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Developing recovery and monitoring strategies for the endemic Mount Graham Red Squirrels (*Tamiasciurus hudsonicus grahamensis*) in Arizona

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Abstract

An important challenge in conservation biology is extracting pertinent information from the available data for endangered species. Rarely do we have enough information to precisely determine an organism's risk of extinction and other factors that affect its management. How, then, can we use limited information to make responsible conservation decisions on controversial species such as the Mount Graham red squirre?

We use several analytical approaches to examine 15 years of abundance data for the Mount Graham red squirrel, in order to propose recovery criteria and to evaluate alternative conservation strategies. We analysed the historical population dynamics using a diffusion approximation model and showed that the main threat to the population was not the overall growth rate (which may well be greater than 1) but rather the wide range of variation in annual growth rates. We have used information on the distribution of growth rates and abundance to classify the species as threatened under the Endangered Species Act (ESA). We have then presented a simple demographic model to examine the effects of proportional changes in vital rates on the population growth rate (λ). The elasticity values obtained for Mount Graham red squirrels indicate that the population is far more sensitive to changes in survival rates (particularly adult survival) compared to reproduction. Our analyses suggest that management should focus on refining monitoring techniques, reducing sources of variability, improving the survival of adult animals and filling the gaps in the currently available data.

INTRODUCTION

The goal of recovery teams is to improve the condition of an endangered or threatened population until it can be downlisted or delisted. Recovery teams frequently must approach this goal with scant and sometimes questionable data about their species of concern. When waiting indefinitely for more information is not an option, policy decisions must be made as rigorously as possible using the limited data. Conservation biology offers a number of quantitative approaches to population viability analysis (PVA) that we can apply to small, at-risk populations such as the Mount Graham red squirrel(MGRS). These approaches are useful for determining the status of a population, recovery criteria, the potential effect of management options and what types of future research are most critical to the continued management and recovery of the species.

The MGRS (*Tamiasciurus hudsonicus grahamensis*) is a subspecies endemic to the sky island of the Pinaleño Mountains in Arizona. The habitat of this endangered species occurs only at high altitudes (>3267 m), which limits dispersal to other suitable habitats. The MGRS and the Pinaleño (Graham) Mountains of south-eastern Arizona have been a centre of considerable controversy since the 1980s due to the ongoing construction of the Mount Graham International Observatory on one of the highest peaks in the range. In addition to the construction of the observatory in the squirrel's critical habitat, primary threats include habitat loss and disturbance due to human activities such as recreation, road construction, road use and historical unregulated timber harvesting practices. Other threats include insects and disease affecting the primary food sources, fire, weather, competition with introduced Abert's squirrels and the inherent risk of extinction due to small population size.

The US Fish and Wildlife Service added the squirrel to the federal list of endangered species in June 1987. A new recovery team formed in 2002 has the responsibility of outlining recovery criteria and evaluating management options. The team is responsible for identifying population sizes at which the squirrels should be considered recovered, so that they may be downlisted to threatened or removed from endangered species listing altogether. Management options under consideration include silviculture to reduce fire risk, strict controls over access to squirrel habitat, reduction of the introduced Abert's squirrel population and control of insects and tree diseases.

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In this paper we have applied PVA models to an examination of the MGRS as a case study in developing recovery criteria for a small, widely fluctuating population. We used two approaches to examine the extinction risk for the MGRS. Firstly, we analysed time-series of abundance estimates to quantify extinction risks over different time frames and applied these estimates to the development of population thresholds for endangered and threatened status (Gerber & DeMaster, 1999). Secondly, we developed Leslie matrix models of survival and fecundity estimates to identify the vital rates that are most critical to overall population growth (Caswell, 2001) and the relative efficacy of proposed management strategies.

METHODS

Our analyses rely on abundance data collected by the Arizona Game and Fish Department(AGFD), the US Fish and Wildlife Service and the USDA Forest Service (AGFD, unpublished results). MGRS abundance was measured indirectly by a biennial midden survey (Fig. 1). Since the squirrels are territorial and rarely share middens or occupy more than one midden at a time, active midden counts are thought to represent an accurate index of population size (Young, 1995). In the few cases where occupancy of a midden is not clear, the midden is counted in the optimistic survey but not in the conservative survey, thereby providing minimum and maximum estimates. Thus our analysis relies on four data sets: conservative and optimistic counts for both spring and autumn.

Estimating extinction risk from abundance data

We used the Dennis, Molholland & Scott (1991) diffusion approximation method to estimate the infinitesimal mean (μ) and variance (σ^2) of the growth rate, which then allowed us to evaluate probabilities for the future behaviour of stochastic populations. Together, these parameters allowed us to estimate a probability distribution that described the most likely range of future population sizes. This method assumes that the primary source of variation in the growth rate is environmental and does not incorporate density dependence or demographic stochasticity. Using the diffusion approximation method, we estimated μ and σ^2 for the autumn and spring surveys and used these estimates to examine the probability of extinction for both conservative and optimistic abundance estimates.

We assumed a current population size of 247 squirrels from the Autumn 2001 conservative estimate (AGFD, unpublished results). The calculation of an extinction risk required a quasi-extinction threshold (N_q), below which populations would not be expected to recover (Ginzburg *et al.*, 1982). The actual quasi-extinction threshold is not known for MGRS, so we explored the sensitivity of results to different assumptions about the size of N_q ($N_q = 50$, 100). With this information, we calculated distributions for the cumulative probability of extinction and the mean and median times to extinction for each scenario.

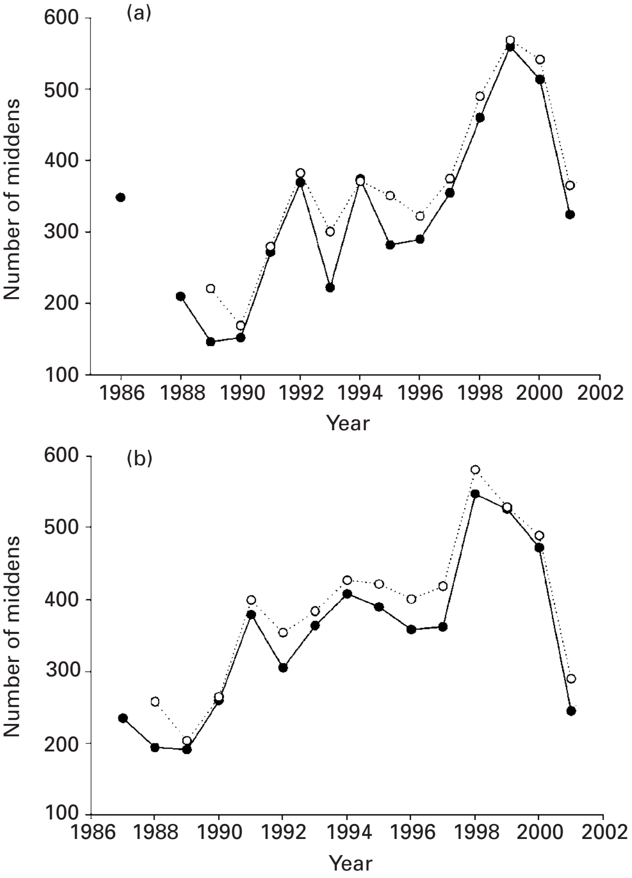

Fig. 1. Optimistic (· · · ○ · · ·) and conservative (–●–) midden count estimates of the Mount Graham red squirrel from the biannual midden survey for (a) spring and (b) autumn. One squirrel is assumed to occupy one midden at a time. If midden occupation was not clear it was counted in the optimistic but not in the conservative survey.

Developing Endangered Species Act classification criteria

We applied our analysis of extinction risk to the determination of squirrel's status as endangered or threatened and to the establishment of quantitative criteria for recovery and delisting. The method developed by Gerber & DeMaster (1999) allows us to use the growth rate estimates from our diffusion approximation modelling and to incorporate the sampling error that is inherent in the fluctuating population. This approach is based on a probability-driven model of population demographics, which establishes threshold levels for threatened and endangered status by projecting a growth rate back from N_q. We have defined the endangered threshold (N_{end}) as the population size at which the population has a 95% chance of remaining above N_q over a 10 year period. The threatened threshold (N_{th}) is the population size with a 95% chance of remaining above N_q for 35 years. These criteria are then used to determine the squirrel's categorical status under the Endangered Species Act (ESA). We have estimated that the 5th percentile of the λ distribution is the growth rate (corresponding to our stated 95% criterion) that will encompass the probable variation and produce conservative estimates. If the population model indicated a greater than 5% chance that the population would fall below the quasi-extinction level in the next 10 years, listing as endangered would be warranted. Similarly, a 5% chance of such a decline occurring over 35 years would result in listing as threatened. We performed these calculations for four subsets of census data autumn *versus* spring, conservative *versus* optimistic) in order to quantify the full range of plausible results.

To further examine the monitoring process and make recommendations for future data needs, we re-ran the model using progressively smaller subsamples of the census data (Gerber, DeMaster & Kareiva, 1999). We applied the previously described techniques to find the 5th percentile of λ from all subsets of data ranging from 7–15 consecutive years in length, as well as data from alternating years. For any given number of abundance estimates, ranging from 15 to 7, all sequential combinations of data were used. For example, there were 9 possible 7-year samples that could be taken from the 15-year dataset. Distributions of possible population growth rates resulting from each sample were subjected to the risk classification protocol described above.

Table 1. Estimates of demographic parameters for red squirrels

		Juvenile	Year 2	Year 3+
Low	Litter Size[1]	0	1.00	1.00
	% Breeding[1]	0	0.29	0.29
	Survival	0.21[2]	0.44[3]	0.39[4]
Average	Litter Size[1]	0	1.50	1.50
	% Breeding[1]	0	0.50	0.63
	Survival	0.33[4]	0.57[5]	0.73[3]
High	Litter Size[1]	2.00	2.00	2.00
	% Breeding	0.43[6]	0.63[1]	0.80[1]
	Survival	0.45[5]	0.66[4]	0.74[5]

Data are from either MGRS or other populations of *Tamiasciurus hudsonicus*. The product of litter size, % of females breeding and age-specific survival determines fecundity. Together fecundity and survival, as determined by these parameters, make up the Leslie matrix used to calculate growth rates and elasticities. Low to high years represent increasingly favourable conditions based on factors such as food quality and weather.
Sources: [1] Young. (1995); [2] Boutin & Larsen (1993); [3] Davis & Sealander (1971); [4] Kemp & Keith (1970); [5] Halvorson & Engeman (1983); [6] Boutin & Larsen (1998). Q2
MGRS, Mount Graham red squirrels.

Identifying optimal management actions

In addition to analysing extinction risks and listing status, we used Leslie matrix models (Caswell, 2001) to determine which aspects of life history would be most sensitive to management. Demographic data are sparse for MGRSs, so a range of data was compiled from studies of red squirrels on Mount Graham (Young 1995), in Montana (Halvorson & Engeman, 1983) and in Canada (Kemp & Keith 1970; Davis & Sealander, 1971; Boutin & Larsen, 1993; Larsen & Boutin, 1994; Becker, Boutin & Larsen, 1998: Table 1).

To encompass the uncertainty in vital rates for the MGRS, matrices were constructed using high, average and low estimates for survival, percentage breeding and litter size from the available data. A stage-classified matrix was used, with three classes: juvenile (in the autumn following their first summer), yearlings (born in the previous summer) and squirrels in their third or greater summer. Reproductive rates were estimated by multiplying litter size, percentage breeding and age-specific survival. Because juveniles are capable of reproducing, but are only likely to do so when food levels are very high, they were considered to be reproductive only in the high-estimate matrix. We then analyzed these matrices to obtain values of λ and generated elasticity matrices to illustrate the relative impact of changes in each parameter on λ.

RESULTS

Extinction risk from abundance data

Our time-series analysis yielded mean annual growth rates (λ) ranging from 1.04–1.10, signifying an increasing population. However, the 5th percentile values, which incorporate the variation in the growth rate, ranged from 0.921–0.963 (Table 2), which predicts up to an 8% Q1 annual decline. Values of lambda and their confidence intervals, as well as the mean and median times to extinction, are given in Table 3. The extinction risk Q1 metrics vary considerably and depend on which survey was used. The variance in growth rates for each survey leads to predictions of as low as 10 years up to 32 years for the median time at which these parameters lead to a quasi-extinction level of 100. Figure 2 shows the cumulative probability of extinction for spring and autumn conservative and optimistic population estimates.

Developing Endangered Species Act classification criteria

The 5th percentile values of λ ranged from 0.921 for the conservative autumn counts to 0.963 for the optimistic spring counts (Table 2). By the most pessimistic estimate (autumn conservative, which has the lowest growth rate), therefore, the squirrels have a 5% chance of decreasing by 8% annually. At this rate, a population of at least 227 squirrels would be necessary to expect, with 95% confidence, a population of > 100 within 10 years, thus defining the endangered threshold as 227. However, to expect such viability over 35 years with the same conditions would require 1761 squirrels (threatened status), which is nearly three times the highest abundance estimate, to data, of 560. By these criteria and assuming $N_q = 100$, we arrive at threatened status under all four datasets (Table 2).

Testing smaller subsets of data revealed the significance of the sharp decline in population from 1999 to 2001

Table 2. Fifth percentile λ values for each census and the associated threshold levels for classification as endangered and threatened under the criteria of Gerber & DeMaster (1999), where $N_q = 100$

Census	Estimate	$5^{th}\%$ λ	N	N_{end}	N_{th}	Classification
Spring	Conservative	0.925	326	217	1514	Threatened
	Optimistic	0.963	367	146	379	Threatened
Autumn	Conservative	0.921	247	227	1761	Threatened
	Optimistic	0.932	292	201	1156	Threatened

N_{end} represents the population level at which, if the population were to average the rate of decline indicated by the fifth percentile λ (5th% λ) value, it would reach 100 animals in 10 years. Nth is the population level at which the population would reach 100 in 35 years at the same rate of decline. Where N, the last abundance estimate, lies in reference to these thresholds determines the endangered species Act classification.

Table 3. Results of diffusion approximation analysis (Dennis *et al.*, 1991) for the estimation of extinction risk as applied to the four sets of abundance data for Mount Graham red squirrels

					Mean years to extinction		Median years to extinction	
Season	Estimate	μ	λ (90% CI)	σ^2	($N_q = 50$)	($N_q = 100$)	($N_q = 50$)	($N_q = 100$)
Spring	Conservative	0.0338	1.10 (0.95,1.23)	0.1270	55	34	30	15
	Optimistic	0.0422	1.08 (0.96, 1.31)	0.0719	47	30	34	20
Autumn	Conservative	0.0036	1.04 (0.92, 1.17)	0.0756	452	257	69	24
	Optimistic	0.0095	1.04 (0.93,1.16)	0.0601	185	112	73	32

The parameters μ and σ^2 summarise the annual transitions in abundance data and are used to calculate mean and median years to extinction thresholds of 50 or 100 years.
CI, confidence interval.

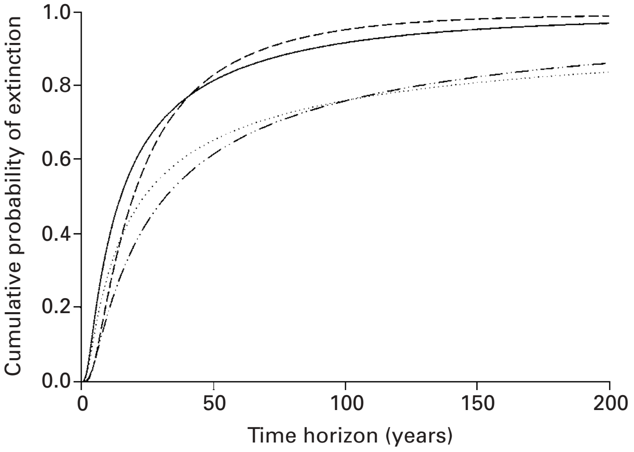

Fig. 2. Cumulative probability of extinction functions for Mount Graham red squirrels. Both optimistic surveys (counting questionable middens) and conservative surveys (not counting questionable middens) were conducted in both spring and autumn. Each provides a different estimate of extinction risk. —, spring conservative; · · ·, autumn conservative; - - - -, spring optimistic: —·—, autumn optimistic.

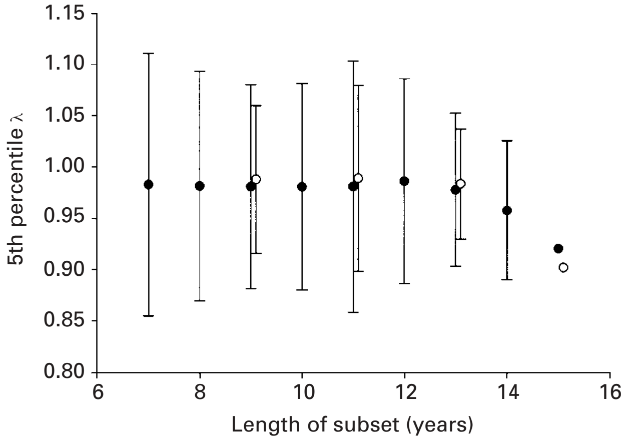

Fig. 3. Values of 5th percentile λ for all subsets of consecutive census data (autumn conservative estimates ranged from 7–15 years). Subsets using only alternate years were also considered for 9, 11 and 13 year intervals. Error bars represent 95% confidence intervals of the 5th percentile λ. ●, every year; ○, alternate years.

(Fig. 3). Mean values of λ were similar for sample subsets of 7–13 years, although the variation was considerable. Counts that did not include the sharp decrease from 1999 to 2001 underestimated the potential for decline that has now been realised. Thus, most shorter subsets are overly optimistic (Fig 4); those that include the decline will call for listing the squirrels as endangered, but the majority will advocate delisting. In contrast, inclusion of > 13 years tended to increasingly call for listing the squirrels as threatened. Longer monitoring periods are more likely to encompass periods of sharp increase or decline but also temper such drastic changes with intervals of moderate change. Subsets that only examined every other year of census data gave similar results, but with less variation (Fig. 3).

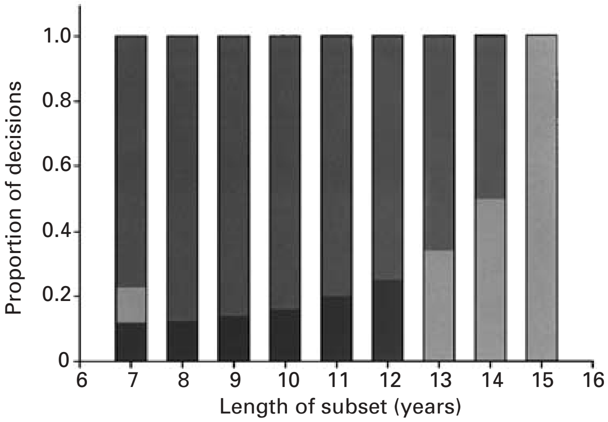

Fig. 4. Proportion of listing decisions made by subsets of census data ranging from 7–15 years, for the autumn conservative census. Sample size is 9 for the 7-year subsets, 8 for the 8-year subsets and so on, decreasing to 1 for the full 15 years of data. ■, endangered; □, threatened; ▨, delisted.

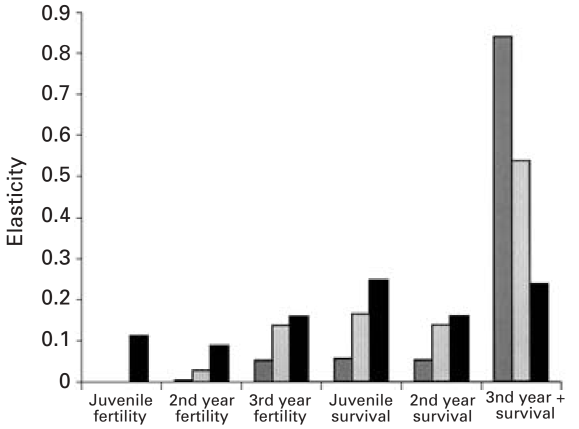

Fig. 5. Elasticity values of λ to changes in age-specific survival and reproduction values for all entries into the population projection matrix. □, low, ▨, average, ■, high.

Optimal management actions

Estimates of λ for low, average and high matrix models are 0.583, 0.916 and 1.230, respectively. The elasticity values obtained for MGRSs indicate that the population is far more sensitive to changes in survival rates (especially adult survival) than reproduction. In particular, our analyses suggest that survival of squirrels ≥ 3 years old was a critically important parameter in all matrices. Elasticity values were also high for juvenile survival in the high-estimate matrix (the only case where juveniles were assumed to reproduce: Fig. 5). This suggests that management should focus on the survival of older animals in order to have the maximum impact on the growth rate. For example, using the average matrix, a 20% increase in adult survival will increase λ by 12%. More data are needed in order to determine which factors (e.g. predation, habitat loss) affect the survival of squirrels in their 3rd year or older.

DISCUSSION

Our results suggest that the Mount Graham red squirrel (MGRS) should be listed as threatened under the Endangered Species Act (ESA). This result is consistent across the four available sets of midden survey data. Threatened status for the MGRS makes sense: overall, the population is not declining, but rather has increased throughout the monitoring period ($\lambda > 1$), even with the decline from 1999 to 2001. It is, however, a small population sensitive to catastrophic events that could quickly push the abundance below the minimum viable population level. The population also exhibits wide variation in annual growth rates, suggesting that one year of recovery from a previous decline does not guarantee future viability. While the abundance data does not suggest an immediate risk of extinction (i.e. endangered status), the repeated fluctuations suggest that the population is not viable and therefore merits ESA protection.

Analysis of data subsets reveals that the last years of data are necessary for listing the squirrels as threatened. The fraction of subsets that suggested threatened status (Fig. 4) are those that contain the 1999–2001 decline. If this recent decline is not included, then all such subsets of data suggest delisting as the optimal decision. The diffusion approximation model used in classifying the species is most effective when the environmental stochasticity affecting growth rates is small to moderate and that range of fluctuation is encompassed in the census data. This was not the case for the midden survey data prior to 1999, since the addition of more data points increased the variability considerably and changed our conclusions based on the model. Environmental stochasticity is likely to continue increasing in future years, as the impact of insects and disease and climate change affect the habitat both directly and through the increased risk of fire. As such, careful monitoring of the population and the continual integration of new data into the classification model is critical for assessing the species' status.

The goal of a recovery team is to increase or stabilise a population until it is no longer in danger of extinction in the near future. Our criteria suggests thresholds of 1514 (spring survey) and 1761 (autumn survey) for delisting. For a population that has not exceeded 580 individuals between 1986 and 2001 and is endemic to a habitat threatened by development, fire and insect infestations, this threshold may far exceed the carrying capacity for Mount Graham. Thus, the chance of delisting the squirrels may be low to zero, since the threshold we propose does not appear to be feasible.

The choice of N_q will affect this target number. It is generally difficult to identify a precise number for minimum viable populations. In our analysis, we assumed quasiextinction values of 50 and 100 based on rules of thumb suggested in the conservation biology literature (Frankel & Soulé, 1986) and empirical data from species with similar life histories. Our results are robust to uncertainty associated with N_q. For example, using conservative abundance estimates for both spring and autumn, N_q would have to be as low as 40 for the squirrels to be delisted. Forty is an unlikely choice for N_q, because at this small population size the squirrels would probably encounter additional problems of demographic stochasticity, skewed sex ratios and loss of genetic variation that would harm their chances for recovery. However, using the same criteria a quasiextinction level of 250 would be needed to classify the squirrels as endangered. Since they have recovered more than once from populations levels of less than 250, this value is unsuitable for a quasi-extinction threshold. Therefore, the uncertainty associated with the minimum viable population size would not affect listing decisions at this time, as long as N_q is between 40 and 250. Since the abundance changes from year to year, the range of N_q values for which the decision remains the same will shift, but will probably remain robust for the purpose of classification despite our lack of knowledge regarding the absolute minimum viable population size.

Our matrix analysis suggests that adult survival as well as the survival of reproducing juveniles are critical life history parameters. Therefore management options that focus on the survival of adult squirrels will be the most productive for managing a healthy population. Most management options being considered, such as silviculture to reduce fire threat and limit or prevent insect and disease spread, or the management of the exotic competitor Abert's squirrels, are aimed not at any particular life stage but at general preservation of habitat and protection of food sources. Steps have already been taken to minimise direct human-caused mortality from traffic, pets, or other impacts by restricting access to the primary habitat, although the telescope construction is still underway. If further steps can be taken to reduce adult mortality, in particular, such actions should be emphasised, on the basis of our analysis of the life history of red squirrels. In the absence of information on specific threats to adults and juveniles, managers should continue pursuing options to protect the habitat and food sources for the squirrels in general.

The quality of the monitoring data is central to our confidence in gauging extinction risk and making listing decisions. Explicit understanding of observation error and the reliability of the midden survey is necessary for establishing exactly how much the population is fluctuating. Optimistic and conservative estimates can provide widely different classification thresholds and while the 'right' answer probably lies somewhere in between, a narrowing of the range will greatly support listing decisions. Knowledge of the effects of small population size for this species will allow us to refine estimates of N_q, which is less important than survey reliability but will also support the classification process. The effects of different management options on adult survival may narrow the range of options to those that would have the greatest impact on the growth rate for the least effort expended. The risk and impact of fire and other catastrophic events, by their very nature, are difficult to quantify, but any analysis of these threats and measures to prevent catastrophe is important to the long-term survival of the Mount Graham red squirrel.

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REFERENCES

Becker, C. D., Boutin, S. & Larson, K. W. (1998). Constraints on first reproduction in North American red squirrels. *Oikos* **81**: 81–92.

Boutin, S. & Larson, K. W. (1993). Does food availability affect growth and survival of males and females differently in a promiscuous small mammal, *Tamiasciurus hudsonicus? J Anim Ecol* **62**: 364–370.

Boutin, S. & Larson, K. W. (1998). ***.

Caswell, H. (2001). *Matrix population models: construction, analysis, and interpretation*, 2nd edition. Sunderland, MA: Sinauer Associates.

Davis D. W. & Sealander, J. A. (1971). Sex ratio and age structure in two red squirrel populations in Northern Saskatchewan. *Can Field Nat* **85**: 303–308.

Dennis, B., Mulholland, P. L. & Scott, J. M. (1991). Estimation of growth and extinction parameters for endangered species. *Ecol Monogr* **61**: 115–143.

Frankel, O. H. & Soulé, M. E. (1981). *Conservation and evolution*. Cambridge: Cambridge University Press

Gerber, L. R. & DeMaster, D. P. (1999). A quantitative approach to Endangered Species Act classification of long-lived vertebrates: application to the North Pacific humpback whale. *Conserv Biol* **13**: 1203–1214.

Gerber, L. R., DeMaster, D. P. & Kareiva, P. M. (1999). Gray whales and the value of monitoring data in implementing the U.S. Endangered Species Act. *Conserv Biol* **13**: 1215–1219.

Ginzberg, L. R., Slobodkin, L. B., Johnson, K. & Bindman, A. G. (1982). Quasi-extinction probabilities as a measure of impact on population growth. *Risk Anal* **2**: 171–181.

Halvorson, C. H. & Engeman, R. M. (1983). Survival analysis for a red squirrel population. *J. Mammal* **64**: 332–336.

Kemp, G. A. & Keith, L. B. (1970). Dynamics and regulation of red squirrel (*Tamiasciurus hudsonicus*) populations. *Ecology* **51**: 763–779.

Larsen, K. W. & Boutin, S. (1994). Movements, survival and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. *Ecology* **75**: 214–223.

Young, P. S. (1995). Monitoring the Mt. Graham red squirrel. In *Storm over a desert mountain*: 226–246. Istock, C. A. & Hoffman, R. S. (Eds). Tucson: University of Arizona Press.