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

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ABSTRACT

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

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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 ($\hat{c}$), 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 $\hat{c}$ 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 ($\Delta QAIC_c < 2$) (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