>PC1</b>	0.71	0.29	2.41	0.01
	<b>PC3</b>	0.82	0.26	3.07	0.37
	<b>PC2</b>	-0.29	0.32	-0.89	0.002

Table 3.5: model selected to explain settlement selection by translocated red squirrel (*Tamiasciurus fremonti fremonti*) in the White Mountains, Arizona, USA, when density of red squirrel residents is included. The model is a generalized linear model, with binomial family and logit link. The variables in the model are PC1, PC3 and local density around a buffer of 100m from the settlement or random point.

	<b><i>Coefficient</i></b>	<b><i>SE</i></b>	<b><i>Z</i></b>	<b><i>p</i></b>
<b><i>Intercept</i></b>	-0.001	0.88	-0.002	0.99
<b><i>PC1</i></b>	0.70	0.72	0.97	0.32
<b><i>PC3</i></b>	1.56	0.63	2.46	0.01
<b><i>Residents density (100 m)</i></b>	-0.46	0.21	-2.17	0.03

*Supplemental material*

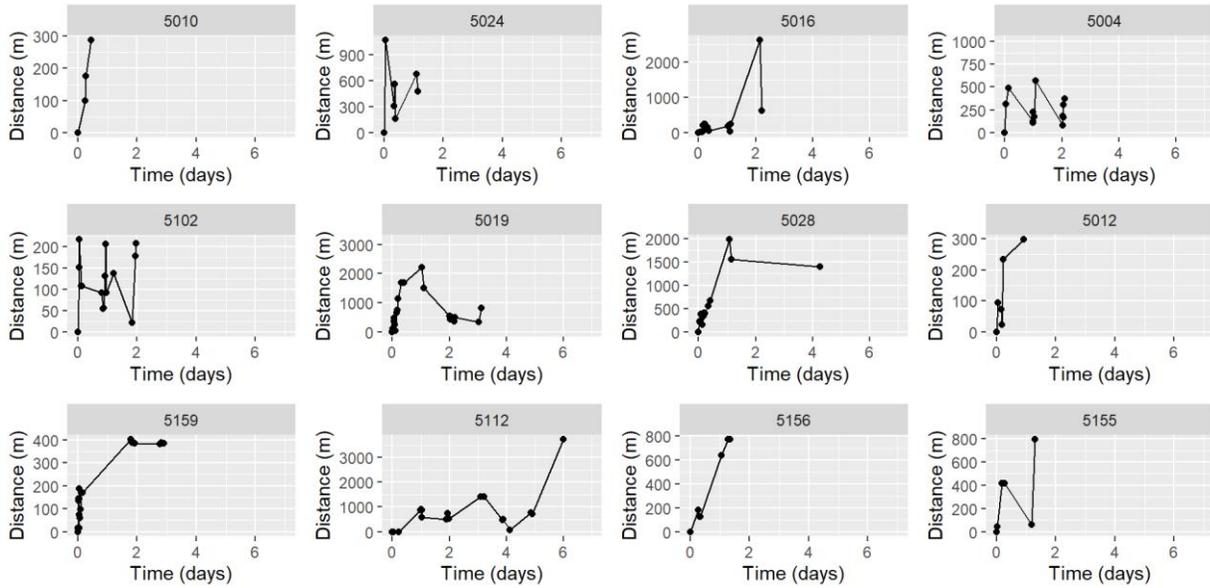


Figure 3.8: Distance (m) from the release point as a function of days post-release for translocated red squirrel (*Tamiasciurus fremonti fremonti*) in the White Mountains, Arizona, USA, from 2018 to 2020, that dies or went missing after translocation, but before settlement behavior was observed.

Table 3.6: Comparisons of spatial scales (canopy cover, tree height, slope, TPI, TRASP) during exploratory movements, testing for differences in environmental covariates between red squirrel (*Tamiasciurus fremonti fremonti*) telemetry locations and the average covariate value within a specific buffer in the White Mountains, Arizona, USA. Models were ranked using Akaike's Information Criterion adjusted for small sample sizes (AICc) and  $w$  is AICc model weight.

THREE HEIGHT					
Buffer Radii (m)	AICc	$\Delta$ AICc	$w$	Log Likelihood	Cumulative $w$
500	-123.29	0.00	0.489	62.65	0.489
600	-123.02	0.27	0.428	62.51	0.916
400	-119.75	3.54	0.083	60.88	1.000
300	-107.84	15.45	0.000	54.92	1.000
270	-104.60	18.69	0.000	53.30	1.000
240	-101.13	22.16	0.000	51.57	1.000
900	-100.95	22.34	0.000	51.48	1.000
210	-99.81	23.47	0.000	50.91	1.000
190	-99.34	23.95	0.000	50.67	1.000
160	-97.05	26.23	0.000	49.53	1.000
130	-95.37	27.91	0.000	48.69	1.000
70	-93.49	29.80	0.000	47.74	1.000
100	-93.27	30.01	0.000	47.64	1.000
1200	-90.14	33.15	0.000	46.07	1.000
TPI					
	AICc	$\Delta$ AICc	$w$	Log Likelihood	Cumulative $w$
600	-76.68	0.00	0.160	39.34	0.160
500	-76.57	0.11	0.151	39.29	0.311
400	-75.90	0.78	0.108	38.95	0.419
1200	-75.77	0.92	0.101	38.88	0.520
900	-75.66	1.02	0.096	38.83	0.616
300	-74.80	1.89	0.062	38.40	0.678
270	-74.46	2.22	0.053	38.23	0.731
240	-74.22	2.46	0.047	38.11	0.778
210	-74.04	2.65	0.043	38.02	0.820
190	-73.94	2.74	0.041	37.97	0.861
160	-73.84	2.85	0.039	37.92	0.900
130	-73.69	2.99	0.036	37.85	0.935
100	-73.54	3.15	0.033	37.77	0.969
70	-73.43	3.25	0.031	37.72	1.000
TRASP					
	AICc	$\Delta$ AICc	$w$	Log Likelihood	Cumulative $w$
190	-76.41	0.00	0.112	39.20	0.112
210	-76.35	0.06	0.109	39.18	0.221
160	-76.29	0.12	0.106	39.14	0.327

240	-76.11	0.29	0.097	39.06	0.424
270	-75.95	0.46	0.089	38.98	0.514
130	-75.94	0.46	0.089	38.97	0.603
300	-75.75	0.65	0.081	38.88	0.684
100	-75.47	0.94	0.070	38.74	0.754
1200	-75.10	1.30	0.059	38.55	0.813
70	-75.09	1.32	0.058	38.55	0.871
400	-74.59	1.81	0.045	38.30	0.916
900	-74.08	2.33	0.035	38.04	0.951
500	-73.52	2.88	0.027	37.76	0.978
600	-73.14	3.27	0.022	37.57	1.000
SLOPE					
	<b>AICc</b>	<b>ΔAICc</b>	<b>w</b>	<b>Log Likelihood</b>	<b>Cumulative w</b>
1200	-84.66	0.00	0.400	43.33	0.400
1500	-84.66	0.00	0.400	43.33	0.800
600	-80.36	4.30	0.047	41.18	0.847
500	-79.88	4.79	0.037	40.94	0.883
900	-79.73	4.93	0.034	40.87	0.917
400	-78.88	5.78	0.022	40.44	0.940
300	-78.44	6.22	0.018	40.22	0.957
270	-77.92	6.74	0.014	39.96	0.971
240	-77.18	7.49	0.009	39.59	0.981
210	-76.31	8.35	0.006	39.16	0.987
190	-75.69	8.97	0.005	38.85	0.991
160	-74.67	10.00	0.003	38.33	0.994
130	-74.18	10.48	0.002	38.09	0.996
100	-74.12	10.55	0.002	38.06	0.998
70	-73.80	10.86	0.002	37.90	1.000
CANOPY COVER					
	<b>AICc</b>	<b>ΔAICc</b>	<b>w</b>	<b>Log Likelihood</b>	<b>Cumulative w</b>
500	-101.73	0.00	0.462	51.87	0.462
400	-101.21	0.52	0.357	51.61	0.819
600	-99.62	2.11	0.161	50.81	0.981
300	-93.90	7.83	0.009	47.95	0.990
270	-92.09	9.64	0.004	47.05	0.993
240	-90.98	10.76	0.002	46.49	0.996
210	-90.19	11.54	0.001	46.10	0.997
190	-89.96	11.77	0.001	45.98	0.998
160	-88.59	13.14	0.001	45.29	0.999
130	-87.76	13.97	0.000	44.88	0.999
100	-87.00	14.73	0.000	44.50	1.000
70	-86.92	14.81	0.000	44.46	1.000

900	-81.81	19.92	0.000	41.91	1.000
1200	-76.32	25.41	0.000	39.16	1.000

Table 3.7: Rankings of candidate models for point selection functions by translocated red squirrel (*Tamiasciurus fremonti fremonti*) in the White Mountains, Arizona, from 2018 to 2020, USA during exploratory movements. Covariates include tree height, percent slope, topographic position index (TPI) and topographic radiation aspect index (TRASP). K is the number of model parameters and w is the AICc model weight.

<b>Models</b>	<b>K</b>	<b>AICc</b>	<b>ΔAICc</b>	<b>w</b>	<b>Log Likelihood</b>	<b>Cumulative w</b>
Tree Height + TPI	2	-132.677	0.000	0.415	68.344	0.415
Tree Height + TPI + Slope	3	-132.104	0.573	0.312	69.063	0.727
Tree Height + TPI + TRASP	3	-130.670	2.007	0.152	68.346	0.879
Tree Height+ TPI + TRASP + Slope	4	-130.091	2.586	0.114	69.064	0.992
Tree Height	1	-123.287	9.391	0.004	62.645	0.996
Tree Height + Slope	2	-121.693	10.984	0.002	62.852	0.998
Tree Height + TRASP	2	-121.283	11.394	0.001	62.647	0.999
Tree Height + TRASP+ Slope	3	-119.688	12.989	0.001	62.855	1.000
TRASP + TPI + Slope	3	-89.699	42.978	0.000	47.861	1.000
TPI + Slope	2	-88.896	43.781	0.000	46.454	1.000
TRASP + Slope	2	-84.820	47.857	0.000	44.416	1.000
Slope	1	-84.662	48.015	0.000	43.333	1.000
TRASP + TPI	2	-78.532	54.145	0.000	41.272	1.000
TPI	1	-76.683	55.994	0.000	39.343	1.000
TRASP	1	-76.406	56.271	0.000	39.205	1.000

Table 3.8: Comparisons of spatial scales (canopy cover, tree height, slope, TPI, TRASP) during settlement movements, testing for differences in environmental covariates between red squirrel (*Tamiasciurus fremonti fremonti*) settlement locations (n = 12) and 5000 random available points in the White Mountains, Arizona, USA. Midden density and average midden distance have been instead compared between settlement locations and 43 random available points. Models were ranked using Akaike’s Information Criterion adjusted for small sample sizes (AICc) and w is AICc model weight.

<b>CANOPY COVER</b>					
<b>Buffer Radii (m)</b>	<b>AICc</b>	<b>ΔAICc</b>	<b>W</b>	<b>Log Likelihood</b>	<b>Cumulative w</b>
100	368.11	0.000	0.176	-182.056	0.176
130	368.70	0.585	0.131	-182.348	0.307
70	368.74	0.628	0.129	-182.37	0.436
160	368.95	0.835	0.116	-182.473	0.552
190	369.18	1.063	0.103	-182.587	0.656
210	369.30	1.190	0.097	-182.651	0.753
240	369.66	1.542	0.081	-182.827	0.834
270	369.80	1.690	0.076	-182.901	0.910
300	370.01	1.897	0.068	-183.004	0.978
400	374.48	6.367	0.007	-185.239	0.985
500	375.22	7.103	0.005	-185.607	0.990
600	375.30	7.186	0.005	-185.649	0.995
900	376.41	8.299	0.003	-186.205	0.998
1200	376.92	8.802	0.002	-186.457	1.000
<b>TREE HEIGHT</b>					
<b>Buffer Radii (m)</b>	<b>AICc</b>	<b>ΔAICc</b>	<b>W</b>	<b>Log Likelihood</b>	<b>Cumulative w</b>
70	367.98	0.000	0.215	-181.991	0.215
100	368.74	0.755	0.147	-182.368	0.362
130	369.91	1.924	0.082	-182.953	0.444
160	369.97	1.983	0.080	-182.982	0.523
270	370.17	2.181	0.072	-183.081	0.595
300	370.18	2.192	0.072	-183.087	0.667
190	370.23	2.247	0.070	-183.114	0.737
240	370.23	2.251	0.070	-183.116	0.806
210	370.39	2.407	0.064	-183.194	0.871
400	370.81	2.825	0.052	-183.403	0.923
600	371.98	3.998	0.029	-183.99	0.952
500	372.03	4.046	0.028	-184.014	0.980
900	373.65	5.662	0.013	-184.822	0.993
1200	374.84	6.858	0.007	-185.42	1.000
<b>SLOPE</b>					
<b>Buffer Radii (m)</b>	<b>AICc</b>	<b>ΔAICc</b>	<b>W</b>	<b>Log Likelihood</b>	<b>Cumulative w</b>
600	376.61	0.000	0.084	-186.305	0.084
900	376.63	0.017	0.084	-186.313	0.168
1200	376.64	0.027	0.083	-186.318	0.251
500	376.76	0.151	0.078	-186.38	0.329

300	376.92	0.311	0.072	-186.46	0.402
400	376.93	0.320	0.072	-186.465	0.473
270	376.98	0.368	0.070	-186.489	0.544
70	377.03	0.417	0.068	-186.514	0.612
240	377.06	0.445	0.068	-186.527	0.679
210	377.09	0.477	0.066	-186.543	0.746
190	377.12	0.512	0.065	-186.561	0.811
100	377.18	0.570	0.063	-186.59	0.875
160	377.20	0.588	0.063	-186.599	0.937
130	377.21	0.597	0.063	-186.604	1.000
<b>TPI</b>					
<b>Buffer Radii (m)</b>	<b>AICc</b>	<b>ΔAICc</b>	<b>W</b>	<b>Log Likelihood</b>	<b>Cumulative w</b>
100	372.90	0.000	0.166	-184.45	0.166
70	373.10	0.200	0.150	-184.55	0.316
130	373.16	0.258	0.146	-184.579	0.461
160	373.67	0.772	0.113	-184.835	0.574
190	374.25	1.346	0.085	-185.123	0.658
210	374.61	1.705	0.071	-185.302	0.729
240	375.01	2.111	0.058	-185.505	0.787
270	375.33	2.430	0.049	-185.665	0.836
300	375.54	2.639	0.044	-185.769	0.880
400	376.17	3.269	0.032	-186.084	0.912
500	376.70	3.797	0.025	-186.348	0.937
1200	376.81	3.910	0.023	-186.405	0.961
600	377.03	4.133	0.021	-186.516	0.982
900	377.30	4.402	0.018	-186.651	1.000
<b>TRASP</b>					
<b>Buffer Radii (m)</b>	<b>AICc</b>	<b>ΔAICc</b>	<b>W</b>	<b>Log Likelihood</b>	<b>Cumulative w</b>
100	376.94	0.000	0.081	-186.468	0.081
1200	376.99	0.056	0.078	-186.496	0.159
900	377.00	0.061	0.078	-186.499	0.237
70	377.04	0.101	0.077	-186.518	0.314
130	377.07	0.133	0.075	-186.535	0.389
160	377.19	0.256	0.071	-186.596	0.460
190	377.22	0.279	0.070	-186.607	0.531
210	377.23	0.292	0.070	-186.614	0.600
240	377.27	0.334	0.068	-186.635	0.669
400	377.30	0.365	0.067	-186.65	0.736
270	377.31	0.372	0.067	-186.654	0.803
300	377.32	0.386	0.066	-186.661	0.869
500	377.36	0.418	0.065	-186.677	0.935
600	377.36	0.423	0.065	-186.679	1.000
<b>AVERAGE MIDDEN DISTANCE</b>					
<b>Buffer Radii (m)</b>	<b>AICc</b>	<b>ΔAICc</b>	<b>W</b>	<b>Log Likelihood</b>	<b>Cumulative w</b>
100	70.15	0.000	0.497	-32.9973	0.497

130	71.29	1.142	0.281	-33.5683	0.777
70	71.75	1.601	0.223	-33.7979	1.000
<b>MIDDEN DENSITY</b>					
<b>Buffer Radii (m)</b>	<b>AICc</b>	<b><math>\Delta</math>AICc</b>	<b>W</b>	<b>Log Likelihood</b>	<b>Cumulative w</b>
100	67.97	0.000	0.495	-31.907	0.495
70	68.76	0.790	0.333	-32.3019	0.828
130	70.09	2.120	0.172	-32.9667	1.000

Table 3.9: Rankings of candidate models for settlement site selection by translocated red squirrels (*Tamiasciurus fremonti fremonti*) in the White Mountains, Arizona, USA, between 2018 and 2020, with available habitat features measured at 5000 random points throughout our study area. Covariates include the first three components of a principal components analysis using GIS-based vegetation and topographic covariates measured at settlement points and random available points. K is the number of model parameters and w is the AICc model weight.

<b>Models</b>	<b>K</b>	<b>AICc</b>	<b><math>\Delta</math>AICc</b>	<b>w</b>	<b>Log Likelihood</b>	<b>Cumulative w</b>
PC1 + PC3	3	364.249	0.000	0.614	-179.122	0.614
PC1 + PC2 + PC3	4	365.771	1.521	0.287	-178.881	0.901
PC1	2	369.600	5.350	0.042	-182.799	0.944
PC3	2	370.965	6.716	0.021	-183.481	0.965
PC1 + PC2	3	371.541	7.292	0.016	-182.768	0.981
PC2 + PC3	3	371.577	7.328	0.016	-182.786	0.997
PC1	1	375.522	11.273	0.002	-186.761	0.999
PC2	2	377.345	13.096	0.001	-186.671	1.000

Table 3.10. Rankings of candidate models for settlement site selection by translocated red squirrel (*Tamiasciurus fremonti fremonti*) in the White Mountains, Arizona, USA, from 2018 to 2020, with available habitat features measured at 43 available points in forested areas throughout our study area. Covariates include the first three components of a principal components analysis using GIS-based vegetation and topographic covariates, mean midden density, and mean inter-midden distance measured at settlement points and available points. K is the number of model parameters and w is the AICc model weight.

<b>Models</b>	<b>K</b>	<b>AICc</b>	<b>ΔAICc</b>	<b>w</b>	<b>Log Likelihood</b>	<b>Cumulative w</b>
midden density + PC1 + PC3	4	52.92	0.000	0.72	-22.01	0.72
PC1 + PC3	3	56.52	3.60	0.12	-25.00	0.84
average middens distance + PC1 + PC3	4	57.71	4.80	0.07	-24.41	0.91
midden density	2	59.02	6.10	0.03	-27.39	0.94
1	1	59.29	6.37	0.03	-28.60	0.97
average middens distance	2	60.57	7.66	0.02	-28.17	0.99
average middens distance + midden density	3	61.25	8.34	0.01	-27.39	1.00