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Modelling the population dynamics of the Mt. Graham red squirrel: Can we predict its future in a changing environment with multiple threats?

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ARTICLE INFO

Article history:

Received 25 April 2005

Received in revised form

31 January 2006

Accepted 24 February 2006

Available online 17 April 2006

Keywords:

Conservation

SEPM

Endangered species

Introduced species

Sciurus aberti

Arizona

ABSTRACT

The Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*; MGRS) is among the most critically endangered mammals in the United States and is isolated on the periphery of the species' range, potentially increasing its conservation priority. To investigate potential threats to the population and provide a tool for land managers, we developed a spatially explicit population dynamics model. We tested model predictions using available range-wide data from the literature and field work specific to the MGRS. A general model input data set using mean life history values overpredicted MGRS abundance. However, we found significant correlation with known squirrel abundance using a general data set with curtailed fecundity and survival. A model with MGRS-specific data provided the best fit to observed population size. We investigated potential impacts of two major threats to the MGRS: competition from introduced Abert's squirrels (*Sciurus aberti*) and increased levels of predation. Predation and particularly competition could have significant effects on the future population of the MGRS. Careful attention must be used to model the viability of fringe populations as peripheral populations can have a different life history than populations found in the range core.

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1. Introduction

Effective management of any endangered population requires a thorough understanding of factors impacting population dynamics. These factors include not only proximal, human-driven causes of decline such as habitat loss, but also inter-specific interactions and the relative contribution of innate life history characteristics that ultimately drive population dynamics. Red squirrels (*Tamiasciurus hudsonicus*) are common inhabitants of forests of North America (Steele, 1998). Their distribution in the western United States extends through the Rocky Mountains to a southern terminus in the

arid lands of south-eastern Arizona. At the terminus the distribution of red squirrels becomes fragmented into montane islands of high elevation forest in the Pinaleno Mountains, Graham County, Arizona, USA (Brown, 1984). The southernmost population, the Mt. Graham red squirrel (*T. h. grahamensis*), is endemic to the Pinaleno Mountains, and as a peripheral population (Lesica and Allendorf, 1994; Vucetich and Waite, 2003) has greater conservation priority due to potentially unique characteristics.

The Mt. Graham red squirrel (MGRS) is restricted to about 12,200 ha of coniferous forest from 2362 m elevation to a summit of 3267 m (Hatten, 2000). The area where the MGRS occurs

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doi:10.1016/j.biocon.2006.02.010

is dominated by Engelmann spruce (*Picea engelmannii*) and corkbark fir (*Abies lasiocarpa* var. *arizonica*) at the highest elevations, with Douglas-fir (*Pseudotsuga menziesii*) and south-western white pine (*Pinus strobiformis*) becoming more frequent as elevation decreases (Hutton et al., 2003). Conifer seeds of these four species are the main food resource for MGRSs. The population is separated by >100 km of low elevation desert scrub and grassland from populations of the nearest related subspecies (*T. h. lychnuchus*: Brown, 1984). MGRSs gained notoriety associated with efforts to construct an astro-physical complex in the late 1980s and the subspecies was protected under the United States' Endangered Species Act in 1987 (United States Fish and Wildlife Service, 1993; Istock et al., 1994; Warshall, 1994). Despite >15 years of legal protection abundance remains low, down to 214 from a high of 562 squirrels in 1999, and the population faces several threats to the extent that it is considered critically endangered by the IUCN (Belitsky, 2000).

One threat to the MGRS is competition by Abert's squirrels (*Sciurus aberti*), an introduced tree squirrel (United States Fish and Wildlife Service, 1993). Abert's squirrels may competitively exclude MGRSs from some environments (Minckley, 1968; Gehlbach, 1981; Brown, 1984; Hoffmeister, 1986; United States Fish and Wildlife Service, 1993; Hutton et al., 2003). Abert's squirrels may reduce food resources for MGRS (Nash and Seaman, 1977; Brown, 1984; Edelman and Koprowski, 2005) because there is considerable dietary overlap between the species (Steele, 1998; Hutton et al., 2003). Abert's squirrels may also kleptoparasitise middens (larderhoards) of red squirrels (Ferner, 1974; Hall, 1981; Hutton et al., 2003) resulting in a direct loss of cached food resources. The impact on red squirrels may be significant since *S. aberti* are known to reduce cone crops by as much as 74% due to herbivory and granivory (Larson and Schubert, 1970; Snyder, 1990; Allred et al., 1994).

Forest management can also impact the MGRS. Thinning operations that open forest canopy to reduce fire risk may change microclimates and increase predation (Hakkaraïnen et al., 1997; Carey, 2002; Thompson et al., 2003). A diversity of mammalian and avian predators are known for the MGRS (Hoffmeister, 1956; Schauffert et al., 2002) such as the Mexican spotted owl (*Strix occidentalis luca*), the Northern goshawk (*Accipiter gentilis*) and the Bobcat (*Lynx rufus*) (Koprowski unpublished data). Evidence across the geographic range of the species suggests that predation significantly impacts on population size, accounting for 19–70% of mortality (Kemp and Keith, 1970; Rusch and Reeder, 1978; Wirsing et al., 2002).

Spatially explicit population models (SEPMs) have successfully been used to predict dynamics of squirrel populations (Rushton et al., 1999; Lurz et al., 2003), their spatial spread (Rushton et al., 1997; Lurz et al., 2001), and impacts of different management regimes (Rushton et al., 2002; Lurz et al., 2003). Furthermore, SEPMs can be used to explore site-specific management impacts (Lurz et al., 2003). Here we develop a SEPM to investigate dynamics of MGRSs in relation to the key population drivers. SEPMs require detailed information on life history patterns (Conroy et al., 1995; Ruckelhaus et al., 1997). Area or population specific data are not always available for some life history parameter ranges and general species data from comparable populations in other geograph-

ical locations are often used in population modelling of this type (Howells and Edwards-Jones, 1997; Mladenoff and Sickley, 1998; South et al., 2000; Buenau and Gerber, 2004). However, it is unclear if data derived from studies of populations within a species' main distributional or 'core' range can adequately predict demography of fringe populations such as the MGRS population in the Pinaleño Mountains. This may be significant if these populations differ genetically and/or demographically, as is often the case in peripheral populations (see Hoffman and Blows, 1994; Lomolino and Channell, 1995). Our objective was to create a SEPM that could be used for the conservation of the MGRS and use this model to evaluate potential threats. To this aim we collected life history data from literature that covers the entire geographical range of the red squirrel and data from surveys of the MGRS population. Using extant data on population fluctuations of MGRSs, we tested multiple life-history scenarios and performed an analysis to determine which life history set adequately describes the population dynamics of MGRSs. Using the best model we investigated the potential effects of competition by introduced Abert's squirrels and increased predation levels linked to changes in forest management.

2. Methods

We used the previously successful approach of Rushton et al. (1997, 1999, 2000, 2002) and modelled: maximum dispersal distance, the maximum distance over which males would search to find a mate, adult mortality, juvenile mortality, fecundity (litter size), and the proportion of females breeding. We added an additional variable for cache size to represent the larder-hoarding strategy of *T. hudsonicus* (Gurnell, 1984).

2.1. Description of the model

The model had two main components: The first component was the geographic information system (GIS) which stored the position of home ranges in the landscape. Secondly, an individual-based population dynamics model simulated individual life histories and dispersal within the GIS-held landscape. Our population model was written in the programming language C and integrated with the GIS component through a UNIX-shell environment (Rushton et al., 1997, 1999). The model was stage-structured (Caswell, 1989), in so far as discrete stages were recognised in the population, but the life history processes of mortality, fecundity and dispersal were modelled stochastically at the level of the individual within the different age classes. Coordinates of each available midden in each year were used as the spatial reference point with which to model dynamics of individuals. We assumed squirrels would occupy home ranges centred on a midden site and an individual squirrel could occupy each midden within the landscape (Steele, 1998). Two age classes were modelled, adults and juveniles. We modelled the life history of each squirrel on a monthly time step. Middens known to have been destroyed by fire were removed from the available 'midden pool' following these events.

Reproduction occurred once a year in April (month 4: Koprowski, 2005). The proportion of females breeding was

varied as a model input. Females were allowed to breed subject to the availability of a male within the maximum mating distance. This distance over which males were allowed to travel for mating was varied as an input. We estimated the number of young produced in each litter by drawing deviates from a Poisson distribution whose mean was varied as a model input (following Akcakaya et al., 1995; Rushton et al., 2000). The sex ratio of young was assumed to be 50:50 (Steele, 1998).

We modelled mortality in each month at the individual level for adults and juveniles. Probability of death for each individual was determined by sampling deviates from a uniform distribution in the range 0–1, with mortality occurring if the deviate was in the mortality range. Thus, for an individual subjected to adult mortality of, e.g. 4.0%, all deviates in the range 0–0.96 corresponded to the individual surviving, those greater than 0.96 and up to 1.0 to it dying.

Mortality and fecundity in tree squirrels are strongly linked to food supply (e.g. Koprowski, 1991) but their effects on population size and viability will be buffered by cached food. We modelled the size of the cache and its exploitation explicitly, with cache size varied as an input. Cache size was modelled in terms of months over which food stored in the cache would last. It was assumed that in good seed years squirrels would create midden caches that were larger and effectively provided food for a longer period into the next season than would years with low seed production (Gurnell, 1984, 1987; Steele, 1998). We assumed adults would utilise other food sources when caches were depleted and therefore only modelled a direct food dependant mortality effect for juveniles (Barkalow et al., 1970; Koprowski, 1991). While food was available in a squirrel's midden, the associated juvenile squirrels were subjected to reduced mortality and adults to increased fecundity relative to periods of higher mortality and reduced fecundity when all stores had been consumed.

Most dispersal of young and sub-adult squirrels takes place in autumn so we modelled dispersal in August, September and October (months 8–10). All young stayed in their mother's natal area until dispersal. We assumed for simplicity that the maximum dispersal distance modelled applied to both sexes. The dispersing animal sampled the landscape up to a maximum dispersal distance from their natal home

range and settled at an existing empty midden location within the landscape. Any animal that could not find a home range was assumed to have perished in the landscape.

2.2. Parameterising the model: home ranges, life history characteristics and food availability in the field

Midden sites were derived from field surveys of the Pinaleno Mountains (Hatten, 2000; Buenau and Gerber, 2004). A total of 1293 known midden locations were available for squirrels in the simulation scenarios. We assessed midden occupancy from 1991 to 2004 by visiting the conspicuous cone scale piles (Finley, 1969) and noting sign of active cone caching and feeding (Rasmussen et al., 1975; Mattson and Reinhart, 1996). A 1996 fire in the Pinaleno Mountains severely damaged 39 middens, removing these sites as possible larderhoard locations (Froehlich, 1996), and we removed them as possible sites within the model simulation in the appropriate year.

Ranges for life history parameters and cone crops for the MGRS were obtained from yearly monitoring efforts, current work in the Pinaleno Mountains, and MGRS specific literature (see Table 1; Young, 1990, 1991; Young et al., 1992, 1993, 1994, 1995, 1996, 1997, 1998, 1999; Stromberg and Patten, 1993; Kreighbaum and Van Pelt, 1996; Koprowski et al., 2000, 2001, 2002, 2003; Koprowski, 2005; Frank, 2006; Miller and Yoder, 2006). Proportion of animals breeding was assessed by observation of individuals for evidence of lactation or scrotal testes. Fecundity (litter size) was assessed by repeated observation of juveniles emerging from nests. Beginning in 2001, squirrels were live-trapped, ear tagged, and radio-collared (reviewed in Koprowski, 2002, 2005). Weekly monitoring of animals by radio-telemetry permitted quantification of adult survival (proportion of adults surviving interval) and enabled us to monitor maximum distance moved by males to find a mate. Juvenile dispersal distances were calculated from known dispersal movements by ear tagged juveniles from natal middens. Up to 1992, seed crops were assessed qualitatively as either 'poor' or 'good'. Seed production since 1993 was estimated from the same 28 (19 spruce-fir, 9 mixed-conifer) plots distributed among monitored areas (Koprowski et al., 2005). Three 0.25 m² seed traps were randomly placed within a 10 m × 10 m plot at each location. Seeds for a given

Table 1 – Life history parameters of Mt. Graham red squirrels, Pinaleno Mountains, Arizona and literature averages for red squirrels across their range

Parameter	Mt. Graham specific			Literature average		
	Mean	Minimum	Maximum	Mean	Minimum	Maximum
Adult mortality (%) ^a	47	22	73	34.73	26.8	47
Juvenile mortality (%) ^b	50			61.82	25	81
Fecundity (num/litter)	2.35	1	5	3.69	1	7
Females breeding (%)	56	29	99	77.14	47	99
Maximum mate distance (m) ^c	418.7	92	923			
Dispersal distance (m)	460.5	0	1885	257	0	4500

a Estimates for Mt. Graham red squirrel adult mortality were generated from trapping efforts and telemetry data rather than overwinter survival or turnover.

b Only one mortality study was performed on juveniles of the Mount Graham red squirrel (Kreighbaum and Van Pelt, 1996).

c No maximum mate distance data were found in collected literature and our estimate represents maximum movements of radio-collared Mount Graham red squirrel males during the breeding season.

Table 2 – Cone crop ratings from 1987 to 2002, Pinaleno Mountains, Arizona

Year	Crop rating
1987	Poor ^a
1988	Poor ^a
1989	Poor ^a
1990	Good ^a
1991	Poor ^a
1992	Poor ^b
1993	Good ^c
1994	Poor ^c
1995	Poor ^c
1996	Poor ^c
1997	Good ^c
1998	Poor ^c
1999	Poor ^c
2000	Poor ^c
2001	Good ^c
2002	Poor ^c

a Based on Engelmann Spruce cone counts (Stromberg and Patten, 1993).
b Personal communication with Vicki L. Greer, University of Arizona.
c Seed trap data.

year were collected from seed traps in spring of the following year. Conifer seeds contained in each trap were separated and tallied by species. Years were classified as 'poor' or 'good' by natural dichotomies (Table 2).

The same suite of life-history parameters was obtained from literature for red squirrel populations from Central Arizona to Alaska (Hamilton, 1939; Layne, 1954; Smith, 1967, 1968; Wood, 1967; Davis, 1969; Krasnowski, 1969; Wrigley, 1969; Kemp and Keith, 1970; Millar, 1970; Zirul, 1970; Davis and Sealander, 1971; Modafferi, 1972; Dolbeer, 1973; Ferron and Prescott, 1977; Kelly, 1978; Rusch and Reeder, 1978; Halvorson, 1982; Halvorson and Engeman, 1983; Erlein and Tester, 1984; Gurnell, 1984; Lair, 1985; LaPierre, 1986; Boutin and Schweiger, 1988; Sun, 1989; Klenner, 1990; Sullivan, 1990; Uphoff, 1990; Boutin and Larsen, 1993; Larsen, 1993; Larsen and Boutin, 1994; Berteaux and Boutin, 2000; Humphries and Boutin, 2000; Anderson and Boutin, 2002; Wheatley

et al., 2002; Haughland and Larsen, 2004). Values from this set were used in one instance in the specific MGRS life history collection where MGRS specific data were scarce (juvenile survival) but the one value available from the MGRS population was in the range of values from the general literature.

2.3. Running the model

2.3.1. Sensitivity analysis

We used latin hypercube sampling (LHS) to generate suites of life history inputs from each parameter in the general red squirrel and MGRS specific data ranges (Table 3), following the methodology of Rushton et al. (2000). Five hundred sets of inputs were randomly generated based on a uniform distribution. For each set, values were randomly selected over the observed minimum to maximum range of each life history parameter to capture the whole universe of probable inputs. We randomly allocated 348 adult squirrels, the known population size in 1986, into the 1293 available middens with sex varied at random. An even sex ratio was assumed. We investigated persistence of red squirrels over 20 years for MGRS and general red squirrel inputs. The final population predicted at year 20 was used as a variable in a partial correlation analysis against the life history parameters used in each run to generate sensitivity analysis results for each life history collection.

2.3.2. Model testing

We compared general input range based on *T. hudsonicus* literature and a MGRS specific range. We also created a series of curtailed general ranges to reflect reduced fecundity and survival found at the edge of a species range. The fit of model predictions based on these scenarios was compared to observed population census data (1987–2002).

2.3.3. Assessing the potential impacts of Abert's squirrel competition and increased mortality due to predation

The potential impact of Abert's squirrels on food availability was modelled by reducing the available cache size to individual red squirrels. Based on the best fit model (Table 4) we investigated possible reductions in food availability and thus cache size using observed reductions in cone crops due to Abert's

Table 3 – Mount Graham red squirrel life history parameter ranges input for a sensitivity analysis of a spatially explicit population model (G = good; P = poor)

Parameter	General red squirrel		Mt. Graham red squirrel	
	Minimum	Maximum	Minimum	Maximum
Fecundity (G) (young/female)	3.7	7	2.6	5.0
Fecundity (P) (young/female)	1	3.6	1.0	2.5
Females breeding (G) (%)	47	79	56	99
Females breeding (P) (%)	79	99	29	56
Adult mortality (%)	26.8	47	22	73
Juvenile mortality (G) (%)	25	62	25	60
Juvenile mortality (P) (%)	62	81	60	81
Litter frequency (per year)	1	1	1	1
Dispersal distance (m)	0	4500	0	4500
Maximum mate distance (m)	92	923	92	923
Food cache size (months)	2	18	2	18

Table 4 – Input parameter ranges for validation of spatially explicit red squirrel model for two data sets

Parameter	General red squirrel		Mt. Graham red squirrel	
	Good	Poor	Good	Poor
Fecundity (young/female)	3.69		3.0	2.35
Adult mortality (%)		0.34		0.46
Juvenile mortality (%)	0.61		0.50	0.81
Proportion breeding (%)	0.77		0.99	0.56
Cached food (months)	6		6	16
Maximum mate distance (m)		923		923
Dispersal distance (m)		4500		4500

The parameter range for the general red squirrel data set is the curtailed range that represents an average to poor range for the red squirrel.

squirrels (Larson and Schubert, 1970; Snyder, 1990; Allred et al., 1994). We simulated an increase in Abert’s squirrel competition through a reduction in the available cached food by 20%, 56% and 74% (minimum, maximum, and midpoint of observed effect published in the literature). We also considered that Abert’s squirrels might currently have an impact on MGRSs and predicted population size based on food cache increases of 20%, 56% and 74% (potential but not maximal increases) should Abert’s squirrels be removed from MGRS range.

Effects of increased predation on population size were investigated by imposing additional mortality on adults. Increases in predation rates by avian predators were simulated by increasing adult mortality for the months (October–May) that raptors are known to have taken red squirrels on the mountain. The magnitude of likely increases in predation rates for the MGRS in the Pinaleno Mountains due to opening of the forest canopy as a result of fire prevention measures is unknown. We therefore explored two plausible scenarios covering increases of 5% and 10% in mortality rates as observed for another red squirrel population in response to high levels of predation (Wirsing et al., 2002).

3. Results

3.1. Sensitivity analysis

The variables that were significant determinants of predicted population size depended on the life-history data set used in the model. Using the general life-history data set, adult mortality ($f = 150.51, p < 0.001$) and duration of cache ($f = 30.87, p < 0.001$) were the most significant life-history parameters (model $r^2 = 0.27$). For the MGRS-specific analyses (model $r^2 = 0.67$) adult mortality ($f = 561.19, p < 0.001$) and duration of cache ($f = 360.95, p < 0.001$) were also significant. However, the results of the sensitivity analysis using the MGRS life-history data set (Fig. 1) were also significant for three variables connected to reproduction for good years: juvenile mortality ($f = 20.38, p < 0.001$), fecundity ($f = 24.13, p < 0.001$), and proportion of females breeding ($f = 29.07, p < 0.001$). This indicates that the relative importance of life-history parameters differed between the two data sets. In effect the observed MGRS-specific data set indicate a constraining influence of variables linked to reproduction on population size.

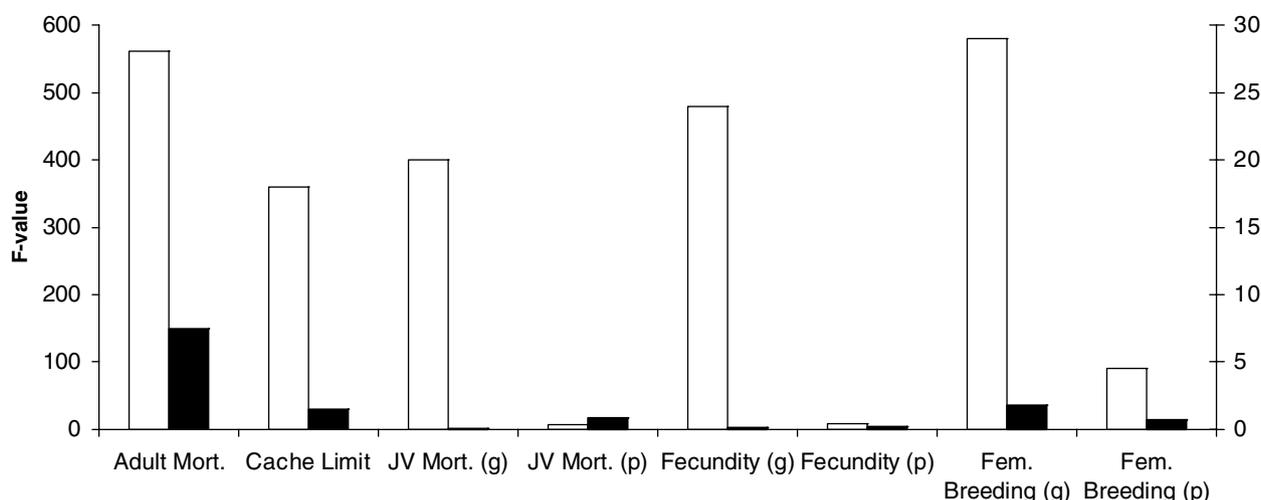


Fig. 1 – Plot of F-values (absolute value) of sensitivity analysis results for red squirrels, illustrating the relative importance of different life history parameters for a model populated by general red squirrel (filled bars) and Mt. Graham red squirrel (unfilled bars) life-history parameters. Adult mortality and cache size are plotted on the primary axis (left) and juvenile mortality, fecundity, and proportion females breeding are plotted on the secondary axis (right). In a good cone year parameters are indicated by a ‘g’ and in a poor cone year with a ‘p’.

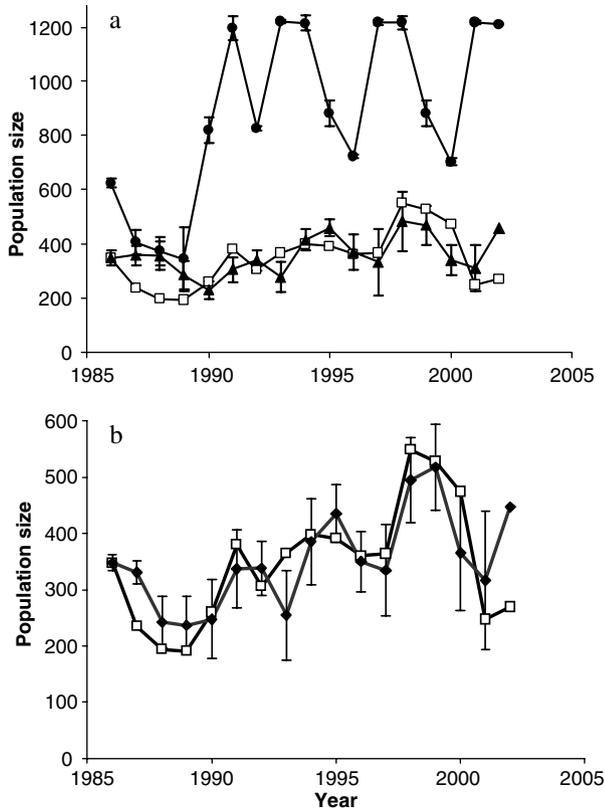


Fig. 2 – Spatially explicit population model predictions for red squirrels: (a) comparison of observed (open squares) and predicted population estimates (mean ± 1SD) using general (closed circles) and a curtailed general (closed triangles: $r = 0.539, p < 0.03$) life history data sets and (b) comparison of observed (open squares) and predicted population estimates (mean ± 1SD) using Mt. Graham red squirrel specific (closed diamonds: $r = 0.741, p < 0.001$) life history ranges.

3.2. Model testing

A general life history range (Table 1) vastly overpredicts MGRS numbers (Fig. 2a). Results from model simulations give a significant correlation of observed and predicted population estimates for the curtailed general range with reduced fecundity ($r = 0.539, p < 0.03$: Table 4, Fig. 2a) and particularly the MGRS scenarios ($r = 0.741, p < 0.001$: Table 1, Fig. 2b).

3.3. Impacts of Abert’s squirrel and predation on population size

Competition for food and impacts of Abert’s squirrels on seed or cone production has the potential to reduce population viability of MGRSs (Fig. 3). We also considered potential changes to another major life-history variable driving the red squirrel population dynamics in the Pinaleno Mountains – adult mortality. Based on plausible scenarios, both increased predation and competition from Abert’s squirrels can have significant negative consequences. At the levels simulated, the potential impact of Abert’s squirrels competition is surprisingly high. Increases in predation of the MGRS led to considerably lower population levels (Fig. 4).

4. Discussion

What can modelling tell us about the population dynamics of MGRSs and future management? Firstly, strong agreement exists between predicted and observed population densities for squirrels from 1987 to 2002, but only for data generated on the Pinaleno Mountains, or where the generalised life history data were constrained at levels lower than the mean for the species over its full geographical range.

Results of sensitivity analyses were different for general life history and MGRS specific model runs. Whilst adult mortality and duration of cache size were significant predictors

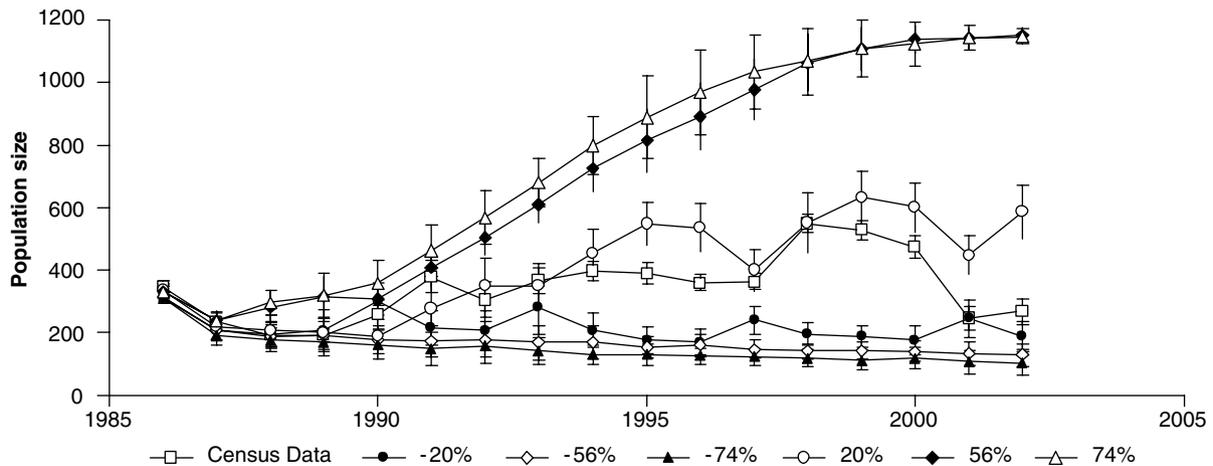


Fig. 3 – Spatially explicit population model predictions for Mt. Graham red squirrel population sizes (mean ± 1SD) illustrating possible impacts of cache size reductions and increases from 1986 to 2002 due to Abert’s squirrel foraging compared to observed population sizes (census data).

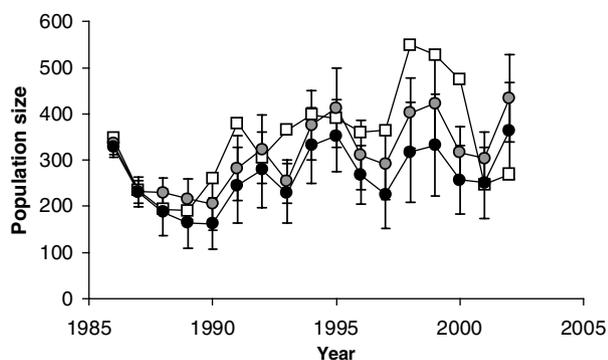


Fig. 4 – Observed (open squares) and predicted Mount Graham red squirrel population sizes (mean ± 1SD) illustrating the impact of increased predation levels of 5% (grey circles) and 10% (closed circles). Predictions generated by a spatially explicit population model developed for the Mt. Graham red squirrel.

of population size for both sets of model runs, other reproductive parameters were significant predictors of population size for the MGRS population. This suggests that many aspects of the population dynamics of squirrels were of critical importance for the MGRS population. These results also suggest that MGRSs might be more susceptible to extinction since deviation in any one of the demographic variables is likely to result in changes in population size. We found large differences in fecundity and mortality for red squirrels (Table 5) and variation in life history patterns for populations at the edge of the species range in relation to the core range have been documented for other species (Aldridge and Brigham, 2001). Populations at the edge of their range may also show genetic (Vucetich and Waite, 2003), and morphological differences (Lesica and Allendorf, 1994). Furthermore, abundance in peripheral populations is often lower and more variable than in core populations (Hengeveld and Haeck, 1982; Brown, 1984).

The red squirrel gives us the unique opportunity to study a system where the core and fringe of the population are still extant. In many conservation situations we may be limited to data derived from previous studies focused on the core population. However, it is peripheral populations that are more likely to remain than core populations in cases of anthropogenic-caused extinctions (Lomolino and Channell, 1995). In modelling for conservation purposes we need to be concerned with how to model populations on the periphery of a species range and be aware of the differences between core and peripheral populations, since models that do not take into account local demographic patterns are unlikely to

recapitulate system behaviour or to be accurate predictors of the impact of management. Whilst previous modelling attempts worked well with general literature data for populations in habitats typical for the species’ distribution range (e.g. Howells and Edwards-Jones, 1997; Rushton et al., 1997; Mladenoff and Sickley, 1998; Rushton et al., 1999; South et al., 2000) our results indicate caution may have to be exercised when predicting dynamics of fringe populations.

Assessing the relative significance of current levels of predation and interspecific competition for the Mt. Graham red squirrel is difficult because the two variables are confounded. We addressed this issue by estimating the proportion of known kills in the population over the period 2002–2005 and also by assessing how much of the total cone crop could have been removed by the competing Abert’s squirrel and then manipulated the impacts of increases in competition or predation in the model proportionally. The most interesting feature is that competition with the non-native has the potential for a much greater impact on squirrel population size than plausible increases in predation. This is a situation mirrored in the UK where the introduced grey squirrel (*Sciurus carolinensis*) poses a similar threat to the red squirrel (*Sciurus vulgaris*) and has led to extensive declines in range (Gurnell et al., 2004) whilst predation from reintroduced predators such as goshawks has had limited impact (Petty et al., 2003).

For conservation and management, our SEPM illustrates the most important need is to understand the relationships between MGRSs and its habitat at a local scale. Importantly the model emphasizes the need to understand the relationship of predation and resource availability, including interspecific competition, to MGRS mortality. MGRSs face a difficult future, as habitat is lost to a variety of disturbances. Insect damage has reduced available resources in large sections of the spruce-fir forest (Koprowski et al., 2005) and large catastrophic wildfires (such as in 2004; Koprowski et al., 2006) are still a threat (USDA Forest Service, 2000). Incorporating these processes into our initial model will lead to a more accurate tactical tool that will allow conservation managers to minimise the likelihood of extinction of the MGRS.

The MGRS appears to be a species that suffers from being endemic to a small isolated mountain range at the periphery of its range and subject to multiple threats from habitat loss, forest disturbance, and interspecific competition. In a sense MGRSs are a paradigm for imperilled mammals. The conservation of many species will stand or fall based on our ability to manage multiple threats. European red squirrels are threatened by an introduced species and disease (Tompkins et al., 2002; Gurnell et al., 2004), Delmarva fox squirrels (*Sciurus niger cinereus*) combat habitat degradation and fragmentation (United States Fish and Wildlife Service, 2003), large carnivores

Table 5 – Comparison of critical life history traits for red squirrels generated from the literature averages (minimum, maximum, and mean) and for studies of the endangered Mt. Graham red squirrel (MGRS)

	Minimum	Maximum	Mean	MGRS	SD difference
Adult mortality	26.8	47	34.73	47	1.66
Fecundity	2.77	5.4	3.69	2.35	1.46

SD difference shows the deviation of the MGRS value and the literature mean.

face threats of habitat loss and poaching in the rocky mountains (Noss et al., 1996), arctic foxes (*Alopex lagopus*) are imperilled by the loss of the wolf (*Canis lupus*), climate change, and increased red fox (*Vulpes vulpes*) density (Hersteinsson et al., 1989), and multiple threats are seen frequently for island populations (e.g. Cuaron et al., 2004). Our model has shown that future work should move some focus to monitoring the effects of competition and predation on the MGRS. Detailed raptor surveys and monitoring of the introduced Abert's squirrel, could aid the population by alerting managers of increased risks. Actions can then be taken against these threats. In addition, the relationship between resource availability (whether fresh cones are available in larderhoards) and life history is important. Careful monitoring of cone crops and the effects of climate, natural and anthropogenic influences on crop size are important for conservation of MGRS. We believe that modelling of the form reported here has a major role in determining the relative significance of different conservation threats and offers real opportunities for enhancing conservation through prioritising potential intervention.

Acknowledgements

The comments of two anonymous reviewers improved the quality of this manuscript. We thank the many field biologists that have contributed to the collection of data on the status and ecology of Mt. Graham red squirrels. Funding for this research was provided by the Arizona Game and Fish Department, USDA Forest Service, University of Arizona's Office of the Vice President for Research, and Arizona Agricultural Experiment Station. W. Van Pelt was instrumental in the acquisition of funding and is owed a debt of gratitude. Mt. Graham International Observatory personnel provided logistical support to clear roads and maintain field camps. All research was conducted under permit from the University of Arizona's Institutional Animal Care and Use Committee, USDA Forest Service, Arizona Game and Fish Department, and the US Fish and Wildlife Service, Endangered Species Office. We also thank Mark Shirley and Oliver Lurz for assistance in the early stages of the project.

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