

Functional semelparity drives population dynamics and endangers a peripheral population



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ABSTRACT

Despite increased risk of extinction through stochastic events, peripheral populations are conservation priorities as the distribution of endangered species tends to contract to the periphery of historic ranges rather than toward the core. Trailing-edge populations and mountain isolates, which may become more common as climate change drives range shifts, are an important realm of inquiry and contain important reserves of genetic variation. We use long-term monitoring data from the southernmost population of a widespread species to test the hypothesis that peripheral populations display distinct demographic profiles from core populations. The red squirrel (*Tamiasciurus hudsonicus*) is predicted to recede from its southern border in response to climate-induced habitat change. We estimate key demographic parameters for this endangered population using survival and reproduction schedules and compare the dynamics to core populations of this and related species. This peripheral population exhibits higher adult mortality, and suffers associated impacts on reproductive output, which results in a demography distinct from core populations and phylogenetically similar species. Poor adult survival, similar to a population that experiences extremely high hunting pressure, has resulted in this normally iteroparous species becoming functionally semelparous at the periphery. Understanding differences in demographic function between peripheral and core populations is key if management strategies are to be effective in supporting continued persistence of at risk populations in the face of range shifts of species or habitats driven by environmental change.

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1. Introduction

Informed management of populations facing certain future ecosystem change requires accurate assessments of population size and key demographic parameters, which often can be obtained only through long-term research and monitoring programs (Magurran et al., 2010). Frequently, different stage or age classes of populations experience diverse mortality pressures or exhibit variation in reproductive value (Reid et al., 2004). Early indications of ecological imbalance, future population collapse, or expansion can be recognized by close monitoring of demographics and age distributions. Fine-scale knowledge of variation in species' survival and fecundity between life stages or ages should improve the cost-effectiveness of management programs by allowing conservation effort to be applied where and when the greatest impact can be realized. For example, where mature individuals display the highest reproductive values, efforts could target these individuals for protection (Arrigoni et al., 2011) or removal in the case of invasive species (Harris

et al., 2009). As climate change leads to altered species distributions (Parmesan, 2006) and less stable environmental conditions, the demographic function of populations can be severely impacted. Populations at the periphery of a species range often display atypical demographic profiles (Vucetich and Waite, 2003; Goldstein et al., 2015). Managers who seek to mitigate the demographic impacts of altered species distributions will require knowledge of peripheral population dynamics and to appreciate the differences from the core of the species range.

Traditional wisdom states that population density is reduced in peripheral populations, and therefore these populations are more vulnerable to extinction through stochastic catastrophes (Alvarez, 2001; Hardie and Hutchings, 2010). Peripheral populations may arise in locations that are geographically distant from the range center or in environments that are remote from the center of the species' ecological niche (Martínez-Meyer et al., 2013), factors that often, but do not always, align. Genetic drift, isolation, or divergent selection pressures can result in peripheral populations becoming genetically distinct from populations within the core of the range (Lesica and Allendorf, 1995). The preservation of genetic diversity within a species is essential to increase the likelihood of persistence in a changing environment where future selection pressures are uncertain and decreased diversity hampers potential adaptation (Frankel, 1974). Despite the increased

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probability of extinction, peripheral populations have recently been recognized as conservation priorities as endangered species ranges often contract to the periphery of the historic range rather than the core (Channell and Lomolino, 2000; Calkins et al., 2012). Increasingly, changing climate is driving species range shifts, generally toward higher latitudes and elevations but also in complex locally-dependent patterns (Lenoir and Svenning, 2015). Such range shifts demonstrate the increased importance of leading edge peripheral populations (Gibson et al., 2009) in conservation research, triage, and planning.

Additionally, previously contiguous or central populations may become peripheral and isolated as habitats shift in response to predicted climate change. The phylogeography of mountain isolates at the trailing edge of the species range indicate how populations have shifted, recombined, and altered in size as a result of glacial cycles (Hampe and Petit, 2005; Galbreath et al., 2009; Semlitsch and Drake, 2015). A detailed understanding of the population dynamics of current peripheral populations or mountain isolates and how these populations differ in demography from core populations will improve the management and conservation prospects of wildlife populations experiencing, or predicted to experience, catastrophic range shift and isolation. When long-term demographic data are available mortality and fecundity schedules, or life tables, can be powerful analytic and comparative tools to probe the demographic trends of peripheral and core populations. Life tables, whether static or cohort-based, record and standardize the vital statistics of a group of individuals or a population. Dynamic-composite life tables, which compile information from multiple cohorts over time aligned by age class, often feature in long-term studies of wild animal populations (Barkalow et al., 1970; Nixon et al., 1975) and have the advantage of accounting for some inter-annual variation in survival and fecundity. Life tables rely on the assumption that vital rates vary only by age and not by year and that sampling is consistent across all age classes (Anderson et al., 1981).

Peripheral ranges are concentrated where the interplay of climate and geology leads to the extension of distribution outside of the core (Browne and Ferree, 2007). For example, mountain ranges in the North American Intermountain West extend the distribution of high latitude habitats and species far to the south, into the Madrean archipelago of sky islands in the southwestern United States and northern Mexico. The North American red squirrel (*Tamiasciurus hudsonicus*, hereafter red squirrel) exhibits a complex phylogeography that includes 25 subspecies, half of which inhabit the Intermountain West (Steele, 1998). A recent phylogeographic study of this species highlighted that the red squirrel is a species complex with three major groups (*T. hudsonicus*, *T. fremonti*, *T. douglasii*) (Hope et al., 2016), however we continue to use the traditional species names in this paper for clarity, and remain mindful of the complexity of relationships within the group. With its wide distribution, the larder-hoarding red squirrel is an ideal species in which to examine variation in demographic patterns among populations located in the periphery and core of the range. Individuals fiercely defend a territory that ranges in size between 0.24 and 0.98 ha centered on the larderhoard, or midden, in which they cache food for overwinter survival (Gurnell, 1987; Steele, 1998). The strong association with a midden means that this species is relatively easily monitored for survival and reproduction (McAdam et al., 2007) and the dynamics of populations throughout Canada and the United States have been studied across the species range.

The southernmost population of red squirrels (Mount Graham red squirrel, MGRS; *T. h. grahamensis*) has been isolated on Mount Graham, the tallest peak in the Pinaleno Mountains of Graham County, in southeastern Arizona, USA (32°42'06" N, 109°52'17" W) (Steele, 1998) since glacial retreat and associated habitat shifts between 9000 and 10,000 years ago constrained coniferous forest to the highest elevations. The federally endangered MGRS has been the subject of a long-term monitoring program since 1989 (Sanderson and Koprowski, 2009) with a subset of individuals residing within five main study areas marked and/or radiotracked since 2002. We use long-term monitoring

data available for MGRS to test the hypothesis that peripheral populations display demographic patterns that are distinct from core populations. We compile dynamic composite cohort life-tables and calculate standard life-table statistics for known-age animals and those first captured as adults and compare demography of the MGRS to other non-peripheral populations of red squirrels and other related species. Conservation and management of imperiled species can benefit from detailed demographic information on target populations ensuring that valuable conservation funds can be directed to improving the survival of critical age or stage classes. In the face of increasing range shifts and fragmentation as a result of changing climate (Opdam and Wascher, 2004) that increase the frequency of peripheral populations, it is imperative to formulate demographically based management techniques tuned to the unique demographics of these marginal populations. Our findings have direct implications for the conservation and continued persistence of MGRS and other peripheral populations.

2. Methods

2.1. Study area and species

The MGRS is endemic to Mount Graham (3267 m). The population is currently estimated at 274 animals (Arizona Game and Fish Department, 2015). The squirrel is restricted to mature cone-producing forested habitat >3000 m in elevation dominated by Englemann spruce (*Picea englemanni*) and corkbark fir (*Abies lasiocarpa* var. *arizonica*) at higher elevations with Douglas fir (*Pseudotsuga menziesii*) and southwestern white pine (*Pinus strobiformis*) components at low elevation (Hutton et al., 2003). The five study areas, totaling approximately 400 ha, were established in the spruce-fir and mixed conifer habitats. The MGRS suffers heavy predation by avian and mammalian predators (Schauffert et al., 2002), and has experienced losses from intense forest fires (Blount and Koprowski, 2012) and insect outbreaks (Zugmeyer and Koprowski, 2009).

2.2. Trapping and radio telemetry

Squirrels were captured at middens 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, marked with colored ear tags, and fitted with a radio collar (SOM 2190, Wildlife Materials International: Koprowski et al. (2008)). Resident adult animals captured between May 2002 and December 2014 inclusive were fitted with a radio collar if their mass was ≥200 g. Juvenile squirrels ≥100 g were radio collared between September 2010 and August 2013 inclusive (mean collar weight ~ 5 g). Collared animals were located ≥12 times/month 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.

2.3. Life table analysis

We considered disappearance from the population to be equivalent to mortality given that this species is rarely observed to shift home range once established (Berteaux and Boutin, 2000) and the high intensity of monitoring effort by radio-telemetry, live-trapping, and visual observations during censuses. Ages and fates were known definitively for animals first captured as juveniles ($n = 89$). We constructed separate dynamic composite cohort life tables for males and females of known age with age classes equaling years. Data from 220 MGRS of unknown age, first captured as adults, were treated separately and incorporated into adjusted life tables under assumptions described below in Section 2.4. We calculated demographic statistics without assuming

a stable age distribution (Caughley, 1977) and follow the notation scheme of Krebs (1994).

We calculated the number alive (n_x) for each age class in each annual interval (March – February) from monitoring records that enabled computation of survivorship (l_x ; n_x / n_0), number dying (d_x ; $n_x - n_{x+1}$), and death rate (q_x ; d_x / n_x) for each age class. Life expectancy for each class (e_x) was the mean number of age classes (years) remaining for individuals that reached the beginning of an age class. We found the median survivorship for each sex using Kaplan Meier survival analysis and compared the survivorship of males and females using the Breslow statistic (χ^2). The departure of the sex ratio in an age class from presumed equality was tested for significance using a goodness-of-fit G-test. We classified females as reproductive when litters emerged from the nest and were observed at the midden site associated with the mother. We calculated the proportion of reproductive females on a yearly basis. We determined mean litter size per female in each age class using observations of 53 litters of known age mothers and 80 litters of mothers with estimated minimum ages and looked for trends using general linear modeling. We summed the product of the mean number of female young per female (b_x) and survivorship (l_x) to find the net reproductive rate (R_0). The mean generation length (G), or the average length of time for a female to replace herself with a female offspring, was also derived from l_x and b_x and was used to approximate the innate capacity for increase (r_m) = $\ln(R_0 / G)$. We used this estimation to approach the exact value of $r_m = r$ through an iterative calculation using the Euler-Lotka equation $\sum e^{-rx}(l_x b_x) = 1$. The finite rate of increase λ was calculated as e^r . We calculated reproductive value (V_x), as number of expected present and future female offspring per female age class, and residual reproductive value (RV_x) or the expected future female offspring per female age class, were expressed in animal units such that $V_0 = R_0$ (Schwartz et al., 1998).

2.4. Incorporating unknown age adults into the life table

The majority (71.7%) of the animals radio-collared were first captured as adults of unknown age. We incorporated these animals into the n_x column under 2 different assumptions: 1) using ages estimated at time of first capture based upon physiological clues such as the animal attaining an adult body mass > 200 g, adult pelage, and indications of pregnancy or previous breeding i.e. protruding or darkened teat condition/coloration (138 additional females, 151 additional males) and 2) the assumption that all animals collared as adults were collared at 12 months of age (141 additional females, 151 additional males). Three additional females were included in under assumption 2, but not assumption 1, because their estimated ages were not recorded in the field. We evaluated the effect of including the additional animals under the various assumptions on e_x and R_0 for females and on e_x for males and compared survivorship distributions using Kaplan-Meier survival analysis and the Breslow statistic as above.

2.5. Contrasting peripheral with core populations

We identified peer-reviewed literature that reported the results of long-term demographic studies of North American red squirrels and

other tree and ground squirrels. We compiled and compared data on e_x and litter size where possible to those of MGRS. We examined the correlation between the life expectancy curves of the MGRS and other core-range populations using Pearson product-moment correlation.

3. Results

3.1. Survivorship

Longevity did not differ greatly between known age females ($n = 49$; Table 1) and males ($n = 40$; Table 2) and mortality was consistent over time (Fig. 1). Survivorship of females (median \pm SE = 1.47 \pm 0.26 year) was greater than that of males (median \pm SE = 0.96 \pm 0.05 year; $\chi^2 = 4.33$, d.f. = 1, $p = 0.038$). Life expectancy for known age females and males at the 0 age class was 1.76 years and 1.22 years respectively. The ratio of females:males was higher than presumed equality in the 1 and 2 year age classes of known aged animals (Table 3). The age distributions of squirrels sampled in each age class for each year during the study are not stable and we provide the proportions of animals in each age alongside the total number of marked squirrels present during each study year in Supplementary Material A1.

3.2. Fecundity

The mean number of litters produced by each age class did not differ by age ($F_{6,318} = 1.029$, $p = 0.406$) or whether age was known or estimated ($F_{1,318} = 0.409$, $p = 0.523$). When only reproductive females were considered, litter size differed by age ($F_{6,174} = 2.483$, $p = 0.025$) but not whether age was known or estimated ($F_{1,174} = 2.334$, $p = 0.128$) and no interaction was observed ($F_{3,174} = 0.897$, $p = 0.444$). Litter sizes produced by females in the 2-year-old age class were larger than those produced by the 4-year-old age class (post hoc Tukey's HSD, $p = 0.022$). Approximately 60% of females that were alive in the 1 and 2-year-old age classes produced a litter (Table 3). The majority of females only successfully produced 1 litter (64.8%) with much smaller percentages producing 2 or ≥ 3 litters, 20.9% and 14.3% respectively.

The generation length was short at approximately 20 months (1.697 years, Table 1). The net reproductive rate for known age females was $R_0 = 1.1158$. The innate capacity for increase r_m was approximated at 0.0645 but through iterative calculations was found to approach $r = 0.0654$. The finite rate of increase, a useful metric, was therefore evaluated as $\lambda = 1.0676$. The reproductive and residual reproductive values were highest for 1-year-old females and females in the 0 age class respectively then slowly decreased until death. No litters were produced by the 0 age class but all other ages were productive.

3.3. Adjusted life tables

The restrictions on the most conservative life tables were relaxed by including unknown aged animals under different assumptions (Supplementary Material A2). These life tables included a larger sample of squirrels including some older animals, whose ages were not known exactly but were estimated, and hence more age classes. The population level life table statistics changed the least when the minimum estimated

Table 1
Life table statistics calculated for female Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) of known age from Mount Graham, Pinaleño Mountains, southeastern Arizona, USA, which were collared between 2002 and 2014.

Age class (years)	Number alive n_x	Survivorship l_x	Number dying d_x	Death rate q_x	Life expectancy (years) e_x	Number of ♀ young b_x	Reproductive value V_x	Residual reproductive value RV_x
0	49	1.000	16	0.327	1.765	0.000	1.116	1.116
1	33	0.673	16	0.485	1.379	0.857	1.657	0.800
2	17	0.350	8	0.471	1.206	0.950	1.552	0.602
3	9	0.184	6	0.667	0.833	0.971	1.137	0.167
4	3	0.061	3	1.000	0.500	0.500	0.500	0.000
$R_0 = 1.116$		$G = 1.697$	$r_m = 0.0645$		$r = 0.0654$		$\lambda = 1.068$	

Table 2

Life table statistics calculated for male Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) of known age from Mount Graham, Pinaleno Mountains, south-eastern Arizona, USA, which were collared between 2002 and 2014.

Age class (years)	Number alive n_x	Survivorship l_x	Number dying d_x	Death rate q_x	Life expectancy (years) e_x
0	40	1.000	23	0.575	1.225
1	17	0.425	11	0.647	1.206
2	6	0.150	2	0.333	1.500
3	4	0.100	2	0.500	1.000
4	2	0.005	2	1.000	0.500

ages for unknown aged adults (assumption 1 above) were combined with the known age animals (Table 4). Survivorship did not differ between females and males when unknown aged adults were incorporated into the dataset of known aged animals either using minimum estimated ages (median ± SE females = 1.91 ± 0.11 year, males = 1.73 ± 0.07 year; $\chi^2 = 1.76$, d.f. = 1, $p = 0.18$) or by assuming animals were collared at 12 months of age (median ± SE females = 1.62 ± 0.15 year, males = 1.48 ± 0.09 year; $\chi^2 = 2.28$, d.f. = 1, $p = 0.13$). Survivorship differed between the known age and adjusted life tables only in males (minimum estimated age $\chi^2 = 19.61$, $p < 0.01$; collared at 12 months $\chi^2 = 18.15$, $p < 0.01$).

3.4. Comparisons between peripheral and core-range populations

The peripheral red squirrel population at Mount Graham experiences the highest life expectancy at age 0 (Fig. 2). Other core red squirrel populations show an increase in life expectancy from age 0, as do many core populations of other sciurids such as *Sciurus* and Nearctic ground squirrels (Fig. 2), and attain highest life expectancy after reaching reproductive maturity at 1 to 3 years. The Pearson's correlation coefficients for comparisons between the life expectancy of the MGRS and 12 of the 14 squirrel populations considered were strongly negative, confirming that MGRS populations did not follow the typical pattern. One eastern gray squirrel (*S. carolinensis*) population that experienced severe hunting pressure was also found to have a life expectancy curve that decreased from age 0 (Fig. 2; Mosby, 1969) and was strongly and positively correlated with the MGRS population ($r = 1.00$ $p = 0.009$).

MGRS produced litters with sizes that were among the smallest reported in the literature (Table 5) though methods varied between surveys. Eastern populations that inhabit deciduous or mixed conifer landscapes had larger mean litter sizes than western populations or those that lived in boreal or montane conifer habitat. The peripheral MGRS experiences low adult survival and fecundity compared to core populations of red squirrels.

4. Discussion

Long-term multigenerational field-based studies provide invaluable insight into the population dynamics, mortality and reproduction regimes of wild animal populations (Clutton-Brock and Sheldon, 2010). Such studies must be tailored to the ecological vagaries of the target species to avoid undue bias in identification or non-capture of individuals of a particular physiological or behavioral profile (Kidd et al., 2015). Anderson et al. (1981), in their critique of life tables, noted that the basic assumptions of constant survival and recovery of marked animals over time of the life table model are often violated. They found that age-specific variation in reporting rate and survival rate can lead to mortality being overestimated.

Monthly monitoring of the MGRS population ensured that animals were regularly recorded to reduce the probability of missing demographic events such as reproduction or mortality but sample sizes of each age during each year were small, particularly at older ages (Supplementary Material A1). Nonetheless, this peripheral and endangered population is highly suited to life-table based population analysis because it has been thoroughly documented within the study area since 2002. The variation in the proportion of animals in each age class over time may have caused us to overestimate mortality (Anderson et al., 1981) but these problems are common in studies with relatively small sample sizes of marked animals and the other red squirrel populations that we compare to this peripheral population are equally vulnerable to mortality overestimation. Age-specific patterns of mortality and reproduction in the MGRS differ perceptibly from those in other well-studied core populations of the North American red squirrel. Compared to other red squirrel populations and phylogenetically similar species, MGRS experience poor adult survival and display life expectancy curves similar to a population under high hunting pressure (Mosby, 1969), which results in a normally iteroparous species that becomes

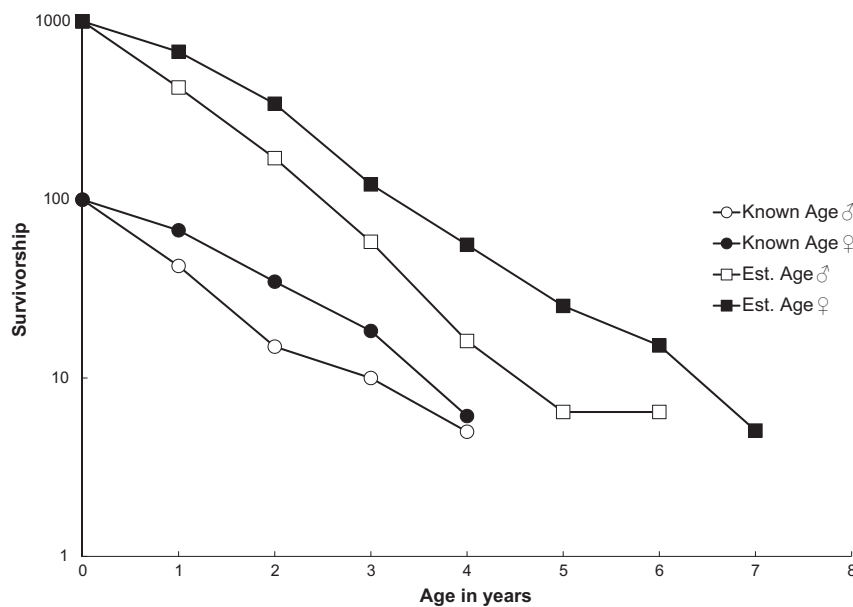


Fig. 1. Sex specific survivorship curves for radio-collared Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) of known age (scaled to 100 individuals) and of known age + adults of estimated minimum age (scaled to 1000 individuals) on the c. 400 ha study area on Mount Graham, Pinaleno Mountains, southeastern Arizona. See Tables 1, 2, and Supplementary Material A2 for sample sizes.

Table 3
Age specific sex ratios, mean litter size (\pm SE), and proportion of females in an age class reproducing for the groups of known age animals and the known age and minimum estimated age squirrels together for the Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) in southeastern Arizona, USA.

Age class	Known age			Minimum estimated age			Proportion of females reproducing
	Sex ratio F:M	N litters	Mean litter size	Sex ratio F:M	N litters	Mean litter size	
0	1.23	0	0				0
1	1.94*	27	2.73 \pm 0.15	1.01	60	2.70 \pm 0.13	0.628
2	2.83*	17	2.88 \pm 0.26	1.28	38	3.13 \pm 0.15	0.607
3	2.25	8	2.00 \pm 0.38	1.33	21	2.67 \pm 0.28	0.727
4	1.5	1	1.00	2.2	7	2.00 \pm 0.38	0.500
5				2.5	4	2.50 \pm 0.87	1.000
6				1.5	1	4.00	0.333
7				7:0	2	3.50 \pm 0.50	0.667
All		53	2.63 \pm 0.13		133	2.80 \pm 0.09	0.547

* $G \geq 4.47$, $p \leq 0.034$.

functionally semelparous. As a federally protected species the MGRS is not hunted by humans but does experience heavy predation pressure by avian and mammalian predators (Schauffert et al., 2002) and is isolated in a difficult environment. These factors mimic the effects of anthropogenic hunting on the demography of the population causing high mortality and non-typical life expectancy patterns with juveniles at age 0 having the highest life expectancy (Sibly et al., 1997; Thorington et al., 2012). Adult MGRS may suffer heavier predation pressure than juveniles on Mount Graham and adults in other core populations because they range much more widely than other subspecies of red squirrel to acquire resources in this scarce environment (Koprowski et al., 2016). The reproductive potential of this species' iteroparous life history strategy is not achievable under the current environmental conditions that cause poor adult survival. Prolonged hunting pressure in ungulates causes emergence of suboptimal reproductive strategies and early senescence after release from hunting pressure due to selection for a less iteroparous life history (Benton et al., 1995; Ericsson et al., 2001). Similarly, high predation on adult guppies (*Poecilia reticulata*) causes heritable changes in life history and reproductive strategies (Reznick et al., 1990). MGRS demography is profoundly influenced by low adult survival and this has clear ecological and potentially evolutionary consequences.

The short lifespan and yearly decrease in life expectancy in the MGRS creates a cascade of impacts on the reproduction potential of this endangered subspecies. The majority of females that reproduce only do so once in their lifetime. The demographic challenges of life at the periphery of the species' range result in this population in which individuals are functionally semelparous. Semelparity in an otherwise iteroparous mammal implies further lost opportunities for population increase beyond the lack of additional chances for reproduction (Weladji et al., 2006). Primiparous mothers are often less successful at raising young to maturity or produce smaller litters than those with previous experience (Clutton-Brock, 1984; Forslund and Pärt, 1995; Mar et al., 2012). Even within the limited sample of multiparous females in MGRS especially as age increases, litter sizes were largest on average for 2-year-old females. Long-term research on core red squirrel reproductive success indicates that other metrics of reproductive success such as weaning success, juvenile mass at weaning, and juvenile survival to one year of age also increased for post-primiparous females until senescence (Descamps et al., 2008). If such trends hold true at the

range periphery, then the majority of offspring produced each year are of sub-optimal quality, compounding already poor population-wide survival prospects.

Despite the demographic challenges imposed by poor survival and reproductive output for an individual red squirrel on Mount Graham, the population maintains demographic stability with a slightly positive instantaneous rate of growth and $\lambda > 1$. Habitat and MGRS abundance have decreased during the last two decades due to catastrophic environmental events such as fire and insect outbreak (Koprowski et al., 2005; Blount and Koprowski, 2012). In tandem, the availability of unoccupied middens in non-damaged habitat (Sanderson and Koprowski, 2009) and apparent demographic stability indicate that the population does not have the capacity to increase in abundance and take advantage of vacant middens and re-approach carrying capacity following stochastic population loss events. With environmental instability in the region predicted to increase due to the changing climate (Opdam and Wascher, 2004), the MGRS may not have the demographic capacity to overcome increased environmental stressors.

In their treatment of trailing edge peripheral populations, Hampe and Petit (2005) discuss the importance of understanding the performance and function of valuable relict populations that harbor a larger than expected proportion of unique genetic diversity within species. Here, we have focused on the basic demographic underpinnings of an endangered montane isolate at the low-latitude extremes of a well-studied mammalian model species to elucidate the functional differences that can manifest in peripheral populations. Our results suggest that typical conservation actions may be less effective in peripheral populations that exhibit atypical demographic profiles (Rushton et al., 2006). In this population, poor adult survival appears to constrain the capacity for population increase. Research predicts that populations composed of younger and inexperienced animals are more susceptible to effects of variability in weather or habitat conditions (Gordon et al., 2004). Our analysis indicates that improving the survival of adult female squirrels enough to allow additional reproduction opportunities would increase the number and potentially the quality of juveniles entering the population and could lead to greater population resilience at the range periphery. Results suggest that this non-resilient population is currently vulnerable to catastrophic events such as fire or other tree mortality episodes (i.e. beetle infestation) and resources should continue to be directed to preventing such occurrences. Further investigations

Table 4
Population level life table statistics and life expectancy at the 0 age class calculated for the Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) in the study area population on Mount Graham, Pinaleno Mountains, southeastern Arizona, USA. Assumptions about the age of unknown individuals are detailed in the text. Combining the known age juveniles and the adults with estimated minimum ages based on observations at first capture resulted in life table statistics that were most similar to when known age animals only were considered, while greatly increasing the sample size. Complete life tables for the male and female squirrels of known age + estimated age adults are included in Supporting Information.

Age assumption	R_0	G	r_m	r	λ	Female e_0	Male e_0
Known age only	1.1158	1.6972	0.0645	0.0654	1.0676	1.77	1.23
Known age + estimated minimum age adults	1.1006	1.7826	0.0538	0.0524	1.0538	1.74	1.18
Known age + all adults are 12 months at first capture	1.0297	1.7139	0.0171	0.0141	1.0142	1.67	1.18

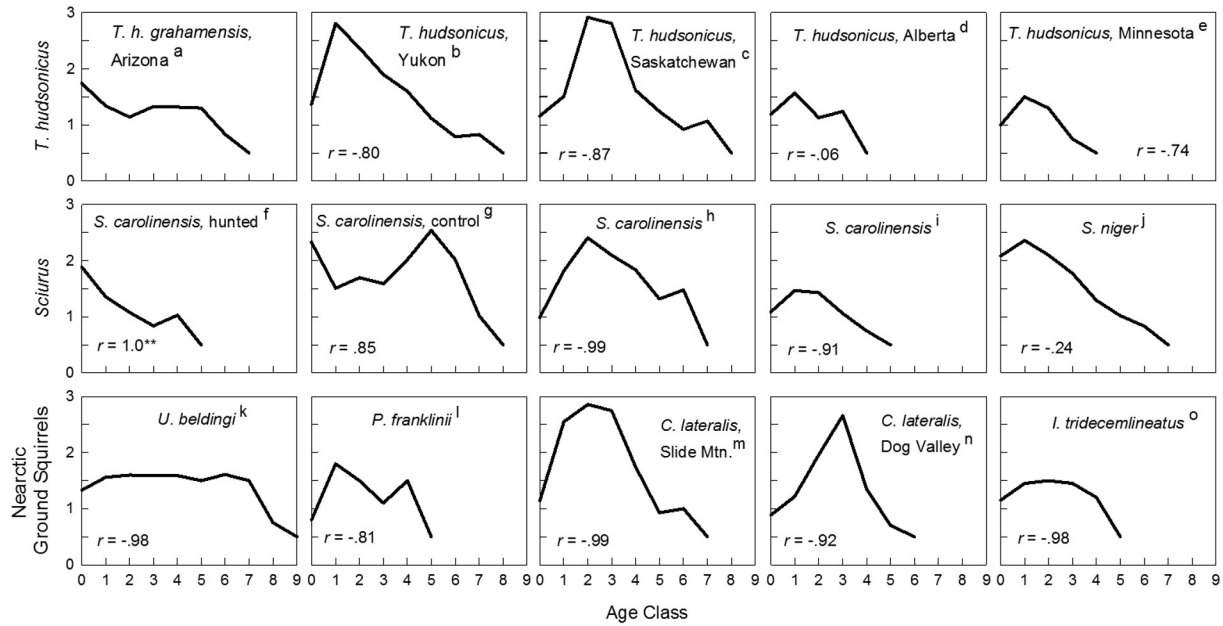


Fig. 2. Life expectancy in years by age class of the Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) and 14 other populations of red squirrels and closely related squirrels including *Sciurus* species, and Nearctic ground squirrel species. Data are derived from females only unless otherwise specified. Pearson's product-moment correlation between the Mount Graham red squirrel and each species is displayed. ** Indicates significance at the 0.01 level. ^a This study, ^b *T. hudsonicus* Yukon, Canada derived from figure (McAdam et al., 2007), ^c *T. hudsonicus* Cree Lake, Saskatchewan, Canada both sexes (Davis and Sealander, 1971), ^d *T. hudsonicus* Rochester, Alberta, Canada both sexes (Kemp and Keith, 1970), ^e *T. hudsonicus* Minnesota derived from figure (Erlie and Tester, 1984), ^f *Sciurus carolinensis* hunted population, Virginia (Mosby, 1969), ^g *S. carolinensis* control population, Virginia (Mosby, 1969), ^h *S. carolinensis* North Carolina sexes combined (Barkalow et al., 1970), ⁱ *S. carolinensis* West Virginia, sexes combined (Smith and Smith, 2006), ^j *S. niger* Illinois spring and summer born young sexes combined (Koprowski, 1985), ^k *Urocyon beldingi* California (Sherman and Morton, 1984), ^l *Poliocitellus franklinii* Minnesota (Erlie and Tester 1984), ^m *Callospermophilus lateralis* Slide Mountain, California (Bronson, 1979), ⁿ *C. lateralis* Dog Valley, California (Bronson, 1979), ^o *Ictidomys tridecemlineatus* Minnesota (Erlie and Tester, 1984). Full references for studies cited in this figure are available in Supplementary Material A4.

into the sources of mortality for adult females will guide potential conservation actions and should improve cost-effectiveness of conservation measures, which could include habitat manipulation, midden supplementation, or captive breeding. Examples of targeted demographic management of populations first arose in game species populations managed for recreation purposes, such as ungulates or fish (Schwartz et al., 1992; Gwinn et al., 2015), in which highly reproductive size or age classes were protected from harvest to improve the abundance and fitness of future offspring. Conservation managers are also beginning to utilize targeted management for species of conservation interest to achieve more natural metapopulation dynamics in anthropogenically-altered landscapes (Miller et al., 2013; Davies-Mostert et al., 2015).

At risk populations of species across the globe may benefit from targeted demographic intervention and further research is necessary to understand optimal strategies that may vary across taxa. Our long-term demographic profile of the MGRS identifies demographic targets for conservation management and highlights that peripheral populations require specialized management distinct from that formulated for core range populations.

The proportion of marked squirrels in each age class by year (A1), Life tables including unknown aged adults (A2), full references from Table 5 (A3), and full references from Fig. 2 (A4) are available online. Supplementary data associated with this article can be found in the online version, at <http://dx.doi.org/10.1016/j.biocon.2016.11.017>.

Table 5
Mean litter sizes of red squirrels (*Tamiasciurus hudsonicus*) from across their range arranged in ascending order.

Mean litter size	Method	Habitat	Location	Source
2.8 ± 0.09	Emerged young	Montane conifer	Mt. Graham, Arizona, USA	Current study
2.8	Nest young	Mixed conifer	Central Alberta, Canada	Larsen and Boutin (1994)
3.0	Nest young	Mixed conifer	Central Alberta, Canada	Becker (1992)
3.02	Nest young	Boreal conifer	Yukon, Canada	McAdam et al. (2007)
3.2	Nest young	Northern conifer	Saskatchewan, Canada	Davis (1969)
3.3	Embryos	Montane conifer	Summit County, Colorado, USA	Dolbeer (1973)
2.88–3.75	Placental scars/embryos/nest young	Montane conifer	Cascade Mts., British Columbia, Canada	Smith (1968)
3.4	Placental scars/embryos	Mixed Conifer	Alaska, USA	Modafferi (1972)
3.4–4.3	Placental scars	Aspen spruce	Rochester, Alberta, Canada	Kemp and Keith (1970)
3.6	Corpora lutea	Mixed conifer	Interior British Columbia, Canada	Millar (1970b)
3.7	Corpora lutea/placental scars	Mixed conifer	Northwest Territories, Canada	Zirul (1970)
4.0	Placental scars	Mixed conifer	Saskatchewan, Canada	Wood (1967)
4.1	Placental scars/embryos	Mixed conifer	Rochester, Alberta, Canada	Rusch and Reeder (1978)
4.2	Embryos	Deciduous	Ithaca, New York, USA	Hamilton (1939)
4.2	Emerged young	Deciduous	Southern Quebec, Canada	Lair (1985)
4.9	Corpora lutea	Mixed conifer	Vancouver Island, Canada	Millar (1970a)
4.5	Placental scars/embryos/nest young	Deciduous	Ithaca, New York, USA	Layne (1954)
5.4	Nest young	Captivity	Montreal, Quebec, Canada	Ferron and Prescott (1977)

Full references for studies included in this table are available in Supplementary Material A3.

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References

- Alvarez, L.H., 2001. Does increased stochasticity speed up extinction? *J. Math. Biol.* 43, 534–544.
- Anderson, D.R., Wywalowski, A.P., Burnham, K.P., 1981. Tests of the assumptions underlying life table methods for estimating parameters from cohort data. *Ecology* 62, 1121–1124.
- Arrigoni, M., Manfredi, P., Panigada, S., Bramanti, L., Santangelo, G., 2011. Life-history tables of the Mediterranean fin whale from stranding data. *Mar. Ecol.* 32, 1–9.
- Barkalow Jr., F.S., Hamilton, R.B., Soots Jr., R.F., 1970. The vital statistics of an unexploited gray squirrel population. *J. Wildl. Manag.* 34, 489–500.
- Benton, T.G., Grant, A., Clutton-Brock, T.H., 1995. Does environmental stochasticity matter? Analysis of red deer life-histories on rum. *Evol. Ecol.* 9, 559–574.
- Berteaux, D., Boutin, S., 2000. Breeding dispersal in female North American red squirrels. *Ecology* 81, 1311–1326.
- Blount, S.J., Koprowski, J.L., 2012. Response of the Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) to postfire conditions. *Southwest. Nat.* 57, 8–15.
- Browne, R.A., Ferree, P.M., 2007. Genetic structure of southern appalachian “sky island” populations of the southern red-backed vole (*Myodes gapperi*). *J. Mammal.* 88, 759–768.
- Calkins, M.T., Beaver, E.A., Boykin, K.G., Frey, J.K., Andersen, M.C., 2012. Not-so-splendid isolation: modeling climate-mediated range collapse of a montane mammal *Ochotona princeps* across numerous ecoregions. *Ecography* 35, 780–791.
- Caughley, G., 1977. *Analysis of Vertebrate Populations*. John Wiley & Sons, London, UK.
- Channell, R., Lomolino, M.V., 2000. Dynamic biogeography and conservation of endangered species. *Nature* 403, 84–86.
- Clutton-Brock, T., Sheldon, B.C., 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends Ecol. Evol.* 25, 562–573.
- Clutton-Brock, T.H., 1984. Reproductive effort and terminal investment in iteroparous animals. *Am. Nat.* 123, 212–229.
- Davies-Mostert, H.T., Mills, M.G.L., Macdonald, D.W., 2015. The demography and dynamics of an expanding, managed african wild dog metapopulation. *Afr. J. Wildl. Res.* 45, 258–273.
- Arizona Game and Fish Department, 2015. *Endangered Mount Graham Red Squirrel Population in Southern Arizona Decreases*.
- Descamps, S., Boutin, S., Berteaux, D., Gaillard, J.M., 2008. Age-specific variation in survival, reproductive success and offspring quality in red squirrels: evidence of senescence. *Oikos* 117, 1406–1416.
- Ericsson, G., Wallin, K., Ball, J.P., Broberg, M., 2001. Age-related reproductive effort and senescence in free-ranging moose, *Alces alces*. *Ecology* 82, 1613–1620.
- Forslund, P., Pärt, T., 1995. Age and reproduction in birds – hypotheses and tests. *Trends Ecol. Evol.* 10, 374–378.
- Frankel, O.H., 1974. Genetic conservation: Our evolutionary responsibility. *Genetics* 78, 53–65.
- Galbreath, K.E., Hafner, D.J., Zamudio, K.R., 2009. When cold is better: climate-driven elevation shifts yield complex patterns of diversification and demography in an alpine specialist (American pika, *Ochotona princeps*). *Evolution* 63, 2848–2863.
- Gibson, S.Y., Van Der Marel, R.C., Starzowski, B.M., 2009. Climate change and conservation of leading-edge peripheral populations. *Conserv. Biol.* 23, 1369–1373.
- Goldstein, E.A., Butler, F., Lawton, C., 2015. Frontier population dynamics of an invasive squirrel species: Do introduced populations function differently than those in the native range? *Biol. Invasions* 17, 1181–1197.
- Gordon, I.J., Hester, A.J., Festa-Bianchet, M., 2004. Review: The management of wild large herbivores to meet economic, conservation and environmental objectives. *J. Appl. Ecol.* 41, 1021–1031.
- Gurnell, J., 1987. *The Natural History of Squirrels*. Facts on File Inc., New York.
- Gwinn, D.C., Allen, M.S., Johnston, F.D., Brown, P., Todd, C.R., Arlinghaus, R., 2015. Rethinking length-based fisheries regulations: the value of protecting old and large fish with harvest slots. *Fish. Fish.* 16, 259–281.
- Hampe, A., Petit, R.J., 2005. Conserving biodiversity under climate change: the rear edge matters. *Ecol. Lett.* 8, 461–467.
- Hardie, D.C., Hutchings, J.A., 2010. Evolutionary ecology at the extremes of species' ranges. *Environ. Rev.* 18, 1–20.
- Harris, C.M., Park, K.J., Atkinson, R., Edwards, C., Travis, J.M.J., 2009. Invasive species control: Incorporating demographic data and seed dispersal into a management model for *Rhododendron ponticum*. *Eco. Inform.* 4, 226–233.
- Hope, A.G., Malaney, J.L., Bell, K.C., Salazar-Miralles, F., Chavez, A.S., Barber, B.R., Cook, J.A., 2016. Revision of widespread red squirrels (genus: *Tamiasciurus*) highlights the complexity of speciation within North American forests. *Mol. Phylogenet. Evol.* 100, 170–182.
- Hutton, K.A., Koprowski, J.L., Greer, V.L., Alanen, M.I., Schaufert, C.A., Young, P.J., Jones, C.A., 2003. Use of mixed-conifer and spruce-fir forests by an introduced population of Abert's squirrels (*Sciurus aberti*). *Southwest. Nat.* 48, 257–260.
- Kidd, L.R., Sheldon, B.C., Simmonds, E.G., Cole, E.F., 2015. Who escapes detection? Quantifying the causes and consequences of sampling biases in a long-term field study. *J. Anim. Ecol.* 84, 1520–1529.
- Koprowski, J.L., Alanen, M.I., Lynch, A.M., 2005. Nowhere to run and nowhere to hide: Response of endemic Mt. Graham red squirrels to catastrophic forest damage. *Biol. Conserv.* 126, 491–498.
- Koprowski, J.L., Goldstein, E.A., Bennett, K.R., Pereira Mendes, C., 2016. Family Sciuridae (tree, flying and ground squirrels, chipmunks, marmots and prairie dogs). In: Wilson, D.E., Lacher Jr., T.E., Mittermeier, R.A. (Eds.), *Handbook of the Mammals of the World/Lagomorphs and Rodents 1 Vol 6*. Lynx Edicions, Barcelona.
- Koprowski, J.L., King, S.R., Merrick, M.J., 2008. Expanded home ranges in a peripheral population: space use by endangered Mt. Graham red squirrels. *Endanger. Species Res.* 4, 227–232.
- Krebs, C.J., 1994. *Ecology: The Experimental Analysis of Distribution and Abundance*. Harper and Row, New York.
- Lenoir, J., Svenning, J.C., 2015. Climate-related range shifts – a global multidimensional synthesis and new research directions. *Ecography* 38, 15–28.
- Lesica, P., Allendorf, F.W., 1995. When are peripheral populations valuable for conservation? *Conserv. Biol.* 9, 753–760.
- Magurran, A.E., Baillie, S.R., Buckland, S.T., Dick, J.M., Elston, D.A., Scott, E.M., Smith, R.I., Somerfield, P.J., Watt, A.D., 2010. Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. *Trends Ecol. Evol.* 25, 574–582.
- Mar, K.U., Lahdenperä, M., Lummaa, V., 2012. Causes and correlates of calf mortality in captive Asian elephants (*Elephas maximus*). *PLoS One* 7, e32335.
- Martinez-Meyer, E., Diaz-Porras, D., Peterson, A.T., Yáñez-Arenas, C., 2013. Ecological niche structure and rangewide abundance patterns of species. *Biol. Lett.* 9.
- McAdam, A.G., Boutin, S., Sykes, A.K., Humphries, M.M., 2007. Life histories of female red squirrels and their contributions to population growth and lifetime fitness. *Ecoscience* 14, 362–369.
- Miller, S.M., et al., 2013. Management of reintroduced lions in small, fenced reserves in South Africa: An assessment and guidelines. *S. Afr. J. Wildl. Res.* 43, 138–154.
- Mosby, H.S., 1969. The influence of hunting on the population dynamics of a woodlot gray squirrel population. *J. Wildl. Manag.* 33, 59–73.
- Nixon, C.M., McClain, M.W., Donohoe, R.W., 1975. Effects of hunting and mast crops on a squirrel population. *J. Wildl. Manag.* 39, 1–25.
- Opdam, P., Wascher, D., 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biol. Conserv.* 117, 285–297.
- Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Syst.* 37, 637–669.
- Reid, J.M., Bignal, E.M., Bignal, S., McCracken, D.I., Monaghan, P., 2004. Identifying the demographic determinants of population growth rate: a case study of red-billed choughs *Pyrrhocorax pyrrhocorax*. *J. Anim. Ecol.* 73, 777–788.
- Reznick, D.A., Bryga, H., Endler, J.A., 1990. Experimentally induced life-history evolution in a natural population. *Nature* 346, 357–359.
- Rushton, S.P., Wood, D.J.A., Lurz, P.W.W., Koprowski, J.L., 2006. Modelling the population dynamics of the Mt. Graham red squirrel: can we predict its future in a changing environment with multiple threats? *Biol. Conserv.* 131, 121–131.
- Sanderson, H.R., Koprowski, J.L., 2009. The Last Refuge of the Mt. Graham Red Squirrel: Ecology of Endangerment. The University of Arizona Press, Tucson, AZ.
- Schauffert, C.A., Koprowski, J.L., Greer, V.L., Alanen, M.I., Hutton, K.A., Young, P.J., 2002. Interactions between predators and Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*). *Southwest. Nat.* 47, 498–501.
- Schwartz, C.C., Hundertmark, K.J., Spraker, T.H., 1992. An evaluation of selective bull moose harvest on the Kenai Peninsula, Alaska. *Alces* 28, 1–13.
- Schwartz, O.A., Armitage, K.B., Van Vuren, D., 1998. A 32-year demography of yellow-bellied marmots (*Marmota flaviventris*). *J. Zool.* 246, 337–346.
- Semlitsch, R.D., Drake, D.L., 2015. Structure and dynamics of *Lithobates sylvaticus* (wood frog) at the periphery of its range in Missouri. *Southeast. Nat.* 14, 329–341.

- Sibly, R.M., Collett, D., Promislow, D.E.L., Peacock, D.J., Harvey, P.H., 1997. Mortality rates of mammals. *J. Zool.* 243, 1–12.
- Steele, M.A., 1998. *Tamiasciurus hudsonicus*. *Mamm. Species* 586, 1–9.
- Thorington, R.W., Koprowski, J.L., Steele, M.A., Whatton, J.F., 2012. *Squirrels of the World*. The Johns Hopkins University Press, Baltimore, Maryland.
- Vucetich, J.A., Waite, T.A., 2003. Spatial patterns of demography and genetic processes across the species' range: null hypotheses for landscape conservation genetics. *Conserv. Genet.* 4, 639–645.
- Weladji, R.B., Gaillard, J.-M., Yoccoz, N.G., Holand, Ø., Mysterud, A., Loison, A., Nieminen, M., Stenseth, N.C., 2006. Good reindeer mothers live longer and become better in raising offspring. *Proc. R. Soc. London, Ser. B* 273, 1239–1244.
- Zugmeyer, C.A., Koprowski, J.L., 2009. Severely insect-damaged forest: A temporary trap for red squirrels? *For. Ecol. Manag.* 257, 464–470.