Low survival, high predation pressure present conservation challenges for an endangered endemic forest mammal

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A B S T R A C T

Knowledge of which population parameters and mortality risks contribute most to population decline and endangerment is necessary to develop informed and actionable conservation plans for threatened and endangered species (Rushton et al., 2006). The federally endangered Mount Graham red squirrel (*Tamiasciurus fremonti grahamensis*) is restricted to the Pinaleño Mountains, in southeastern Arizona, USA. The population is critically threatened with extensive habitat loss from fire as well as by an introduced non-native squirrel species, the Abert's squirrel (*Sciurus aberti*). Recovery is challenged by low survival and poor reproduction, such that the subspecies is functionally semelparous. We calculate survival rates and cause-specific mortality hazards from known-fate individuals to understand the impact of predation on survival and demography in this peripheral population. We document the lowest survival and highest rates of mortality in any population of North American red squirrels in both adult and juvenile age classes (mean annual survival: adults = 0.32, juveniles = 0.26). We attributed the majority of confirmed deaths to avian predation (adults 65%, juveniles 75%), and the daily hazard rate for avian predation was 15 times higher than for mammalian predation and 2 times higher than death from unknown causes. It is likely that the presence of an ecologically similar, non-native tree squirrel subsidizes a diverse avian predator guild, which includes two raptor species of conservation concern. In addition to efforts to remove the non-native Abert's squirrel, we recommend immediate forest restoration efforts in the long term, and habitat augmentation to increase structural complexity, cover, shelter, and food resources in the short term.

1. Introduction

Peripheral populations at the leading and trailing edges of a species range are subject to climatic extremes, persist at low densities, face demographic challenges such as decreased reproductive rates and reduced survival of certain age classes, and are therefore threatened with increased risk of extinction (Hampe and Petit, 2005; Hardie and Hutchings, 2010; Lesica and Allendorf, 1995; Vucetich and Waite, 2003). Peripheral populations, particularly at the trailing edge, can also be biologically important reservoirs of genetic differentiation, and thus important for conservation in the face of rapid environmental change (Hampe and Petit, 2005; Hardie and Hutchings, 2010; Lesica and Allendorf, 1995). Conservation and management of small, peripheral populations relies upon improved understanding of demographic parameters that limit population growth (Arrigoni et al., 2011; Corti et al., 2010; Davies-Mostert et al., 2015).

Survival rate is a fundamental check on persistence and can have a greater impact on population growth rate λ than fecundity, especially in species that do not have high reproductive rates (Sæther and Bakke,

2007) or in isolated, peripheral or small populations (Lande, 1988). Although much concern in recent years has focused on human-caused declines in species survival rates both through indirect means, such as habitat modification (Root, 1998), and direct means such as hunting for sport or subsistence (Festa-Bianchet, 2003), it is as critical to understand the influence of natural trophic relationships on the survival rate of at-risk species. Influences on the survival of certain groups within a population can affect overall population function and demography in different ways. For example, increasing natural levels of predation and the introduction of competition causes a decrease in juvenile recruitment and behavioral modification with demographic effects (Gurnell et al., 2004; Preisser et al., 2005; Wauters et al., 2000; Wolff et al., 1999). Experimental manipulation revealed that predation rates have a greater impact on survival than resource availability in rodents (Desy and Batzli, 1989). Estimation of survival rates and the relative importance of different mortality hazards (e.g. natural predation vs. hunting) among age classes within populations of conservation concern can aid management as well as provide a more complete picture of survival (Olson et al., 2014). Further, quantification of demographic

parameters such as survival and mortality hazards can aid in understanding indirect impacts of introduced, non-native species on endangered populations.

The federally endangered Mount Graham red squirrel (MGRS; *Tamiasciurus fremonti grahamensis*) is one of the southernmost populations of the North American red squirrel species complex (Hope et al., 2016; hereafter red squirrels) and is endemic to the Pinaleño Mountains, in southeastern Arizona, USA. This population has been monitored intensively since 1989 with individual animals in the study marked since 2002. Populations have experienced fluctuations and declines in response to disturbance events that include insect defoliators and wildfire (Koprowski et al., 2005, 2006; Fig. S1). Life expectancy in this peripheral population is shorter than in the core range of the species complex and results in decreased fecundity (Goldstein et al., 2017). Part of the Madrean sky island archipelago, the Pinaleño Mountains are considered a biodiversity hotspot (Warshall, 1995). In addition to unique small mammal taxa, the Pinaleño Mountains provide important habitat to a suite of mammalian carnivores and avian predators that include MGRS in their diet. Predators of MGRS include northern goshawk (*Accipiter gentilis*), Cooper's, sharp shinned, and red-tailed hawks (*A. cooperii, A. striatus, Buteo jamaicensis* respectively), Mexican spotted and great horned owls (*Strix occidentalis lucida, Bubo virginianus*), bobcat (*Lynx rufus*), and gray fox (*Urocyon cinereoargenteus*) (Schauffert et al., 2002). Four predators of red squirrels in other parts of their range, long-tailed weasels (*Mustela frenata*), short-tailed weasels (*Mustela erminea*), American marten (*Martes americana*), and lynx (*Lynx canadensis*) (Digweed and Rendall, 2009; Rusch and Reeder, 1978), are absent in the Pinaleños (Clark et al., 1987; King, 1983; Sheffield and Thomas, 1997; Tumlison, 1987), although long-tailed weasels may have occurred there previously (Hoffmeister, 1956). In Alberta, Canada it is estimated that predators account for > 19% of adult red squirrel mortality, and if it can be assumed that mustelids are responsible for the majority of nestling mortality, predator caused mortality for adult and juvenile age classes combined could be as high as 51–70% (Rusch and Reeder, 1978). However cause-specific mortality in MGRS has not been quantified.

Compared to other red squirrel populations in North America, MGRS suffers increased adult mortality with life expectancy highest at birth and continually decreasing with each successive year of life (Goldstein et al., 2017). An average life expectancy of 1.2–1.8 years for males and females, respectively, suggests this population is functionally semelparous (Goldstein et al., 2017). Further, the presence of an introduced tree squirrel (*Sciurus aberti*), may limit food availability, elicit additional energy expenditure via territorial defense, and serve as a secondary prey source for predators (Derbridge, 2018; Edelman and Koprowski, 2005; Hutton et al., 2003). It is unknown whether the low survivorship observed in MGRS is driven by increased predation pressure or other causes. We collected data from known-fate individuals as part of a long-term study on radio collared animals to assess cause of death and estimate survival. We calculate survival rates and cause-specific mortality hazards in MGRS by sex, age class, and season to understand the impact of predation on survival and demography in this peripheral population. Our results will inform MGRS conservation and recovery efforts as well as current and future forest restoration and habitat management plans.

2. Methods

2.1. Study area

We studied MGRS in mature spruce-fir and mixed-conifer forest in the Pinaleño Mountains of southeastern Arizona, Graham County USA (32.7017° N, 109.8714° W). Our five study areas, totaling approximately 400 ha (Fig. 1), are within MGRS habitat and range in elevation from 2647 m to 3267 m and comprise vegetation communities of mesic mixed-conifer forest dominated by Douglas fir (*Pseudotsuga menziesii*)

and southwestern white pine (*Pinus strobiformis*) and high-elevation spruce-fir forest dominated by Englemann spruce (*Picea engelmannii*) and corkbark fir (*Abies lasiocarpa* var. *arizonica*) (O'Connor et al., 2014; Smith and Mannan, 1994).

2.2. Animal capture and radio telemetry

MGRS were captured at their central larderhoard, or midden, in collapsible single-door live traps (model 201, Tomahawk Live Trap Co, Tomahawk, Wisconsin) baited with peanuts and peanut butter, checked at < 2 hourly intervals and closed to capture at night. Captured squirrels were safely restrained with a cloth handling cone (Koprowski, 2002), marked with colored ear tags, and fitted with a radio collar (SOM 2190, Wildlife Materials International) (Koprowski et al., 2008). We captured and radio collared animals between May 2002 and February 2016 and adults with mass ≥ 200 g were fitted with a radio collar (mean collar weight ~7 g). We also trapped and collared juvenile squirrels ≥100 g between September 2010 and August 2013 (mean collar weight ~5 g; Merrick and Koprowski, 2016a, b). Collared animals were located ≥12 times/month via biangulation and homing and quarterly censuses of all known middens within the study areas ensured that the presence of residents on the study sites was monitored regularly to accurately ascertain disappearance dates. We binned recapture data monthly; animals were recorded as alive and recaptured in a monthly session when they were visually sighted, trapped, and/or had biangulation data from radio-telemetry. When deceased animals (known-fate) were located by homing in on the radio transmitter signal, we recorded all details and collected the remains in an attempt to assign the cause of mortality. All research was carried out under University of Arizona Institutional Animal Care and Use Committee protocol #08-024, Arizona Game and Fish Department scientific collecting permit #SP654189, U.S. Fish and Wildlife Service permit #TE041875-0, and adhered to the American Society of Mammalogists guidelines for the use of wild mammals in research (Sikes, 2016).

2.3. Survival and recapture estimation

We calculated survival and recapture probabilities for the MGRS population using Cormack-Jolly-Seber (CJS) models in Program MARK (White and Burnham, 1999). We investigated survival for the complete population of marked MGRS, 381 animals over 166 occasions. We included separate parameters for age when collared (juvenile: 0–1 year; adult > 1 year), sex (male; female), and time (monthly). The most saturated model included all parameters [$\phi_{sex*age*time}$, $p_{sex*age*time}$] where ϕ represented the monthly survival probability and p represented the monthly recapture probability. Goodness-of-fit of the saturated model was evaluated with the parametric bootstrap procedure to ensure adequate model fit and that CJS assumptions were not violated. We corrected for overdispersion in the saturated models by adjusting the variance inflation factor (ĉ), which we calculated as the quotient of the observed model deviance and the mean deviance of simulated models. We created the candidate set of models by systematically stepping down the parameters on p while retaining the most saturated survival function [$\phi_{sex*age*time}$]. Next, we stepped-down ϕ while retaining the most parsimonious recapture function (Lebreton et al., 1992; Wauters et al., 2008). The Akaike Information Criterion corrected for small sample bias (AIC$_c$, or the quasi-AIC$_c$ after the ĉ correction was made) identified the most parsimonious model that adequately represented the data. We used the model-averaging function in Program MARK when the QAIC$_c$ indicated that multiple models had approximately equal weight in the data (ΔQAIC$_c$ < 2) (Anderson and Burnham, 1999). We estimated the annual value for the survival parameter by raising the monthly estimate to the 12th power and using the delta method to adjust the standard error of the measurement (Powell, 2007).

Fully time-dependent models are often identified by QAIC$_c$ as the most parsimonious choice in large datasets due to the inflated power of
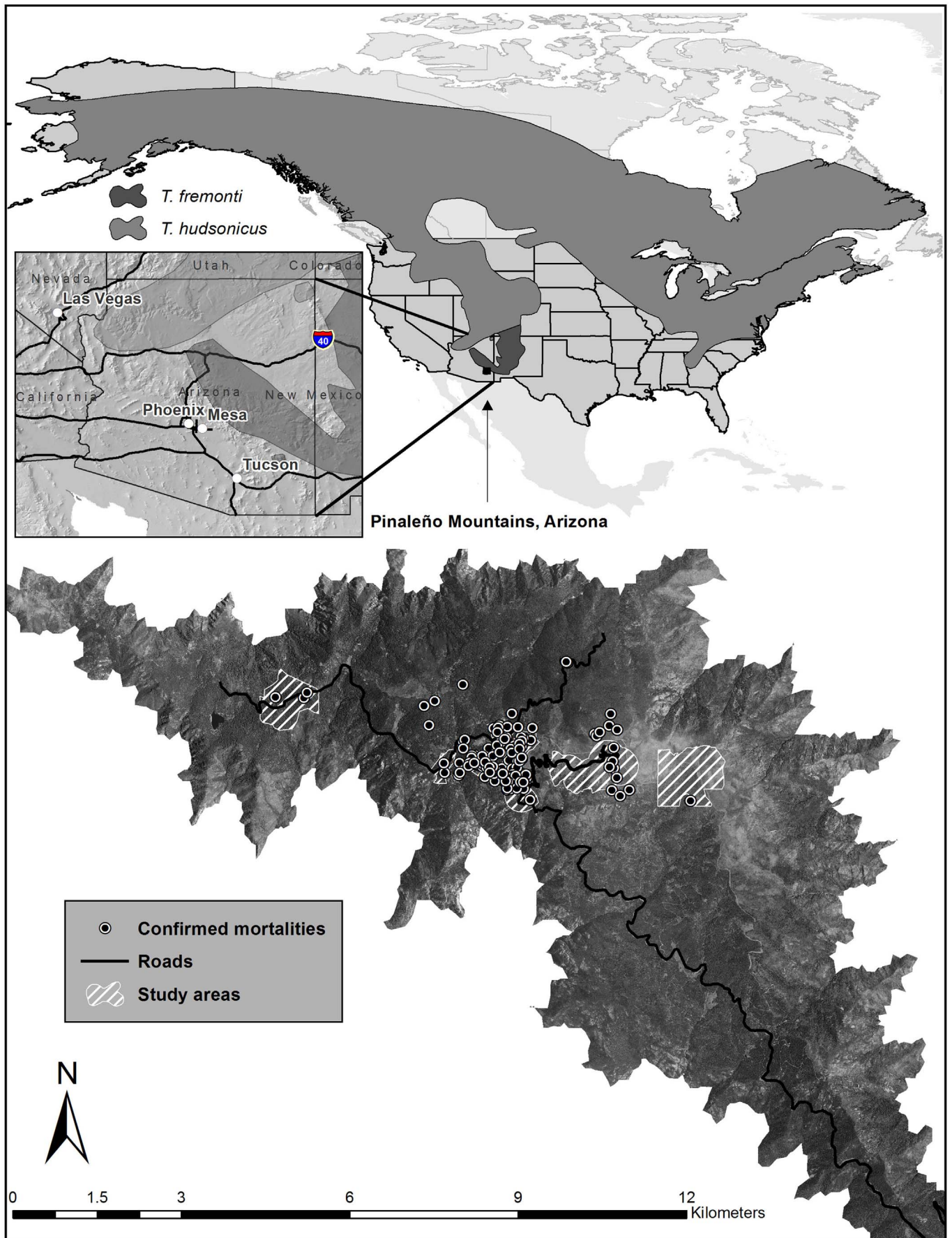
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Fig. 1. Overview of red squirrel distribution in North America, with *Tamiasciurus fremonti* elevated to species status from *T. hudsonicus*, after Hope et al., 2016 (top panel). The Pinaleño Mountains, Arizona, U.S.A. above 2400 m (bottom panel). Five study areas where Mount Graham red squirrels (*Tamiasciurus fremonti grahamensis*) were radio collared are shown with white hatching. Black circles represent mortality sites (n = 135) where remains were collected between 2002 and 2016.

the approach and may not be appropriate for choosing the best model (Frederiksen et al., 2008). When investigating covariates, it is possible to use analysis of deviance to determine the amount of deviance in the global model explained by nested covariates (Skalski et al., 1993). We did find that the most parsimonious model for survival and recapture estimation was fully time-dependent when the capture histories of all 381 marked MGRS were included. Analysis of deviance was not applicable in this case because we were not investigating the impacts of covariates on survival and recapture probability. We instead took the approach of using a subset of the marked animals, those with known fate (i.e. remains and collar found), to examine the importance of age of collaring and sex on survival and recapture. We followed the same procedure as above with 127 squirrels with known fate in the data set over 166 occasions.

2.4. Estimating incidence of cause-specific mortality

To separate mortality events from a possible slipped radio collar, we considered a confirmed mortality any instance where a radio collar with squirrel remains were recovered. Upon recovering remains, we binned mortalities into three categories: avian, mammalian, and unknown. We identified avian-caused mortalities by the presence of plucked fur, a clipped tail, gut piles, and other miscellaneous parts such as ears with tags found on top of logs or on the ground below perches; raptor feces or "white wash" is also often located nearby. We identified mammal-caused mortalities as the recovery of mostly intact carcasses, often cached beneath leaves or other forest debris or placed inside hollow logs, or based on bite mark patterns upon necropsy. We assigned mortalities to the unknown category if cause of death could not be determined due to decomposition or lack of other evidence. This category includes death from natural causes. We recorded the date that remains were recovered as the date of death, recognizing that in some cases actual death may have occurred a few days prior. All remains were collected for tissue samples and when intact specimens were found, necropsy and parasite assays. We assigned age classes to deceased individuals as above (juvenile: 0–1 year; adult > 1 year).

We estimated the incidence and rate of occurrence for each cause of death within a competing risks framework. Competing risks are events that preclude the occurrence of an event of interest (Austin et al., 2016). For example, a squirrel that dies from mammalian predation is no longer at risk of avian predation. In this case, we were interested in estimating the incidence of avian predation, mammalian predation, and death from unknown causes as competing risks. Traditional Kaplan-Meier methods to estimate the probability of an event and Cox proportional hazard models to assess the influence of covariates on the

occurrence of a particular type of event assume competing risks are absent and tend to over-estimate the probability of one type of event in the presence of competing risks (Austin et al., 2016; Lau et al., 2009). For each mortality event type, we estimated the incidence of its occurrence while taking into account other causes of death as competing risks. We used the cumulative incidence ("cuminc") and competing risks regression ("crr") functions in package "cmprsk" (Gray, 2015) in program R 3.3.1 (R Core Team, 2016) to analyze the cumulative incidence of each cause of mortality in the presence of competing risks and to test for the influence of covariates on the incidence of death from each mortality event type. We tested for differences in the incidence of each mortality type in adults and juveniles between sexes and among seasons via a modified χ^2 statistic (Gray, 2015, 1988). We assessed the relative effect of sex and season on cause-specific hazard models while accounting for competing risks via competing risks regression subdistribution hazard models ("crr") (Austin et al., 2016) to search for ecologically meaningful trends in predator impact. We used package "muhaz" (Hess, 2015) to obtain smoothed, kernel-based and locally optimal hazard estimates for each cause of death in adults and juveniles, where we set bandwidth method to "local", and kernel type to "Epanechnikov".

3. Results

3.1. Survival and recapture estimation

We calculated the variance inflation factor (ĉ) by dividing the observed deviance of the saturated model by the mean deviance of 1000 simulated models, after which we rejected the null hypothesis that ĉ = 1 for both the complete set of marked squirrels (ĉ = 1.16; p ≤ 0.001) and the subset of squirrels with known-fate (ĉ = 2.50; p ≤ 0.001) and corrected for overdispersion accordingly. In both cases the saturated models did not violate CJS assumptions or suffer from critical lack of fit as 1 < ĉ < 3. After step down model selection the most parsimonious models were retained (Table 1). These indicated that survival and recapture probabilities were time-dependent for all marked squirrels, as expected. Monthly estimates for survival and recapture in all marked animals varied from 0.688–1.000 and 0.743–1.000 respectively. The annual survival rate for all marked animals was (mean ± SE) 0.368 ± 0.177. Across years, months with the lowest mean survival were April, June, and August, and when binned into seasons, the lowest mean survival occurred in summer and fall (Fig. 2). For the subset of animals with known fate, approximately equal support existed for the survival estimate being constant, influenced by age when collared, and by sex, but interaction between the terms was

Table 1
The four most parsimonious CJS models of the candidate model set with the saturated CJS model for the set of all marked animals (N = 381 squirrels) and the subset of those with known fate (N = 127 squirrels). The most parsimonious model from each set was used to estimate survival and recapture probability in Mount Graham red squirrels (*Tamiasciurus fremonti grahamensis*) in southeastern Arizona, USA. Models were averaged when ΔQAIC$_c$ < 2.

|	Model	QAIC$_c$	ΔQAIC$_c$	No. Par	QDeviance
All marked	$\phi_{(time)}P_{(time)}$	8031.614	0.000	330	5533.996
	$\phi_{(.)}P_{(time)}$	8141.278	109.663	166	5991.237
	$\phi_{(age)}P_{(time)}$	8143.443	111.829	168	5989.244
	$\phi_{(sex)}P_{(time)}$	8144.188	112.574	168	5989.989
	$\phi_{(age*sex*time)}P_{(age*sex*time)}$	9898.357	1866.742	1270	5112.946
Known fate	$\phi_{(.)}P_{(sex)}$	606.412	0.000	3	550.543
	$\phi_{(age)}P_{(sex)}$	606.988	0.576	4	549.106
	$\phi_{(sex)}P_{(sex)}$	608.208	1.795	4	550.325
	$\phi_{(age*sex)}P_{(sex)}$	610.761	4.349	6	548.844
	$\phi_{(age*sex*time)}P_{(age*sex*time)}$	5072.721	4466.309	819	304.228
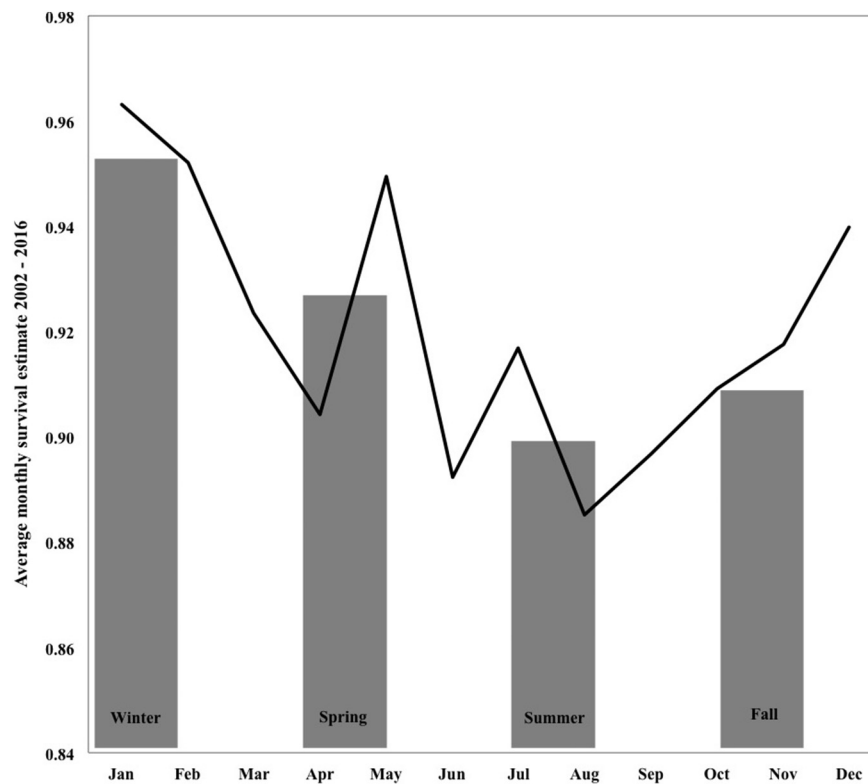
Fig. 2. Estimates of monthly and seasonal survival for all radio-collared Mount Graham red squirrels (*Tamiasciurus fremonti grahamensis*) from May 2002–February 2016 in southeastern Arizona, USA. Seasons were binned as follows: Winter = December–February; Spring = March–May; Summer = June–August; Fall = September–November.

less well-supported. Males and adults had higher survival than females and juveniles respectively (Table 2). Recapture in this subset of marked animals was influenced by sex with females having a higher recapture probability than males (Table 2).

3.2. Cause-specific mortality

Between June 2002 and June 2016 we recovered sufficient evidence to assign a cause of death for 135 individuals (74 males, 61 females; 32 juveniles, 103 adults). We excluded one juvenile female that was killed by a vehicle the day that she was radio collared. Avian predation was the most common cause of mortality for MGRS, with 67% of confirmed deaths attributed to raptors (avian n = 91 (67%), unknown n = 37 (27%), mammalian n = 7 (5%)) (Fig. 3). Across age classes, age at death (estimated days surviving) did not differ between sexes or among causes of death, or seasons (3-factor ANOVA by: sex $F_{1,128} = 0.50$, p = 0.48; cause of death $F_{2,128} = 0.41$, p = 0.67; season $F_{3,128} = 0.94$, p = 0.43). Incidence of death by avian predation and unknown causes differed by age class (Gray's χ^2 statistics: avian predation = 96.9, d.f. = 1, p < 0.001; unknown death = 27.39, d.f. = 1, p ≤ 0.001) (Fig. 4), thus we analyzed data for each age class separately. Proportion of deaths by avian predation was 0.75 in juveniles, and 0.65 in adults; proportion of deaths from unknown causes was 0.25 in juveniles, and 0.28 in adults; proportion of deaths from mammalian predation was 0.07 in adults. We did not observe any instances of mammalian predation in juveniles.

Incidence of death was similar for males and females across mortality event types in adults (Gray's χ^2 statistics by sex: avian predation = 0.29, d.f. = 1, p = 0.59; mammalian death = 0.71, d.f. = 1, p = 0.40; unknown death = 0.002, d.f. = 1, p = 0.96) and in juveniles (Gray's χ^2 statistics by sex: avian predation = 0.15, d.f. = 1, p = 0.70; unknown death = 1.20, d.f. = 1, p = 0.27). Similarly, sex had a minimal effect on each cause-specific hazard after accounting for competing risks (Table 3). Further analysis showed a stronger tendency

for the incidence of death by avian and mammalian predation to vary by season in adults (Gray's χ^2 statistics by season: avian predation = 6.11, d.f. = 1, p = 0.11; mammalian predation = 6.86, d.f. = 1, p = 0.08, unknown death = 4.10, d.f. = 1, p = 0.25) and juveniles (Gray's χ^2 statistics by season: avian predation = 6.22, d.f. = 1, p = 0.10; unknown death = 1.25, d.f. = 1, p = 0.73). Avian predation is more prevalent in the spring and fall, whereas mammalian predation is more prevalent in winter (Fig. 4). The cause-specific hazard for avian predation increased by 16–17% for juveniles and adults, respectively, for every incremental increase in season (winter is the reference value of 1), and the cause-specific hazard for mammalian predation decreased by 42% in adults for each season after winter (Table 3).

3.3. Mortality hazards

In both adults and juveniles, the estimated daily hazard rate differed by mortality event type (adults: $F_{2,200} = 164.2$, p < 0.001; juveniles $F_{1,200} = 303.0$, p < 0.001), with risk of dying from avian predation highest in both age classes (Table 4, Fig. 5). For adults, the hazard of avian predation increases steadily throughout life (Fig. 5). The mean daily hazard rate of dying from avian predation is twice as high as the mean daily hazard of death from unknown causes and 15 times higher than the mean daily hazard of mammalian predation (Table 4). In juveniles, the daily hazard rate of dying from avian predation increases dramatically during the first year of life (Fig. 5) and the mean daily hazard of avian predation is 5 times higher than the hazard of death from unknown causes (Table 4). Further, the mean daily hazard of death from avian predation was 3.5 times higher in juveniles compared to adults (Table 4, Fig. 5).

4. Discussion

Mortality rates in red squirrel populations can fluctuate in forest ecosystems as a function of intrinsic and extrinsic factors that include

Table 2
A. Weighted average estimates of the survival and recapture parameters for all marked and known fate Mount Graham red squirrels (*Tamiasciurus fremonti grahamensis*) in southeastern Arizona, USA from the best-fitting Cormack-Jolly-Seber (CJS) models. B. Mortality estimates for MGRS adults and juveniles compared to estimates reported from other red squirrel populations.

A.

	Group	Monthly estimate		Annual estimate
		Survival	Recapture	Survival
All marked	–	0.920 ± 0.037	0.923 ± 0.034	0.368 ± 0.177
Known fate	Juvenile ♀	0.893 ± 0.030	0.950 ± 0.016	0.257 ± 0.104
	Juvenile ♂	0.896 ± 0.029	0.881 ± 0.020	0.268 ± 0.104
	Adult ♀	0.908 ± 0.016	0.950 ± 0.016	0.314 ± 0.064
	Adult ♂	0.911 ± 0.014	0.881 ± 0.020	0.327 ± 0.061

B.

Annual mortality estimates	Juvenile	Adult
This study	0.74	0.68
Rochester, Alberta[a]	0.67	0.34
Rochester, Alberta[b]	0.59	0.38
Ft. Assiniboine Alberta[c] pre-settlement	0.22	
Ft. Assiniboine Alberta[c] post-settlement	0.73	
Indiana[d] conifer		0.24
Indiana[d] deciduous		0.59
Yukon[e]	0.25	
Yukon[f]	0.27	0.28
Clearwater National Forest, Idaho[g]		0.72
South-central British Columbia[h]		0.10
South-central British Columbia[h] fir	0.25	
South-central British Columbia[h] spruce	0.23	
Prince George British Columbia[i]	0.27	0.25
Cariboo British Columbia[j]	0.28	0.17

[a] Kemp and Keith, 1970, Rochester, Alberta.
[b] Rusch and Reeder, 1978, Rochester, Alberta.
[c] Larsen and Boutin, 1994, Ft. Assiniboine, Alberta.
[d] Goheen and Swihart, 2005, Tippacanoe County, Indiana.
[e] Anderson and Boutin, 2002, Kluane Lakes Yukon - emergence to weaning.
[f] Stuart-Smith and Boutin, 1995, Kluane Lakes Yukon - average across predator exclosure and control plots and years.
[g] Wirsing et al., 2002, Clearwater National Forest, Idaho.
[h] Klenner and Krebs, 1991, south-central British Columbia.
[i] Sullivan, 1990, Prince George British Columbia - mean monthly mortality across treatments.
[j] Sullivan, 1990, Cariboo British Columbia - mean monthly mortality across treatments.

age class, body condition, predation pressure, and resource availability (Kemp and Keith, 1970; Klenner and Krebs, 1991; Rusch and Reeder, 1978; Sullivan, 1990; Wirsing et al., 2002). Here we show that, compared to other ecologically similar *T. hudsonicus* populations, annual survival tends to be lower and predation pressure and associated mortality higher in both juvenile and adult Mt. Graham red squirrel age classes. Juvenile red squirrels in many parts of their range tend to suffer higher mortality compared to adults. In jack pine (*Pinus banksiana*) and white spruce (*Picea glauca*) forests of the Athabasca Sand Hills region of Alberta, Canada, 22% of juveniles were killed prior to settlement, and 73% of the remaining survivors were killed over winter (Larsen and Boutin, 1994). In a white spruce (*Picea glauca*) forest in the Yukon, juvenile mortality from emergence to weaning was on average 25%, and remained similarly low from emergence to settlement (27%), and from settlement through the first winter (16%) (Stuart-Smith and Boutin, 1995). Juvenile mortality was 59–67% in white spruce and jack pine forest in Rochester, Alberta (Kemp and Keith, 1970; Rusch and Reeder, 1978). Once red squirrels reach adulthood and establish their own territories, mortality tends to decrease and annual survival rates increase in many populations. Mean annual adult mortality varied by forest community type in Indiana, from 24% in conifer stands, to 59% in deciduous forest patches (Goheen and Swihart, 2005). Mean adult mortality was 28% in the Yukon (Stuart-Smith and Boutin, 1995), 34–38% in Rochester, Alberta (Kemp and Keith, 1970; Rusch and

Reeder, 1978), but as high as 72% in the Clearwater National Forest, Idaho (Wirsing et al., 2002). In the Pinaleño Mountains, adult mortality was comparable to that observed in juveniles, and the mean annual survival rates we document here are among the lowest reported for either age class of red squirrels.

Avian predation is one of the primary causes of death for both juvenile and adult red squirrels. The majority of observed adult mortalities (88%) in Indiana were attributed to raptor predation (Goheen and Swihart, 2005), as were the majority of juvenile mortalities (94%) in Ft. Assiniboine, Alberta; primarily by northern goshawks (*Accipiter gentilis*) (Larsen and Boutin, 1994). Raptor predation comprised 50% of all confirmed mortalities across age classes and years in Rochester, Alberta and 54–51% of adults and juvenile mortalities, respectively, in the Yukon (Stuart-Smith and Boutin, 1995); the other 50% of mortalities were attributed to mammalian predators and hunter harvest in Alberta (Rusch and Reeder, 1978) and 46–49% attributed to mammalian predators, unknown predators, and starvation in the Yukon (Stuart-Smith and Boutin, 1995). In contrast, mammalian predation, particularly by mustelids, was more common in north-central Idaho (27% avian vs. 35% mammalian) (Wirsing et al., 2002). Red squirrel susceptibility to predation by raptors may vary seasonally and by age class to coincide with key life history events that include breeding, dispersal, and the harvesting and hoarding of food resources. For example, in Alberta, juvenile mortality was highest (42–47%) during the periods
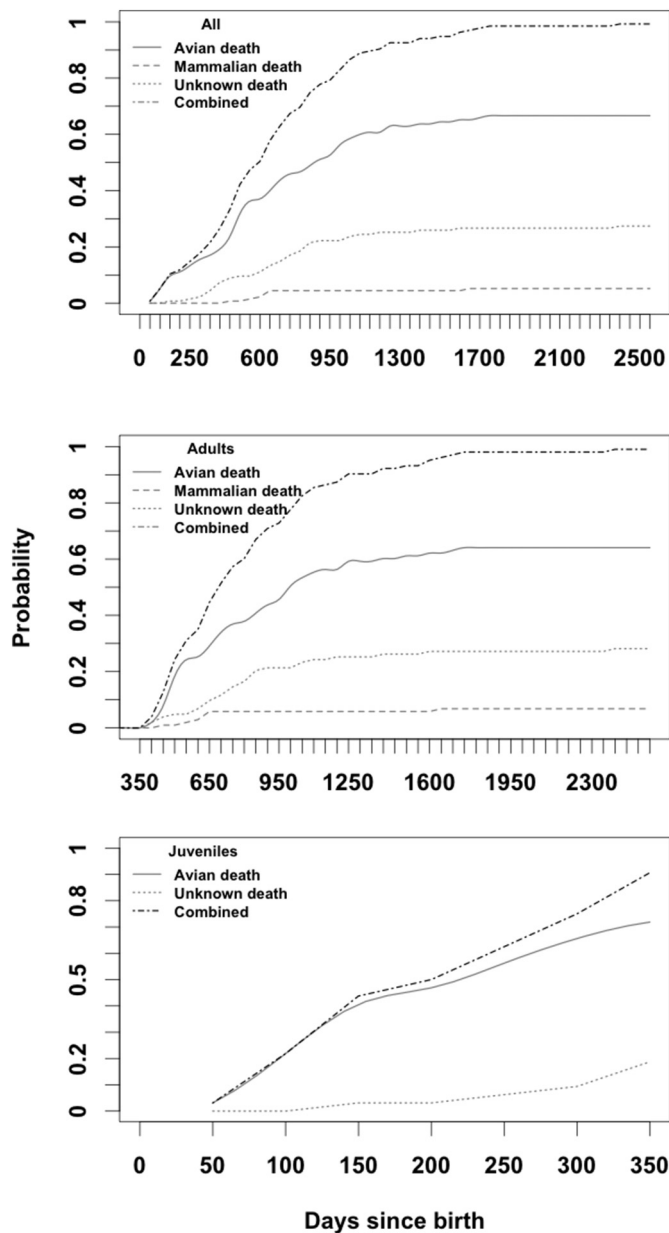
Fig. 3. Cumulative incidence function curves with competing risks (avian predation, mammalian predation, and unknown death) for radio-collared Mount Graham red squirrels (*Tamiasciurus fremonti grahamensis*) from May 2002–February 2016. Top: all animals combined; middle: adults only (≥1 year old); bottom: juveniles only (< 1 year old). We did not document any confirmed mammalian predation events for juveniles during our study.

from parturition to weaning, and between weaning and first spring. Adult male mortality was highest (13%) during the breeding season (March–May), and adult female mortality was highest (25%) during parturition and weaning (Rusch and Reeder, 1978). Risk of predation can increase significantly as juveniles make forays away from their natal territory during dispersal (Larsen and Boutin, 1994). In the Pinaleño Mountains, the majority of documented predation events in both juveniles and adults (75% and 65% respectively) were attributed to avian predators. Observed peaks in avian predation on MGRS in spring and fall correspond with our lowest monthly survival estimates. Seasonal periods of high avian predation and low survival coincide with adult mating activity in the spring and juvenile dispersal and food harvesting in the early fall, behaviors that are characterized by longer forays and extra-territorial movements (Larsen and Boutin, 1994; Layne, 1954; Merrick and Koprowski, 2016a, 2016b; Rusch and Reeder,

1978). Peaks in avian predation events also coincide with the migration and seasonal shifts from summer breeding ranges to wintering ranges of many raptor species (Goodrich and Smith, 2008). Continental movements, dispersal, and home range shifts along elevational gradients in the fall and spring are documented in avian predators commonly observed in the Pinaleño Mountains: Cooper's hawks, red-tailed hawks, northern goshawks, and Mexican spotted owls (Ganey and Balda, 1989; Goodrich and Smith, 2008; Schauffert et al., 2002; Underwood et al., 2006; Wiens et al., 2006; Willey and van Riper, 2007). Although the Madrean Sky Islands do not appear to serve as a major corridor for seasonal raptor migration (McHugh, 2017), some combination of continental and elevational migration may contribute to seasonal peaks in avian predation on MGRS.

While avian predation comprises 65–75% of confirmed mortalities in MGRS adults and juveniles, which is within the range of avian-attributed mortalities documented in other red squirrel populations (27–94% of mortalities), a larger proportion of the population dies each year (63%) in MGRS than is documented in most other populations. Given that the population size in the Pinaleño Mountains has been fluctuating around 250 animals for the last 15 years, low survival attributed in part to high avian predation is a conservation concern. Above average predation pressure in the Pinaleño Mountains and low survival could be the product of degraded habitat and spatio-temporal unpredictability of food and mates that result in increased overall susceptibility to predation as individuals move farther in search of resources. Further, evidence suggests that individuals in poorer condition are more susceptible to predation (Wirsing et al., 2002). An introduced tree squirrel in the Pinaleños may also sustain a higher density of both avian and mammalian predators that increase predation pressure on red squirrels. Abert's squirrels were introduced to the Pinaleño Mountains from their native range in northern Arizona in the 1940's and presently occupy the same areas as red squirrels (Derbridge, 2018; Edelman et al., 2009; Hutton et al., 2003). Though Abert's squirrels do not physically interact with red squirrels (red squirrels are behaviorally dominant in most interactions), nor act as kleptoparasites of red squirrel larder hoards (Edelman et al., 2005), they may compete indirectly for resources such as food and nest sites (Derbridge, 2018; Edelman et al., 2009). Because the two species share avian predators (Keith, 1965; Reynolds, 1963), overlap spatially (on average each red squirrel home range is overlapped by 3 Abert's squirrels), and have overlapping niches (Derbridge, 2018), the presence of Abert's squirrels may contribute to higher predator densities and rates of predation on red squirrels.

Instances where predation pressure by generalist predators disproportionately impacts an endangered population in the presence of an abundant alternate prey source is known as apparent competition (DeCesare et al., 2010; Johnson et al., 2013). In the Pinaleño Mountains, it is likely that introduced Abert's squirrels subsidize a diverse avian and mammalian predator guild. This is of concern for MGRS persistence as some populations in decline become increasingly vulnerable to predation by subsidized predators (Sinclair et al., 1998) and at risk of extinction (DeCesare et al., 2010). Asymmetrical impacts of predators on prey in instances of apparent competition are often associated with a high degree of niche overlap among prey species and human- or disturbance-driven changes to the resource base, communities of prey, or predators. Examples can include habitat destruction or degradation and introduced species of predator and prey (DeCesare et al., 2010; Sinclair et al., 1998). Abundant, non-native feral pigs (*Sus scrofa*) subsidize a recently colonized population of golden eagles (*Aquila chrysaetos*) in the California Channel Islands, a situation that led to population crashes and extirpation of native island foxes (*Urocyon littoralis*), the eagles' secondary prey, on several of the islands (Angulo et al., 2007). In Australia, both introduced predators and increases in alternate prey threaten native mammals with extinction and suppressed population growth via depensatory predation (increased predation at low prey densities) and likely Allee effects (Courchamp et al., 1999) in eastern barred bandicoot (*Perameles gunnii*), quokka (*Setonix*
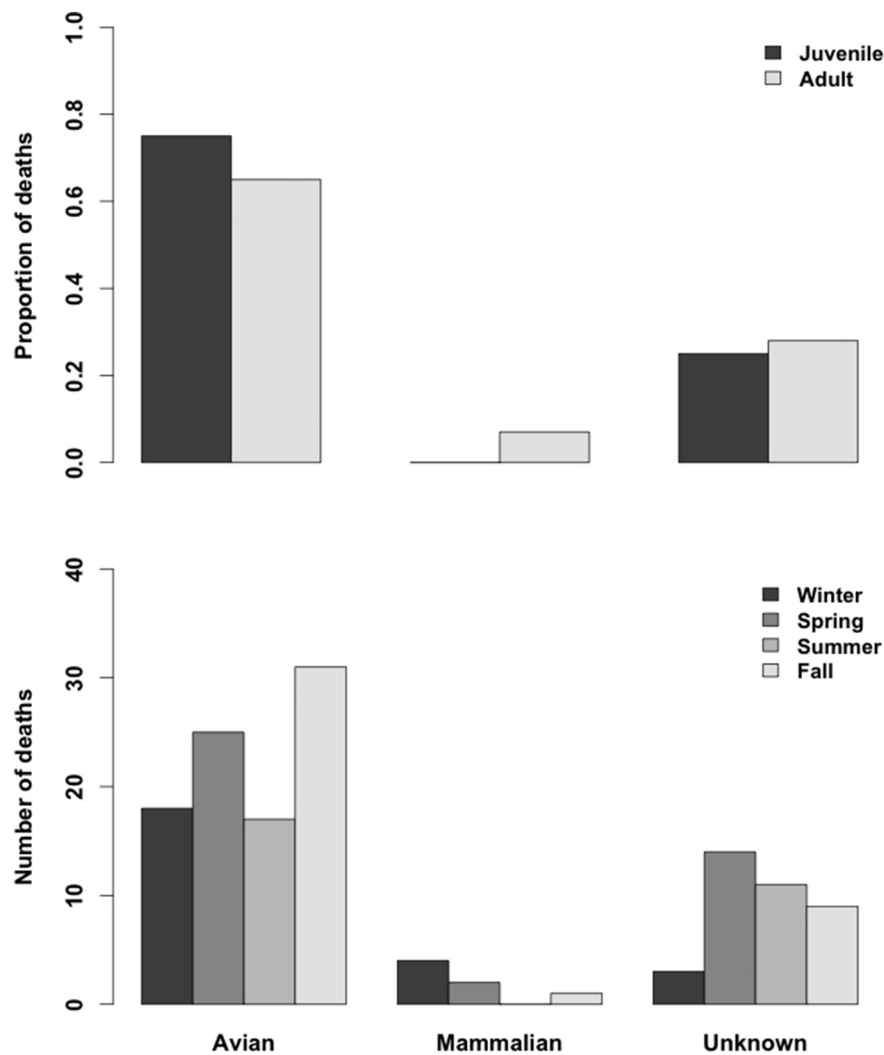
Fig. 4. Proportion of deaths by avian predation, mammalian predation, and unknown causes by age class (juvenile < 1 year, adult ≥1 year) (top), and number of total deaths by season (bottom) for radio-collared Mount Graham red squirrels (*Tamiasciurus fremonti grahamensis*) from May 2002–February 2016. Winter = December–February, Spring = March–May, Summer = June–August, Fall = September–November.

brachyurus), and black-footed rock-wallabies (*Petrogale lateralis*), and apparent competition in spinifex hopping mice (*Notomys alexis*) and sandy inland mice (*Pseudomys hermannsburgensis*) when an alternate prey species increased in abundance (Sinclair et al., 1998). In Europe, parasites, disease, and possibly increased predation on juveniles mediate apparent competition between native Eurasian red squirrels (*Sciurus vulgaris*) and invasive eastern gray squirrels (*S. carolinensis*) and are thought to drive observed declines in the native species (Prenter

et al., 2004; Tompkins et al., 2002, 2003; Wauters et al., 2000). In the Pinaleño Mountains, predation risk in red squirrels may be exacerbated in part by the presence of a non-native, ecologically similar prey species and the degradation of red squirrel habitat as a result of wide-spread tree death and fire (Derbridge, 2018; Edelman and Koprowski, 2005; Koprowski et al., 2005; Wood et al., 2007a), making much of the forest more suitable to Abert's squirrels, a species that thrives in open, fire-adapted forest systems (Hutton et al., 2003).

Table 3
Subdistribution hazard model coefficients and 95% confidence intervals estimated via competing risks regression for each mortality event type (avian, mammalian, and unknown cause) while accounting for competing risks in radio-collared Mount Graham red squirrels (*Tamiasciurus fremonti grahamensis*) from May 2002–February 2016. Coefficients are hazard ratios and can be interpreted as the relative influence of the covariate (sex, season) on the relative increase in the rate of occurrence of the event of interest (avian predation, mammalian predation, and unknown cause of death).

	Avian predation			Mammalian predation			Unknown cause of death		
	exp(coef)	95% C.I.	p	exp(coef)	95% C.I.	p	exp(coef)	95% C.I.	p
Adults									
Sex	0.91	0.56–1.50	0.72	1.461	0.28–7.64	0.65	0.995	0.47–2.10	0.99
Season	1.17	0.93–1.49	0.19	0.424	0.14–1.30	0.13	1.042	0.79–1.38	0.77
Juveniles									
Sex	1.29	0.58–2.87	0.53	NA	NA	NA	0.749	0.19–2.90	0.68
Season	1.16	0.82–1.63	0.40	NA	NA	NA	1.131	0.68–1.88	0.64

Table 4

Mean and standard deviation of smoothed, kernel-based hazard estimates for avian predation, mammalian predation, and unknown cause of death in adult and juvenile radio-collared Mount Graham red squirrels (*Tamiasciurus fremonti grahamensis*) from May 2002–February 2016.

	All			Adults			Juveniles		
	Mean	Std. dev.	ANOVA	Mean	Std. dev.	ANOVA	Mean	Std. dev.	ANOVA
Avian	0.001200	0.000400	$F_{2,300} = 383.7 \; p < 0.001$	0.001051	0.000586	$F_{2,300} = 164.2 \; p < 0.001$	0.003651	0.001501	$F_{1,200} = 303 \; p < 0.001$
Mammalian	0.000076	0.000044		0.000076	0.000044		NA	NA	
Unknown	0.000570	0.000290		0.000515	0.000307		0.000718	0.000784	

Knowledge of which population parameters and mortality risks contribute most to population decline and endangerment is necessary to develop informed and actionable conservation plans for threatened and endangered species. These data allow managers to better understand where limited management and restoration funds may have the most impact. Parameter estimates and cause-specific mortality hazards also provide baseline measures against which future conservation or management actions can be assessed (Olson et al., 2014). Understanding that predation, hunter overharvest, or non-native species drive demographic declines and reduced fitness in threatened populations has led to management recommendations that focus on setting harvest limits or control of both non-native species and predators. Effective law enforcement and licensing programs were recommended to regulate human harvest of Mongolian gazelles (*Procapra gutturosa*) after the determination that harvest was the primary driver of low survival and population decline (Olson et al., 2014). For declining or reintroduced populations of marsupials in Australia, control of non-native predators was recommended in addition to a substantial (2–3×) increase in the number of individuals released in the case of reintroductions to allow populations to stay above a critical population growth rate (Sinclair et al., 1998). Control or eradication of non-native feral pigs along with golden eagles was deemed necessary for the persistence of island foxes in California's Channel Islands (Angulo et al., 2007). Removal of golden eagles is controversial and presents a conservation paradox, as the species is also federally protected (Courchamp et al., 2003). A similar conservation challenge is present in the Pinaleño Mountains. While

state agencies have implemented unlimited hunting in an attempt to control the non-native Abert's squirrel (Arizona Game and Fish Department, 2008), possible control of avian predators is complicated by the fact that two avian predators of MGRS, northern goshawks and Mexican spotted owls, are regionally sensitive and federally threatened, respectively (Arizona Game and Fish Department 2005, 2013).

While control of predators and alternate prey may address proximate causes of reduced survival and population decline in threatened and endangered species, we must recognize that in many cases, anthropogenically-driven landscape alteration and disturbance are often the ultimate drivers of apparent competition and also need to be systematically addressed (DeCesare et al., 2010; Goodrich and Buskirk, 1995). Complete eradication of introduced species and control of native predators may be difficult to implement or to achieve the desired outcome, and can have unintended consequences (Goodrich and Buskirk, 1995). Ecosystem, community, and habitat restoration measures may be more feasible and address ultimate underlying causes of endangerment. Examples of successful community and habitat restoration efforts include re-introduction of ecosystem engineers and keystone species to improve grassland suitability for burrowing owls (*Athene cunicularia hypugaea*) (McCullough Hennessy et al., 2016), wetland restoration to increase vegetative cover for California Ridgway's rail (*Rallus obsoletus obsoletus*) via a non-native grass (Casazza et al., 2016), increasing structural complexity on sea walls to protect oysters from fish predation (Strain et al., 2017), and the addition of artificial rocks to increase amount of shelter sites for velvet geckos (*Oedura lesueurii*), the primary
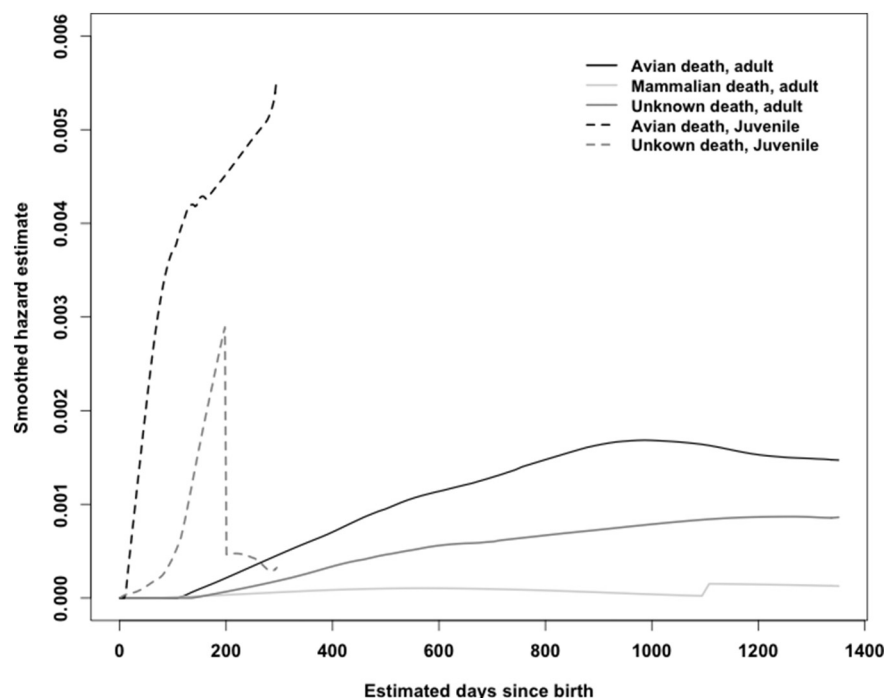

Fig. 5. Smoothed, kernel-based and locally optimal hazard estimates for each cause of death in adult and juvenile Mount Graham red squirrels (*Tamiasciurus fremonti grahamensis*) from May 2002–February 2016. We did not document any confirmed mammalian predation events on juveniles during our study.

prey of the endangered broad-headed snake (*Hoplocephalus bungaroides*) (Webb and Shine, 2000). Mt. Graham red squirrels respond to forest structural characteristics that include mature forest stands with high canopy cover, vertical structural complexity, large woody debris, and dead trees with cavities for nesting (Merrick et al., 2007; Smith and Mannan, 1994). Evidence suggests that following natal dispersal, juvenile tree squirrels tend to settle in places structurally similar to natal sites (Haughland and Larsen, 2004; Merrick and Koprowski, 2016a, b; Wauters et al., 2010). Thus, addressing structural cues that emulate natal sites and augmenting structural complexity in and around natal areas may be a worthwhile focus of restoration efforts and also provide a fruitful arena for adaptive management research.

In addition to high mortality and avian predation pressure, MGRS suffers from extreme inbreeding as a result of isolation and genetic drift (Fitak et al., 2013). While we did not document any mortalities due to genetic abnormalities or defects during this study, decreased litter sizes in MGRS may be a result of inbreeding depression (Fitak et al., 2013; Rushton et al., 2006) and further limit population growth. MGRS are considered a population with extensive genetic differentiation from their nearest congeners (*T. f. mogollonensis*), but are not distinct phylogenetic units (Fitak et al., 2013). Thus, other conservation strategies for this population include a captive breeding program at the Phoenix Zoo, possible genetic augmentation from the White Mountains of Arizona, as well as potential assisted translocations (Fitak et al., 2013).

In the summer of 2017, the 19,604 ha Frye Fire (https://inciweb. nwcg.gov/incident/5221/) impacted 95% of surveyed MGRS territories (Arizona Game and Fish Department, 2017). The mountain-wide MGRS population is currently estimated at 35 animals (down from an estimate of 252 in 2016), thus ensuring survival of the remaining animals is a conservation priority. Tree squirrel populations have the capacity to successfully reestablish with fewer than 35 individuals (Wood et al., 2007b). Population viability analyses to estimate the current minimum viable population size for MGRS as well as the impact of various levels of predation pressure and management actions on population growth and continued persistence is needed (e.g. Rushton et al., 2006). Following widespread habitat loss from fire and record-low population estimates, we have a unique opportunity to implement a suite of conservation actions. In addition to widespread forest restoration efforts for persistence in the long term, we recommend immediate habitat augmentation to increase structural complexity, cover, shelter, and food resources in the short term as well as continued captive breeding efforts and consideration of assisted translocations to reduce predation risk and increase survival and continued persistence in this critically endangered mammal.

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