Nowhere to run and nowhere to hide: Response of endemic Mt. Graham red squirrels to catastrophic forest damage

John L. Koprowski [a,*], Marit I. Alanen [a,1], Ann M. Lynch [b]

[a] *Wildlife Conservation and Management, School of Natural Resources, University of Arizona, Tucson, AZ 85721, USA*
[b] *USDA Forest Service, Rocky Mountain Research Station, 2500 South Pine Knoll, Flagstaff, AZ 86001, USA*

Abstract

A consequence of isolation is increased susceptibility to catastrophe. Insect damage to fragmented and isolated forests has the potential to serve as a catastrophic force; such damage has increased worldwide due to climate change and fire suppression policies. We examined the response of endangered endemic Mt. Graham red squirrels to catastrophic insect damage due to moths, beetles, and introduced aphids. Insects changed the forest environment significantly for the endemic squirrel by reducing basal area and stem densities of live stems, while increasing number and basal area of standing dead stems. Availability of two major foods, fungi and tree seeds, declined in insect-damaged forests relative to trends in undamaged forests. Numbers of Mt. Graham red squirrels declined precipitously in insect-damaged forests suggesting a catastrophe. Conservation options are limited in such situations. Forest-insect induced catastrophes are likely to become more common in the near future as forest health declines due to past management tactics and climate change. Prudent conservation measures include the anticipation of insect outbreaks and effective forest treatments to decrease likelihood of such catastrophes to species of precarious conservation status, while avoiding abrupt changes to critical habitat.
© 2005 Elsevier Ltd. All rights reserved.

Keywords: Tamiasciurus; Bark beetle; Aphid; Forest health; Climate change; Catastrophe; Arizona

1. Introduction

A commonly suggested consequence of geographic isolation is susceptibility to stochastic events that directly increase probability of extinction for a local population (Lande, 1998; Alvarez, 2001); however, such cases are rarely documented (Mangel and Tier, 1994; Akcakaya and Baur, 1996). Phytopathogens and insect herbivores often drive large-scale changes in habitat that indirectly impact many species (Elkinton et al., 1996; Jones et al., 1998). Habitat loss or degradation commonly occurs in forests due to herbivorous insects and these impacts are predicted to increase with current trends in global climate change (Ayres and Lombardero, 2000). Severity of the impact of forest-insect outbreaks on mammal populations in particular is poorly documented (but see Jones et al., 1998) and likely a question of spatial scale. Large and vagile mammals may be able to avoid impacts through emigration or selective use of areas of reduced damage in relatively continuous or fine grained habitat, while other species may avoid local extinction due to their wide distribution relative to insect outbreaks (Potvin, 1980; Forbes and Theberge, 1993; Sturtevant et al., 1996; McKenney et al., 1998). Small mammals, especially those relegated to isolated habitat fragments, may be less able to cope with such catastrophic changes.

---

* Corresponding author. Tel.: +1 520 624 6439; fax: +1 520 740 0143.
  E-mail address: squirrel@ag.arizona.edu (J.L. Koprowski).
[1] Present Address: U.S. Fish and Wildlife Service, Tucson Ecological Services Office, 201 N. Bonita Ave., Suite 141, Tucson, AZ 85745, USA.

The Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) gained notoriety in association with development of an astrophysical complex within its restricted range (Istock and Hoffmann, 1994). These small-bodied tree squirrels (<250 g, Steele, 1998) are endemic to the high elevation coniferous forests (Stromberg and Patten, 1991) of a single montane isolate in the deserts of southeastern Arizona, USA. The subspecies is morphologically (US Fish and Wildlife Service, 1993), genetically (Sullivan and Yates, 1994), and vocally (Yamamoto et al., 2001) distinct. Red squirrels in coniferous forests are larder-hoarders that have great fidelity to a small territory (<2 ha) that surrounds their centralized cone stores (Steele, 1998). The two principal foods of red squirrels are conifer seeds and fungi (Steele, 1998). The Mt. Graham red squirrel was thought to be extinct in the 1960s (Minckley, 1968) but was subsequently rediscovered and listed as endangered, in part due to its isolation and dependence on relict conifer forest (US Fish and Wildlife Service, 1993). Perhaps as much as 11,000 ha of forest might be suitable (Hatten, 2000); however, only a small proportion of the suitable area is occupied by the <300 squirrels that remain (T. Snow, pers. comm.).

Beginning in 1996, the isolated forest inhabited by Mt. Graham red squirrels was changed through a series of insect outbreaks (USDA Forest Service, 2000, 2001, 2002). Intensive monitoring efforts of squirrels at sites in the high-elevation forests had collected data on stand composition, availability of the two principal foods (fungi and tree seeds), and squirrel abundance. Herein, we document decline of an endemic endangered species in areas with tree mortality induced by sequential insect outbreaks of a catastrophic nature.

2. Methods

2.1. Study area

An area of 252.5 ha of high elevation forests was monitored on peaks of the Pinaleño Mountains, Graham County, AZ USA. The study area includes lower elevation (<3050 m) mixed-conifer forest dominated by Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), corkbark fir (*Abies lasiocarpa* var. *arizonica*), and southwestern white pine (*P. strobiformis*), as well as spruce–fir forest (≥3050 m) composed of Engelmann spruce (*Picea engelmannii*) and corkbark fir. The spruce–fir forest study area (180.4 ha) was established on Emerald, Hawk, and High Peaks within the Mt. Graham red squirrel refugium to which human access is limited; the mixed-conifer forest study area (72.1 ha) is found in the vicinity of Columbine Visitor Center. Some researchers postulate that the spruce–fir forest is the most important of the two forest types (reviewed in Istock and Hoffmann, 1994). The study area

contains 17.8% of all known middens in mixed-conifer forest and 66.9% of middens in spruce–fir forest; thus our study investigates the response of forest and squirrels over a significant portion (34.0% of 1234 middens) of the entire range of endangered Mt. Graham red squirrels.

In 1996–1998, a Geometrid moth *Nepytia janetae* Rindge defoliated spruce and corkbark fir trees in high elevation forests surrounding Hawk Peak, High Peak, and Emerald Cienega (Lynch and Fitzgibbon, in press). Populations of two eruptive species of bark beetles developed rapidly in *N. janetae*-defoliated trees, spruce beetle (*Dendroctonus rufipennis* Kirby) in spruce, and western balsam bark beetle (*Dryocoetes confusus* Swaine) in corkbark fir. Bark beetle populations began developing in storm-damaged timber in 1993, a life-history pattern that is typical for these species (Furniss and Carolin, 1977), and then developed rapidly in the *N. janetae*-damaged areas. Spruce beetle outbreaks are notoriously rapid and cause severe damage, often killing the majority of available host trees ≥15 cm diameter breast height (DBH) over extensive areas. The *N. janetae* epizootic collapsed in 1999 (Lynch and Fitzgibbon, in press), but bark beetle outbreaks continued through 2002 (USDA Forest Service, 2002), and scattered individual trees continue to be attacked at present. Late in 1999, spruce aphid (*Elatobium abietinum* (Walker)), was detected in the Pinaleño Mountains (USDA Forest Service, 2000, 2001, 2002). This exotic is a needle phloem feeder that has had frequent outbreaks in Arizona since the late 1980s, causing mortality and decline of Engelmann spruce (Lynch, 2004).

2.2. Habitat characteristics and insect damage

In December 2000, we surveyed a circular plot of 10 m radius (0.0314 ha) surrounding all known red squirrel middens for evidence of spruce aphids and bark beetles (Schmid and Frye, 1977; Lynch, 2004). Presence or absence of aphids (characteristic defoliation or individuals sighted) and bark beetles (round borings with accumulation of frass or wood dust) were noted for each plot.

We used the same 10-m radius circular plot to characterize vegetation at midden sites in late summer and early autumn 1991 and 1994, prior to insect outbreaks in the spruce–fir forest. By 2001, insect damage was apparent throughout spruce–fir and mixed-conifer forest midden sites. We sampled middens sites again in summer 2001 to document changes associated with insect infestations. Initial vegetation measurements were conducted for other objectives (Smith and Mannan, 1994) and thus we were restricted to using these measures in the spruce–fir forests for comparative purposes and lacked such pre-treatment data for the mixed-conifer forest. We noted DBH and species for all live and dead stems ≥10 cm DBH and calculated basal areas. We

transformed data to meet assumptions of normality as necessary and analyzed data sets using Mann–Whitney U tests, t tests, sign tests, and linear regression.

2.3. Epigeous fungi production

We walked a 100-m transect oriented east to west or north to south every two weeks on 28 (19 spruce–fir, 9 mixed-conifer) randomly located plots; occasionally plots were damaged and a new random location was determined. Transects were traversed beginning with the first sighting of epigeous fungi (generally July) and continued until no epigeous fungi were collected (generally September). After tree seeds, fungi are the most important food item for red squirrels and may compose more than 50% of squirrel diets during some seasons (Layne, 1954; McKeever, 1964; Steele, 1998). We collected all epigeous fungi known to be consumed by red squirrels (Steele, 1998; Koprowski, unpublished data) within 0.5 m of transects (0.01 ha). We air dried fungi and calculated total dry biomass as the sum of the mass of all collections of fungi at each plot from July through September. We completed simple linear regressions using time as the predictive variable and total dry biomass of the individual sites as the dependent variable for mixed-conifer and spruce–fir forest plots.

2.4. Conifer seed production

Conifer seeds are the most important food item for red squirrels (Steele, 1998). We estimated seed production since 1993 from the same 28 (19 spruce–fir, 9 mixed-conifer) plots used for the epigeous fungi sampling. Three 0.25 m^2 wire screen seed traps were covered with hardware cloth to reduce pilferage and randomly placed within a 10 m × 10 m plot at each location. We collected seeds for a 12-month period in May of the following year. We separated and tallied conifer seeds contained in each trap by species. We calculated seedfall for each conifer species as the average number of seeds from the three traps on each plot. We completed simple linear regressions using time as the predictive variable and total number of seeds at each of the individual sites as the dependent variable for mixed-conifer and spruce–fir forest plots. An extremely large mast year occurred in 1995; we removed and reanalyzed these data without any changes in trends and typically a strengthening of model fit.

2.5. Squirrel abundance

We were only permitted to monitor endangered Mt. Graham red squirrels using observational methods during this study. We visited all middens within the study area during each quarterly census period (nearly monthly from 1989 until 1996 and quarterly thereafter)

to assess occupancy status (Young, 1994). We evaluated cone caches and feeding sign at middens to assess likelihood of territory occupancy by a resident. Researchers attempted to verify occupancy by sighting a resident red squirrel that was caching cones or defending its midden and visited several times during each quarterly census if necessary. New middens were added as discovered, whereas unoccupied middens were removed from regular census after 3 years without a resident; these middens were visited once each year to verify activity and again joined the regular census if occupied. As a result, we use proportion of middens occupied as our index of population trends.

3. Results

3.1. Vegetation changes and insect infestation

Forest character changed dramatically over the course of insect outbreaks. In December 2000, 99.2% of 238 middens surveyed in the spruce–fir forest had evidence of spruce aphid infestation. Spruce beetle (90.8%) and western balsam bark beetle (53.4%) also were found at most red squirrel middens. Middens in lower elevation mixed-conifer sites were infested by spruce aphid at similar frequency as upper elevation sites (94.1% of 119 middens: $\chi_1^2 = 0.21$, $p > 0.50$) but much less so by spruce beetle (2.5%: $\chi_1^2 = 100.66$, $p < 0.01$) and western balsam bark beetle (31.9%: $\chi_1^2 = 7.87$, $p < 0.05$).

Number of live trees (Fig. 1: $t_{70} = 4.91$, $p < 0.0001$) and basal area of live trees (Fig. 1: $t_{70} = 5.73$, $p < 0.0001$) decreased to 70.0% and 63.3% of pre-infestation, respectively, in the spruce–fir forest. Insect impact was found on each of the dominant tree species. Number of live spruce trees declined 34.7% ($t_{70} = 3.65$, $p < 0.0005$), in agreement with the 39.7% decline in number of corkbark fir trees ($t_{70} = 2.47$, $p < 0.02$). Similar declines occurred in basal area of spruce (33.7%, $t_{70} = 3.35$, $p < 0.002$) and corkbark fir (42.6%, $t_{70} = 2.92$, $p < 0.005$). Conversely, standing dead timber increased significantly at middens. Number of dead stems increased by 108.1% ($t_{70} = 4.77$, $p < 0.0001$) as did basal area of standing dead timber (127.0%, $t_{70} = 5.41$, $p < 0.0001$). Damaged Engelmann spruce trees take several years to die (Lynch, 2004), and additional mortality is expected.

3.2. Epigeous fungi crops

From 1994 until 2000, mean dry weight of epigeous fungi collected from plots in spruce–fir forest was always greater than that collected in mixed-conifer forest; however, mixed-conifer forest exceeded the mean production of spruce–fir forest for the first time in 2001 (one-tailed sign test, $n = 8$, $p < 0.05$). Primarily due to the high
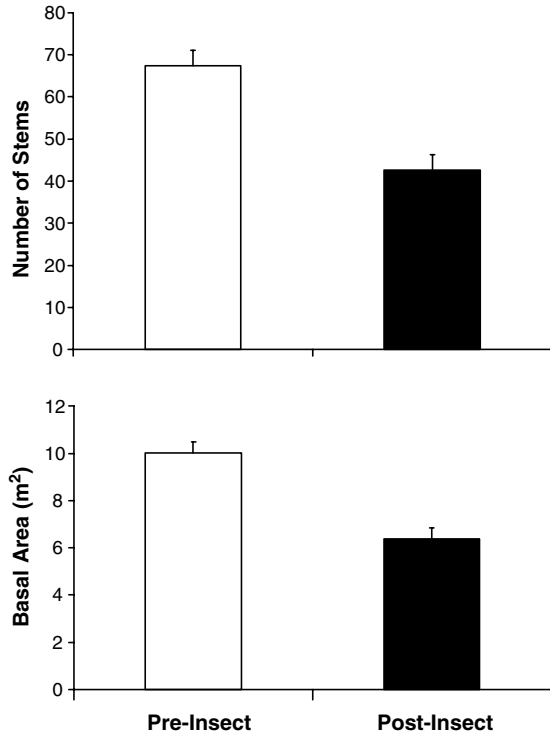
Fig. 1. Mean number and basal area of live tree stems before and after insect infestation in spruce–fir forest, Pinaleno Mountains, Arizona.
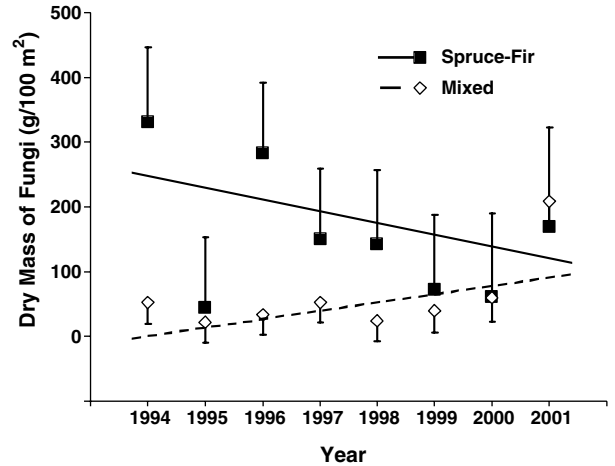

Fig. 2. Epigeous fungi crops in mixed-conifer and spruce–fir forest, Pinaleno Mountains, Arizona.

$F_{1,62} = 1.86$, $p = 0.18$, $R^2 = 0.029$; with 1995 removed: Corkbark fir seeds $= 137.06 - 10.03$ time, $F_{1,54} = 1.79$, $p = 0.19$, $R^2 = 0.033$), Douglas-fir (Douglas-fir seeds $= 70.06 - 4.41$ time, $F_{1,62} = 1.28$, $p = 0.26$, $R^2 = 0.020$; with 1995 removed: Douglas-fir seeds $= 73.09 - 4.77$ time, $F_{1,54} = 1.27$, $p < 0.27$, $R^2 = 0.023$), and Engelmann spruce (Fig. 3: Engelmann spruce seeds $= 88.96 - 8.71$ time, $F_{1,62} = 3.12$, $p = 0.082$, $R^2 = 0.048$; with 1995 removed: Engelmann spruce seeds $= 34.78 - 2.23$ time,

variation between plots, pairwise comparisons of mushroom biomass were not significantly different between spruce–fir and mixed-conifer forest during any year (all $t < 1.32$, $p > 0.20$). Reflective of the different temporal responses of fungi in damaged forests, the difference between mean dry fungal biomass of spruce–fir and mixed-conifer forest decreased in linear fashion from 1994 until 2001 (reduction in fungal Biomass $= 67545.2 - 0.00338$ time, $F_{1,67} = 4.45$, $p = 0.039$, $R^2 = 0.062$). While dry fungal biomass tended to increase from 1994 to 2001 in mixed-conifer forests (fungal biomass in mixed-conifer $= -22772.1 + 0.00114$ time, $F_{1,67} = 3.98$, $p = 0.05$, $R^2 = 0.056$), a similar increase in fungal biomass did not occur in spruce–fir forest (Fig. 2: fungal biomass in spruce–fir $= 44773.1 - 0.00223$ time, $F_{1,67} = 1.38$, $p = 0.25$, $R^2 = 0.02$).

3.3. Seed crops

Seeds of Engelmann spruce, corkbark fir and Douglas-fir (mixed-conifer forests only) were sufficiently common in seed traps to permit analyses of their abundance. Seed crops of each species were highly variable between years and sites; crops did not show a clear temporal relationship over the duration of insect infestation in low elevation mixed-conifer forests, although each showed a slight but non-significant negative relationship, including corkbark fir (Fig. 3: Corkbark fir seeds $= 131.92 - 9.42$ time,
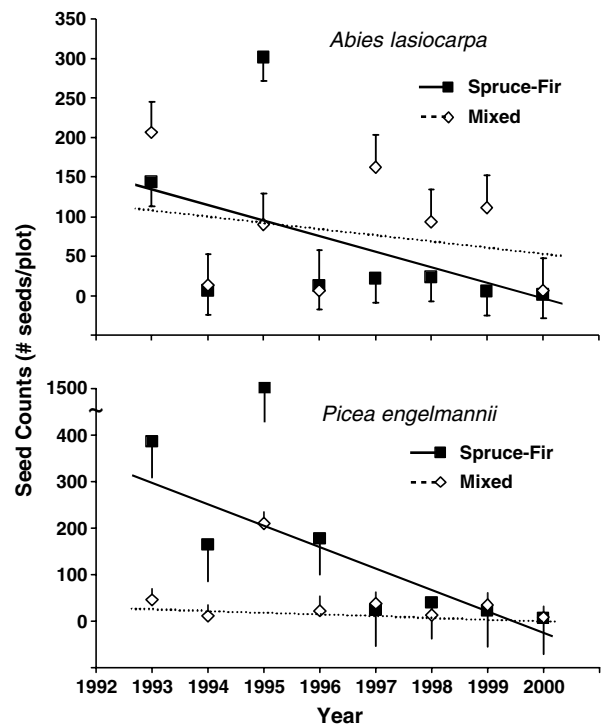

Fig. 3. Seed crops of corkbark fir (*Abies lasiocarpa* var. *arizonica*) and Engelmann spruce (*Picea engelmannii*) in mixed-conifer and spruce–fir forest, Pinaleno Mountains, Arizona. Simple linear regression lines reflect data with the extraordinarily high mast year of 1995 removed.
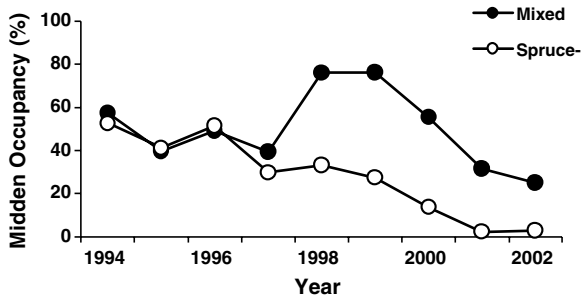
Fig. 4. Occupancy rates of middens by endangered Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) in mixed-conifer and insect-damaged spruce–fir forests, Pinaleno Mountains, Arizona.

$F_{1,54} = 1.15$, $p < 0.29$, $R^2 = 0.021$). In high elevation spruce–fir forests, however, a strong decrease was seen for corkbark fir (Fig. 3: Corkbark fir seeds $= 161.71 - 21.74$ time, $F_{1,94} = 13.53$, $p < 0.001$, $R^2 = 0.126$; with 1995 removed: Corkbark fir seeds $= 90.54 - 12.84$ time, $F_{1,83} = 10.35$, $p < 0.002$, $R^2 = 0.112$) and Engelmann spruce (Fig. 3: Engelmann spruce seeds $= 729.31 - 96.10$ time, $F_{1,94} = 17.61$, $p < 0.0001$, $R^2 = 0.158$; with 1995 removed: Engelmann spruce seeds $= 341.68 - 47.65$ time, $F_{1,83} = 49.77$, $p < 0.0001$, $R^2 = 0.378$).

3.4. Squirrel occupancy

Our mixed-conifer forest study area has supported 54–83 middens while spruce–fir forests contained 120–224 middens from 1994 until 2002. Occupancy of middens is variable, ranging from 2.5% to 76.2% (Fig. 4). The population trend on the low elevation mixed-conifer forests is stable over the 9 years reported here (midden occupancy $= 58.63 - 1.73$ time, $F_{1,8} = 0.51$, $p = 0.50$, $R^2 = 0.068$). In spruce–fir forests, however, midden occupancy exhibited a pronounced decline during the same period (midden occupancy $= 61.06 - 6.54$ time, $F_{1,8} = 66.57$, $p < 0.0001$, $R^2 = 0.905$). Spruce–fir forest was virtually unoccupied at the end of the study (Fig. 4), with only two occupied middens in 2002.

4. Discussion

The consequences of habitat loss for this endemic subspecies are not fully known. Numbers of squirrels have dropped precipitously in the highest elevation forests damaged by insects, whereas low elevation forests with less damage at present have maintained higher, although declining, occupancy rates. Spruce–fir forest has been considered to be the highest quality habitat for Mt. Graham red squirrels (United States Fish and Wildlife Service, 1993), which suggests that the severe degradation of this habitat is problematic for long-term persistence. Such a decline fits the definition of a cata-

strophic decline, one that results in recruitment failure and long-term population decline (Gerber and Hilborn, 2001). Catastrophic events in mammals are most often associated with disease, anthropogenic overharvest, or starvation due to harsh climatic conditions (Yuill, 1987; Deem et al., 2001). Herein, we document a case of a catastrophic decline associated with habitat degradation from insect outbreaks, faced by an exceptionally isolated mammal population.

The insect outbreaks in the Pinaleños severely damaged the mature forest, resulting in a more open forest with few and small trees to produce favored tree seeds, decreased cover from predators, and probably reduced microclimates for shaded midden storage of seeds and epigeous fungal growth (Smith and Mannan, 1994; Steele, 1998). Decreased food availability impacts a number of red squirrel life-history traits. Survivorship and prevalence of reproduction often decrease with food shortage (Gurnell, 1987; Steele, 1998). Territory size seems intimately related to food availability in red squirrels (Smith, 1968). Furthermore, red squirrels in poor body condition are more likely to be killed by predators (Wirsing et al., 2002). Unfortunately, we were not permitted to mark individuals of this endangered species to ascertain the proximate mechanisms of the decline.

Little research has addressed how squirrels respond to insect infestation. Delmarva fox squirrels (*Sciurus niger cinereus*) also declined in areas of bark beetle infestation (Willett, 2002). Red squirrel populations declined significantly in areas with >40% mortality of spruce trees due to beetle infestations in Alaska (Matsuoka et al., 2001) and Colorado (Yeager and Riordan, 1953). Importantly, red squirrels were not observed to completely disappear from areas with high levels of insect infestation and tree mortality, but rather were only reduced in number, persisting within the residual mosaic where conditions remained suitable (Yeager and Riordan, 1953; Matsuoka et al., 2001).

Abandoned cone caches often serve as food for red squirrels (Koprowski, pers. obs.) as could the diversity of insects that remain in insect-damaged forests immediately following outbreaks (Steele, 1998). Trees <11 cm DBH (usually, not <15 cm) are not killed by spruce beetle or western balsam bark beetle (Furniss and Carolin, 1977; Schmid and Frye, 1977; Dymerski et al., 2001) and serve as the canopy of the residual forest. Engelmann spruce can reproduce when 2 m in height (Alexander and Shepperd, 1990), and corkbark fir at 50 years (Alexander et al., 1984) thereby providing a food source for squirrels. However, cones from abandoned middens would not serve as food sources for such an extended time. The decline in seed production seen in spruce–fir plots in this study is undoubtedly due to loss of mature overstory. The residual stand is comprised of few, small trees, which produce low numbers of seeds in these age and size classes (Alexander et al., 1984; Alexander and

Shepperd, 1990). The ability of red squirrels to use remnant forest patches and persist throughout secondary succession is likely the result of their long evolutionary history of association with coniferous forests (Smith, 1970), which enables persistence through historical temporal and spatial patterns of natural disturbance.

Insect outbreaks are a natural occurrence in high elevation conifer forests and compare to catastrophic wildfire in their impact on ecosystems (Veblen et al., 1991). Catastrophic insect outbreaks and wildfires occurred previously in the Pinaleño ecosystem (Anderson and Shafer, 1991; Grissino-Mayer et al., 1995; Swetnam and Baisan, 1996a,b). However, contemporary changes to the scale and frequency of disturbance are of concern (Ayres and Lombardero, 2000; Logan et al., 2003). Forests of the region have been greatly modified by fire exclusion (Swetnam and Baisan, 1996a; Swetnam et al., 2001) and are severely degraded (Dahms and Geils, 1997). Indeed, much of the insect-damaged habitat burned in June and July 2004 during the Nuttall Complex fire that impacted about 11,800 ha (Koprowski et al., 2006). Furthermore, aggressive outbreaks of bark beetles result in dramatic changes in tree species composition and tree size distribution (Schmid and Hinds, 1974; Dymerski et al., 2001). In the Pinaleño Mountains, both predominant tree species in the high elevation spruce–fir forest incurred severe bark beetle outbreaks, and the forest was converted from a high-density, highly-stocked forest of large, mature trees to a low-density forest of pole-sized and smaller trees. Regeneration was abundant, although density and vigor of Engelmann spruce regeneration have been negatively affected by spruce aphid. The future of Engelmann spruce in southwestern United States forests is uncertain due to a steady decline in the presence of spruce aphids (Lynch, 2004) and unpredictable response to projected future temperature regimes (Rehfeldt, 2004). Clearly, the single habitat isolate of Mount Graham red squirrels has incurred multiple, severe insect outbreaks in a short period of time, including outbreaks of a recently introduced exotic. The squirrel may now face unprecedented conditions that could decrease the likelihood of population persistence.

Unusually large and severe outbreaks of several insects in western North American forests, including those describe here, appear to be associated with warmer than usual climate (Logan et al., 2003; Lynch, 2004; Lynch and Fitzgibbon, in press). Insect infestations are predicted to be more common with current trends in global climate change (Ayres and Lombardero, 2000; Logan et al., 2003) and their likelihood must be included in assessments of population viability and trajectory (Gerber and Hilborn, 2001). A dearth of knowledge on the cascade of ecosystem effects that result from such infestations (Leather and Owuor, 1996; Liebhold et al., 2000) must be overcome in order to most effectively anticipate, minimize, and combat further catastrophes.

What are the possible fates that await a species such as the Mt. Graham red squirrel that experiences catastrophic habitat disturbance but exists in disjunct, isolated populations? Persistence of a population can occur through rapid adaptation; however, stochastic events can rather easily offset this potential under most circumstances (Gomulkiewicz and Holt, 1995; Boulding and Hay, 2001). Demographic rescue through recolonization (Brown and Kodric-Brown, 1977) is possible for species with more than a single population; however, the Mt. Graham red squirrel is endemic to the only isolate in which damage has accrued. Persistence at extremely low numbers is a possibility but the demographic and genetic consequences of small populations in a changing environment are of concern (Boulding and Hay, 2001). The alternative is extinction. Active management strategies to reduce the risk of extinction of Mt. Graham red squirrels due to environmental catastrophes should include manipulation of habitat to increase available habitat and population size in the near and distant future. Strategies to meet challenges imposed by demographic catastrophes must also be considered to include the establishment of a captive breeding program. Persistence will likely require significant active management to maintain or achieve desired forest conditions that reduce risk of future catastrophes that impact habitat, while meeting the present ecological requirements of the small population of current residents.

Acknowledgments

References

Akcakaya, H.R., Baur, B., 1996. Effects of population subdivision and catastrophes on the persistence of a land snail metapopulation. Oecologia 105, 475–483.

Alexander, R.R., Shepperd, W.D., 1990. *Picea engelmannii* Parry ex Engelm. In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of

North America, Volume 1, Conifers. USDA Forest Service Agriculture Handbook 654. USDA Forest Service, Washington, pp. 187–203.

Alexander, R.R., Shearer, R.C., Shepperd, W.D., 1984. Silvical characteristics of subalpine fir. General Technical Report RM-115. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Alvarez, L.H.R., 2001. Does increased stochasticity speed up extinction? Journal of Mathematical Biology 43, 534–544.

Anderson, R.S., Shafer, D.S., 1991. Holocene biogeography of spruce–fir forests in southeastern Arizona – implications for the endangered Mt. Graham red squirrel. Madrono 38, 287–295.

Ayres, M.P., Lombardero, M.J., 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Science of the Total Environment 262, 263–286.

Boulding, E.G., Hay, T., 2001. Genetic and demographic parameters determining population persistence after a discrete change in the environment. Heredity 86, 313–324.

Brown, J.H., Kodric-Brown, A., 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58, 445–449.

Dahms, C.,W., Geils, B.W. (Eds)., 1997. An assessment of forest ecosystem health in the Southwest. General Technical Report RM-GTR-295. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Deem, S.L., Karesh, W.B., Weisman, W., 2001. Putting theory into practice: wildlife health in conservation. Conservation Biology 15, 1224–1233.

Dymerski, A.D., Anhold, J.A., Munson, A.S., 2001. Spruce beetle (*Dendroctonus rufipennis*) outbreak in Engelmann spruce (*Picea engelmannii*) in central Utah, 1986–1998. Western North American Naturalist 61, 19–24.

Elkinton, J.S., Healy, W.M., Buonaccorsi, J.P., Boettner, G.H., Hazzard, A.M., Smith, H.R., Liebhold, A.M., 1996. Interactions among gypsy moths, white-footed mice, and acorns. Ecology 77, 2332–2342.

Forbes, G.J., Theberge, J.B., 1993. Multiple landscape scales and winter distribution of moose, *Alces alces*, in a forest ecotone. Canadian Field-Naturalist 107, 201–207.

Furniss, R.L., Carolin, V.M., 1977. Western Forest Insects. USDA Forest Service, Miscellaneous Publication 1339, pp. 1–654.

Gerber, L.R., Hilborn, R., 2001. Catastrophic events and recovery from low densities in populations of otariids: implications for risk of extinction. Mammal Review 31, 131–150.

Gomulkiewicz, R., Holt, R.D., 1995. When does evolution by natural selection prevent extinction? Evolution 49, 201–207.

Grissino-Mayer, H.D., Baisan, C.H., Swetnam, T.W., 1995. Fire history in the Pinaleno Mountains of southern Arizona: Effects of human-related disturbances. In: Debano, L.F., Gottfried, G.J., Hamre, R.H., Edminster, C.B., Ffolliott, P.F., Ortega-Rubio, A. (Eds.), Biodiversity and Management of the Madrean Archipelago: The Sky Islands of Southwestern United States and Northwestern Mexico. General Technical Report RM-GTR-264, USDA Forest Service, Ft. Collins, pp. 399–407.

Gurnell, J., 1987. The Natural History of Squirrels. Facts on File, New York.

Hatten, J.R., 2000. A pattern recognition model for the Mount Graham red squirrel. Technical Report 160. Arizona Game and Fish Department, Phoenix, 32pp.

Istock, C.A., Hoffmann, R.S. (Eds.), 1994. Storm over a Mountain Island. University of Arizona Press, Tucson.

Jones, C.G., Ostfeld, R.S., Richard, M.P., Schauber, E.M., Wolff, J.O., 1998. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. Science 279, 1023–1026.

Koprowski, J.L., Leonard, K.M., Zugmeyer, C.A., Jolley, J.L., 2006. Direct effects of fire on endangered Mt. Graham red squirrels. Southwestern Naturalist, in press.

Lande, R., 1998. Anthropogenic, ecological and genetic factors in extinction and conservation. Researches on Population Ecology 40, 259–269.

Layne, J.N., 1954. The biology of the red squirrel, *Tamiasciurus hudsonicus loquax* (Bangs), in central New York. Ecological Monographs 24, 227–267.

Leather, S.R., Owuor, A., 1996. The influence of natural enemies and migration on spring populations of the green spruce aphid, *Elatobium abietinum* Walker (Hom, Aphididae). Journal of Applied Entomology 120, 529–536.

Liebhold, A., Elkinton, J., Williams, D., Muzika, R.M., 2000. What causes outbreaks of the gypsy moth in North America? Population Ecology 42, 257–266.

Logan, J.A., Régnière, J., Powell, J.A., 2003. Assessing the impacts of global warming on forest pest dynamics. Frontiers in Ecology and the Environment 1, 130–137.

Lynch, A.M., 2004. Fate and characteristics of *Picea* damaged by *Elatobium abietinum* (Walker) (Homoptera: Aphididae) in the White Mountains of Arizona. Western North American Naturalist 64, 7–17.

Lynch, A.M., Fitzgibbon, R.A., in press. Observations on the life history of *Nepytia janetae* in Arizona. Southwestern Entomologist.

Mangel, M., Tier, C., 1994. Four facts every conservation biologist should know about persistence. Ecology 75, 607–614.

Matsuoka, S.M., Handel, C.M., Ruthrauff, D.R., 2001. Densities of breeding birds and changes in vegetation in an Alaskan boreal forest following a massive disturbance by spruce beetles. Canadian Journal of Zoology 79, 1678–1690.

McKeever, S., 1964. Food habits of pine squirrel in northeastern California. Journal of Wildlife Management 28, 402–404.

McKenney, D.W., Rempel, R.S., Venier, L.A., Wang, Y.H., Bisset, A.R., 1998. Development and application of a spatially explicit moose population model. Canadian Journal of Zoology 76, 1922–1931.

Minckley, W.L., 1968. Possible extirpation of the spruce squirrel from the Pinaleño (Graham) Mountains, south-central Arizona. Journal of the Arizona Academy of Science 5, 110.

Potvin, F., 1980. Short term impact of a spruce budworm outbreak on a deer wintering area. Canadian Journal of Forest Research 10, 559–563.

Rehfeldt, G.E. 2004. Interspecific and intraspecific variation in *Picea engelmannii* and its congeneric cohorts: Biosystematics, genecology, and climate change. General Technical Report RMRS-GTR-134, USDA Forest Service, Fort Collins.

Schmid, J.M., Frye, R.H., 1977. Spruce beetle in the Rockies. General Technical Report RM-49, USDA Forest Service, Fort Collins, CO.

Schmid, J.M., Hinds, T.E., 1974. Development of spruce–fir stands following spruce beetle outbreaks. USDA Forest Service, Research Paper RM-131 USDA Forest Service, Fort Collins, CO.

Smith, C.C., 1968. The adaptive nature of social organization in the genus of tree squirrel *Tamiasciurus*. Ecological Monographs 38, 30–63.

Smith, C.C., 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecological Monographs 40, 349–371.

Smith, A.A., Mannan, R.W., 1994. Distinguishing characteristics of Mount Graham red squirrels midden sites. Journal of Wildlife Management 58, 437–445.

Steele, M.A., 1998. Tamiasciurus hudsonicus. Mammalian Species 586, 1–9.

Stromberg, J.C., Patten, D.T., 1991. Dynamics of the spruce–fir forests on the Pinaleno Mountains, Graham Co., Arizona. Southwestern Naturalist 36, 37–48.

Sturtevant, B.R., Bissonette, J.A., Long, J.N., 1996. Temporal and spatial dynamics of boreal forest structure in western Newfoundland: silvicultural implications for marten habitat management. Forest Ecology and Management 87, 13–25.

Sullivan, R.M., Yates, T.L., 1994. Population genetics and conservation biology of relict populations of red squirrels. In: Istock, C.A., Hoffmann, R.S. (Eds.), Storm over a Mountain Island. University of Arizona Press, Tucson, pp. 193–208.

Swetnam, T.W., Baisan, C.H., 1996a. Historical fire regime patterns in the Southwestern United States since AD 1700. In: Allen, C.D. (Ed.), Fire effects in Southwestern Forests: Proceedings of the Second La Mesa Fire Symposium. General Technical Report RM-GTR-286, USDA Forest Service, Ft. Collins, pp. 11–32.

Swetnam, T.W., Baisan, C.H., 1996b. Fire histories of montane forests in the Madrean Borderlands. In: Ffolliott, P.F., DeBano, L.F., Maker, Jr., M.B., Gottfried, G.J., Solis-Garza, G., Edminster, C.B., Neary, D.G., Allen, L.S., Hamre, R.H. (Eds.), Effects of Fire on Madrean Province Ecosystems: A Symposium Proceedings. General Technical Report RM-GTR-289. USDA Forest Service, Ft. Collins, pp. 15–36.

Swetnam, T.W., Baisan, C.H., Kaib, J.M., 2001. Forest fire histories of the sky islands of La Frontera. In: Webster, G.L., Bahre, C.J. (Eds.), Changing Plant Life of La Frontera: Observations on Vegetation in the United States/Mexico Borderlands. University of New Mexico Press, Albuquerque, pp. 95–123.

US Fish and Wildlife Service, 1993. Mount Graham red squirrel recovery plan. US Fish and Wildlife Service, Albuquerque, New Mexico.

USDA Forest Service, 2000. Forest insect and disease conditions in the Southwestern Region, 1999. US Department of Agriculture, Forest Service, R3-00-01.

USDA Forest Service, 2001. Forest insect and disease conditions in the Southwestern Region, 2000. US Department of Agriculture, Forest Service, R3-01-01.

USDA Forest Service, 2002. Forest insect and disease conditions in the Southwestern Region, 2000. US Department of Agriculture, Forest Service, R3-02-01.

Veblen, T.T., Hadley, K.S., Reid, M.S., Rebertus, A.J., 1991. The response of subalpine forest to spruce beetle outbreak in Colorado. Ecology 72, 213–231.

Willett, K., 2002. Population size and habitat use of the Delmarva fox squirrel (*Sciurus niger cinereus*) following an infestation of the southern pine beetle (*Dendroctonus frontalis*) at Chincoteague National Wildlife Refuge. M.S. Thesis. University of Maryland Eastern Shore, Princess Anne, MD.

Wirsing, A.J., Steury, T.D., Murray, D.L., 2002. Relationship between body condition and vulnerability to predation in red squirrels and snowshoe hares. Journal of Mammalogy 83, 707–715.

Yamamoto, O., Moore, B., Brand, L., 2001. Variation in the bark call of the red squirrel (*Tamiasciurus hudsonicus*). Western North American Naturalist 61, 395–402.

Yeager, L.E., Riordan, L.E., 1953. Effects of beetle-killed timber on range and wildlife in Colorado. Transactions of the North American Wildlife and Natural Resources Conference 18, 596–616.

Young, P.J., 1994. Monitoring the Mount Graham Red Squirrel. In: Istock, C.A., Hoffmann, R.S. (Eds.), Storm over a Mountain Island. University of Arizona Press, Tucson, pp. 227–246.

Yuill, T.M., 1987. Diseases as components of mammalian ecosystems: mayhem and subtlety. Canadian Journal of Zoology 65, 1061–1066.