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Population Ecology

Survival and Causes of Mortality in a Northern Population of Western Gray Squirrels

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ABSTRACT We studied survival of radio-marked western gray squirrels (*Sciurus griseus*) and quantified causes of mortality including incidence and severity of notoedric mange in south-central Washington, 1998–2005. We used known-fate models in Program MARK to explore alternative hypotheses on factors related to survival and correlation analysis to investigate parameters that might be related to incidence of mange. The best-supported models indicated that survival varied by year and by sex and that survival of males was lower during the breeding season compared to the non-breeding season. We found little support for differences in survival between juvenile (5–12 months old) and adult squirrels, or for winter severity or size of the acorn crop as significant influences on survival. We determined the likely proximate cause of death for 81 animals; 63% were killed by predators and 37% succumbed to disease, with most disease deaths attributed to mange. Mange was documented in the population during all years and occurred more frequently in animals captured in spring than in animals captured in fall. Counter to our predictions, occurrence of mange was not correlated with 2 measures of winter severity but was strongly correlated with mildness of the preceding winter (number of days with mean air temperature $\geq 0^\circ$ C). Sequential use of nests by individual squirrels during mild winters with temperatures conducive to survival of ephemeral, free-living mites may partially explain the periodic epizootics of notoedric mange in this western gray squirrel population. Continued deterioration of squirrel habitat through fragmentation will place additional stressors on the population and may compound the effects of mange on this threatened species. © 2013 The Wildlife Society.

KEY WORDS notoedric mange, predation, *Sciurus griseus*, survival, Washington State, western gray squirrels.

Western gray squirrels (*Sciurus griseus*) are the largest native tree squirrel in western North America. They occur in mixed oak-conifer habitats along the west coast from north central Washington State south to Baja California (Carraway and Verts 1994). Western gray squirrels are listed as threatened in Washington and as sensitive in parts of Oregon as a result of urbanization and other changes in land use that have reduced availability of quality habitat (Linders and Stinson 2007, Oregon Department of Fish and Wildlife 2008). Although assessment of population size has not been completed for these regions, management authorities are concerned that local populations are declining. Western gray squirrel populations in Washington occur at the northernmost extent of the species' range and therefore represent the current boundary of tolerance along 1 or more gradients (Caughley et al. 1988, Holt 2003). No published, empirical data on annual survival rates currently exist for this species.

Tree squirrels in general follow a pattern of survival typical of many mammals with low survival their first year followed by high survival through adulthood (Steele and Koprowski 2001). Gurnell (1987) reported annual survival rates of 0.50–0.70 as typical of adult tree squirrels and studies of *Sciurus* spp. in North America found survival ranging from 0.45 to 0.69 for adult fox squirrels (*S. niger*; Conner 2001, McCleery et al. 2008) and 0.46–0.58 for adult eastern gray squirrels (*S. carolinensis*; Mosby 1969, Barkalow et al. 1970, Thompson 1978). Survival of adults also may vary seasonally (Rusch and Reeder 1978, Wauters et al. 2008). Abert's squirrels (*S. aberti*), for example, had lower survival in winter than during other periods with seasonal estimates ranging from 0.63 in winter to 0.91 in late-spring and summer (Dodd et al. 2003). Although holoarctic tree squirrels live in environments that can be energetically demanding (Reynolds 1985) and depend to varying degrees on cyclic food sources like tree seeds (Gurnell 1983, Boutin et al. 2006), relationships between adult survival and weather variables (Steele and Koprowski 2001) or availability of food (Nixon et al. 1975, Gurnell 1996, Wauters et al. 2008) have received only weak support in the literature.

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Tree squirrels are known to experience outbreaks of mange, a sometimes fatal disease caused by species of burrowing, sarcoptid mite that remain with the host through successive generations (Sweatman 1971). The organism most frequently identified as causing mange in tree squirrels is *Notoedris centrifera* (Lavoipierre 1964, Cornish et al. 2001). Although the epidemiology of mange in tree squirrels has not been studied, previous research has suggested that mites may occur in healthy mammal populations, erupting periodically to manifest the disease when host animals undergo environmental stress (Lavoipierre 1964, Carlson et al. 1982). During these outbreaks, mite loads on individual squirrels increase, resulting in alopecia (hair loss), thickening of the skin, secondary bacterial and fungal infection, and crusting around the eyes, often resulting in emaciation and death (Sweatman 1971, Cornish et al. 2001). Severe outbreaks causing significant mortality have been documented in western gray squirrel populations in California (Bryant 1921, 1926; Ingles 1947) and in Washington (Cornish et al. 2001). From a wildlife conservation perspective, chronic diseases such as mange pose a potentially serious threat that may increase as resources become fragmented or more limited as a result of anthropogenic habitat loss or climate change (Scott 1988, Holmes 1996).

We studied the survival of western gray squirrels in south-central Washington, USA, from 1998 to 2005. Our study area was in the center of the largest of 3 geographically isolated populations of the species in the state (Linders and Stinson 2007). Our objectives were to estimate survival and determine causes of mortality in this population and to examine possible correlates of survival. We predicted that annual survival would be negatively associated with severity of winter weather and positively associated with size of a primary food resource. We also predicted that survival of juveniles would be lower than that of adults, survival of males would be similar to that of females, and incidence of mange in the squirrel population would be positively associated with severity of the preceding winter.

STUDY AREA

Our study population was located on the Klickitat Wildlife Area, a 5,260-ha state-managed conservation and recreation area in south-central Washington. The wildlife area is located on the eastern slope of the Cascade Mountains, with elevations ranging from 500 m to 600 m. The Cascade Range to the west and the Columbia River Gorge to the south provide for generally dry summers and mild winters with most precipitation falling as rain. Mean daily temperature in winter averaged 0.3° C and ranged from −3.7° C to 4.4° C for the period 1909–2011 (Western Regional Climate Center 2011). Mean daily temperature in summer averaged 18.3° C and ranged from 8.9° C to 27.8° C. Annual precipitation averaged 44 cm with most of that falling during winter. Annual snowfall averaged 65 cm and ranged from 0 cm to 176 cm.

Most of the study area was forested, with Oregon white oak (*Quercus garryana*) and ponderosa pine (*Pinus ponderosa*) dominant in the overstory. Douglas-fir (*Pseudotsuga menziesii*) was a significant component on north-facing slopes. The area occurred in the transition zone between eastside forest and shrub steppe communities, with forest stands and oak woodlands interspersed with open areas of bunchgrasses and forbs. Common understory species included buck brush (*Ceanothus* spp.), antelope bitterbrush (*Pershia tridentata*), and tall Oregon grape (*Mahonia aquifolium*).

METHODS

From 1998 to 2005, we captured western gray squirrels using box traps (Models 105 and 106, Tomahawk Live Traps, Hazelhurst, WI) baited with whole walnuts. We trapped squirrels primarily during spring and fall but also sporadically throughout the year when target-trapping individuals. Traps were set along lines through the study area (1998–1999; Linders et al. 2004) and on 2, 12 × 12 grids (80-m spacing) 1 km apart (2000–2005); we trapped grids for 8–10 consecutive days in spring (Apr–May) and fall (Sep–Oct; Vander Haegen et al. 2005). All animals were handled in accordance with guidelines developed by the American Society of Mammalogy (Sikes et al. 2011).

We handled animals using a cloth handling cone (Koprowski 2002) or with the aid of isoflorane anesthesia. We wore disposable gloves when handling animals and we laundered handling cones before trapping sessions and prior to reusing cones after handling individuals exhibiting mange. Because we handled animals infrequently ($\bar{x} = 1.6$ times/year, SE = 0.05, $n = 218$ individuals) and *Notoedres* mites survive only briefly when not on a host (Gordon et al. 1943), we believe our handling methods did not contribute to spread of mites among individuals. We examined this further by comparing handling frequency for animals known to contract mange with those that showed no indications of the disease.

At each capture, we obtained mass of the squirrel to the nearest gram using a spring-scale; assessed reproductive status by measuring or observing condition of testes, vulva, and teats; noted general physical condition including extent of alopecia related to mange; and attached numbered metal ear tags (No. 1005, National Band and Tag Co., Newport, KY). We classified the degree of mange infection as mild (≤10% of the body involved) or severe (>10% of body involved). In animals where mange infection was classified as mild, typically only the head or head and neck were involved; animals with severe cases frequently had alopecia over much of the torso and limbs. Most adult animals and juveniles of sufficient size (>600 g) were fitted with radio collars (Model SC-2, Holohil Systems, Inc., Carp, ON, Canada) that weighed 15 g and had a projected battery life of 18 months.

We tracked radio-collared animals via homing (White and Garrott 1990) 1–3×/week throughout the year and determined their status either visually or by monitoring the radio signal for indications of movement. During most telemetry locations, investigators attempted to see the animal; therefore, we generally documented kill sites within days of the incident. We inspected kill sites for indications of the predator, including tracks, scat, and white-wash or plucked hair that would indicate a raptor kill. We sent a sample of animals that we suspected to have succumbed to disease to the Washington Animal Disease Diagnostic Laboratory or to the Wyoming State Veterinary Laboratory for necropsy.

Analysis

We conducted survival analysis using known-fate models in Program MARK (Cooch and White 2011) and the associated program RMark in the R programming language (R Development Core Team 2011). We created encounter histories at monthly intervals for the biological years (1 Apr to 30 Mar) 1998–2004. Biological year encompassed the period when females were raising young and extended through the complete winter period, allowing our measures of winter severity to apply directly to this 12-month period. We excluded 2 animals that died within 10 days of release after initial collaring from the analysis to avoid possible inclusion of capture-related mortality. We right-censored radio-marked animals when we suspected failure of the transmitter ($n = 24$) or when the animal apparently slipped the collar (generally within a week of capture; $n = 10$). Right-censoring allows animals with indeterminate fates to remain in the dataset and contribute to survival estimates for the period they were successfully monitored. We classified animals captured in the summer or fall of their birth year as juveniles and recoded them as adults when they entered their first potential breeding season (Apr of the year following their birth). Western gray squirrel females can give birth as 1-year-olds and males are commonly scrotal in their first spring (Washington Department of Fish and Wildlife [WDFW], unpublished data).

We developed a set of candidate models to explore alternative hypotheses on factors related to western gray squirrel survival. This a priori model set included 1) single parameter models for year, season (breeding, Mar–Aug; non-breeding, Sep–Feb), sex, age (adult, juvenile), and weather variables; 2) 2-parameter models where age or sex was combined additively or as an interaction with temporal and weather variables (excluding age-season models because our juvenile age class was not present both periods); 3) 3-parameter models where age or sex were combined with measures of winter severity (see below); and 4) models that included winter severity measures from the previous year to test for delayed effects. In a second step, we used the top model set from the first analysis and added a parameter for size of the annual acorn crop to each model to test for an effect of a primary food source on survival. Data on acorn availability were available only for a subset of years (2000–2004); this 2-step approach allowed us to make maximum use of the survival dataset for the primary analysis and test for effects of acorn crop using a subset of the data.

We considered models differing by ≤ 2 Akaike's Information Criterion (AIC) units from the model with the lowest AIC as potential alternate models; we used model-averaging (Burnham and Anderson 2002) to estimate survival rates and 95% confidence intervals from this top model set. We used the delta method to derive estimates of variance for transformed seasonal survival rates and obtained confidence intervals by transforming the parameter estimates and their standard errors to the logit scale, calculating variance using the delta method, and back-transforming the interval end points. We estimated annual survival rates as the product of seasonal survival rates.

We generated weather variables from data obtained from the Western Regional Climate Center for the Goldendale weather station (No. 453222) located 14 km from the study area and at similar elevation (Western Regional Climate Center 2011). We considered 3 metrics of winter weather derived for the period November–March: 1) number of days with snow depth >10 cm; 2) total measurable precipitation (snow and rain); and 3) number of days with mean air temperature (T_{air}) $< 0^\circ$ C. Deep snow can restrict access to hypogeous fungi, seeds, and other terrestrial food sources and snow depths > 10 cm were reported as detrimental to survival for the ecologically-similar Abert's squirrel in Arizona (Stephenson and Brown 1980, Dodd et al. 2003). Winter precipitation increases the time spent in nests for squirrels in this population (WDFW, unpublished data), potentially increasing exposure to mites while limiting time to search for food. Tree squirrels in northern climates generally operate in T_{air} below their lower critical temperature resulting in increasing thermoregulatory costs as T_{air} declines (Reynolds 1985); conversely, warm temperatures may increase survivorship of sarcoptid mites in nests (Arlian 1989). Lacking published thresholds for T_{air} as an influence on squirrel energy needs or mite survival, we used the long-term mean for winter T_{air} on our study area.

Precisely what causes outbreaks of mange in wild mammal populations is not known; however, environmental conditions that affect the parasite and its host likely play a part (Scott 1988). We used correlation analysis to identify winter weather parameters that might be related to incidence and severity of mange in western gray squirrels. We compared the proportion of mange-infected squirrels captured in spring with weather parameters derived from the previous winter for years 1999–2005.

We used data from a regional assessment of Oregon white oak acorn production (Peter and Harrington 2009) as an index of mast availability for our study area. We collected data on acorn availability on our study site annually from 2002 to 2006 and these local data matched the annual pattern presented for the larger region (WDFW, unpublished data). Using the acorn index from the regional analysis allowed us to include an additional 2 years of data (2000–2001) in our modeling assessment.

RESULTS

We captured 220 individual western gray squirrels between 1998 and 2005. Many animals were captured multiple times, yielding 162 captures during spring and 223 captures during fall. We radio-marked 135 western gray squirrels (75 females and 60 males); we captured 96 as adults and 39 as juveniles. The oldest animal monitored in the radio-marked population was a female first captured as an adult in August 1998 that survived at least through September 2005 to the age of ≥ 8 years. In addition, 2 females also captured as adults survived to $\geq$5 years of age and 4 animals (3 females and 1 male) survived to $\geq$4 years of age.

Prevalence of Mange

We documented mange in the population during all years and it occurred more frequently in animals captured in spring than in animals captured in fall (likelihood ratio $X^2 = 28.5$, $P < 0.001$; Fig. 1). Occurrence of mange in spring-captured squirrels (Mar–May) ranged from 7% to 53% of individuals ($\bar{x} = 25.0\%$, SE = 5.7) among years; in fall (Sep–Nov), 0–31% of animals exhibited indications of mange ($\bar{x} = 8.0\%$, SE = 4.2). Severity of individual cases also varied seasonally, with 40% of spring cases rated severe and all cases in fall (excluding 1998) rated mild. Occasionally, we captured adult animals in the fall that exhibited indications of recovering from mange (i.e., distinct patches of new hair growth) and these animals were not included in mange statistics. A greater proportion of males examined in spring had mange (0.39, $n = 66$) compared to females (0.25, $n = 96$; likelihood ratio $X^2 = 3.76$, $P = 0.052$). Mange was particularly intense on the study area during fall 1998 through summer 1999 when 33 of 56 animals captured (59%) exhibited indications of mange. Excluding 1998, fall occurrence of mange reached a maximum of 9%, whereas spring occurrence was >10% in all years except 2001. Mites from infected animals were identified as *Notoedres centrifera* (Cornish et al. 2001).

We tracked the fate of 24 radio-marked animals documented to have mange in our spring captures. Survival of infected animals appeared related to degree of infection at time of capture; 9 of 14 animals with mild cases recovered fully and survived into the next calendar year, whereas only 3 of 10 animals with a severe case survived. Of the animals with severe cases, 3 were depredated and 4 were found intact but dead, apparently from complications of the disease. All 7 animals died within 1 month of capture and evaluation. Five animals captured with mild cases also were depredated, 3 within 1 month of evaluation and 2 within 5 months; none were found dead from disease.

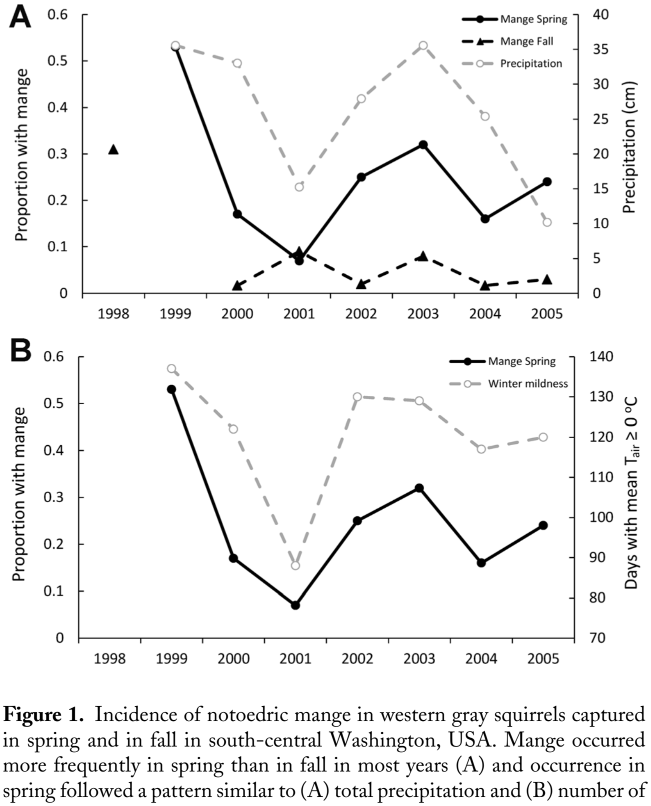

Figure 1. Incidence of notoedric mange in western gray squirrels captured in spring and in fall in south-central Washington, USA. Mange occurred more frequently in spring than in fall in most years (A) and occurrence in spring followed a pattern similar to (A) total precipitation and (B) number of days with mean air temperature (T_{air}) ≥ 0°C (a measure of winter mildness) during the preceding winter (Nov–Mar). Data on mange were unavailable for spring 1998 and fall 1999.

Prevalence of mange as a winter phenomenon was further indicated by the general lack of alopecia in animals evaluated in fall that were later determined to contract the disease. Of the 24 animals documented with mange in spring captures, 18 were captured and evaluated the preceding fall and only 1 exhibited indications of mange. In addition, 10 of 11 animals that were captured in the fall that died from mange prior to the subsequent spring trapping session exhibited no indications of mange in their fall evaluation. Fall weights of adult squirrels that showed no signs of mange in fall were similar for individuals that contracted the disease over the winter ($\bar{x} = 847.0$ g, SE = 16.5, $n = 22$) and for individuals captured in spring exhibiting no indications of mange ($\bar{x} = 868.9$ g, SE = 9.3, $n = 22$; $t_{42} = 1.16$, $P = 0.254$); however, animals contracting mange lost an average of 34.5 g (SE = 11.7, $n = 22$) in mass between fall and spring captures compared to only 1.4 g (SE = 13.7, $n = 17$) for health animals ($t_{37} = 1.88$, $P = 0.069$). Fall weights of animals used in these analyses were similar for males ($\bar{x} = 853.4$ g, SE = 14.7, $n = 18$) and for females ($\bar{x} = 861.0$ g, SE = 12.6, $n = 26$; $t_{42} = 0.39$, $P = 0.698$) so we combined sexes for these analyses. We also compared the number of captures for individuals used in the above analyses for the 12 months prior to our evaluation of their condition in spring to test for a potential relationship between capture frequency and contraction of the disease; mean number of captures for animals that contracted mange (2.05, SE = 0.21, $n = 22$) was slightly less than for individuals that did not (2.28, SE = 0.26, $n = 22$; $t_{42} = 1.09$, $P = 0.064$), suggesting no negative effect of capture frequency.

The relationships revealed between occurrence of mange in spring and weather the preceding winter ran counter to our predictions, with mange strongly but negatively correlated with number of days with $T_{\mathrm{air}} < 0°$ C ($r = -0.819$, $P = 0.024$, $n = 7$) and correlated weakly with both total precipitation ($r = 0.557$, $P = 0.194$, $n = 7$) and number of days with snow depth >10 cm ($r = -0.623$, $P = 0.135$, $n = 7$). The annual pattern of mange incidence in spring matched the pattern of T_{air} (number of days with $T_{\mathrm{air}} \geq 0°$ C, a measure of winter mildness) and precipitation the preceding winter (Fig. 1). Incidence of mange was not correlated with size of the acorn crop the preceding fall ($r = -0.074$, $P = 0.901$, $n = 5$).

Mortality Causes

We determined the likely proximate cause of death for 81 animals; 63% were killed by predators and 37% succumbed to disease. Most (77%) of the disease deaths were attributed to mange based on the condition of the body and from laboratory results for 9 animals sent for analysis where presence of *Notoedres* mites was confirmed and mange was identified as a likely contributor to the animals' death. Animals dying from mange were in generally poor condition, displaying significant loss of body mass, alopecia, and thickening of the skin and infected sores on the body. We often retrieved these animals from nests where they had died or from the base of trees beneath nests. Timing of mortality varied by cause, with loss to disease occurring primarily in winter and early spring (Nov–Apr) with few cases in late-spring through fall (May–Oct; Fisher's exact test $P = 0.0083$, $P = 0.017$, $n = 81$). Loss to predation exhibited no seasonal pattern (Fig. 2).

We could attribute most predation events to avian (25%) or mammalian (34%) predators based on sign at the kill site. In most of the remaining (41%) cases, we only found the collar and small amounts of blood or squirrel hair at the site. Mammalian predators of western gray squirrels in our study included bobcats (*Lynx rufus*; identified by tracks, scat, or caching of the kill) and coyotes (*Canis latrans*; identified by tracks or scat). Avian predators were difficult to identify from sign but likely included red-tailed hawks (*Buteo jamaicensis*) and northern goshawks (*Accipiter gentilis*), which we observed at kill sites. We also have witnessed barred owls (*Strix varia*) and great horned owls (*Bubo virginianus*) killing this species elsewhere in Washington (WDFW, unpublished data). One adult male was killed by collision with an automobile.

Survival Analysis

Two models were within 2 ΔAIC_c units of the top-ranked survival (S) model (Table 1); the 3 top models totaled 53% of the model weight and comprised what we considered to be the best-supported model set. Model S_{time} was the top-ranked model and indicated that survival of western gray squirrels varied annually (Fig. 3); 2 of the 3 top models contained the time parameter, providing additional evidence of annual variation in survival. Two of the top 3 models also

Table 1. Model selection results for survival (S) of western gray squirrels in south-central Washington, 1998–2004, showing second-order Akaike's Information Criterion (AIC_c), differences in AIC_c values from the top model (ΔAIC_c), model weight (w_i), number of parameters (K), and model deviance.

Model[a]	AIC_c	ΔAIC_c	w_i	K	Deviance
S(time)	651.2	0	0.212	7	344.5
S(sex + time)	651.3	0.096	0.202	8	342.6
S(sex × season)	652.4	1.172	0.118	4	351.7
S(age + time)	653.2	2.008	0.077	8	344.5
S(sex + season)	653.5	2.292	0.067	3	354.8
S(season)	654.2	2.951	0.048	2	357.5
S(sex + precip + temp)	655.2	3.986	0.029	4	354.5
S(sex + precip)	655.6	4.411	0.023	3	357.0
S(sex)	656.0	4.754	0.019	2	359.3
S(precip)	656.3	5.040	0.017	2	359.6
S(sex × precip)	656.3	5.064	0.016	4	355.6
S(null)	656.5	5.307	0.014	1	361.9
S(age × precip)	656.8	5.617	0.012	4	356.2
S(sex + snow)	656.9	5.712	0.012	3	358.3
S(sex + snow + temp)	656.9	5.716	0.012	4	356.3
S(snow)	657.5	6.239	0.009	2	360.8
S(sex + precipPY)	657.6	6.373	0.008	3	358.9
S(sex + tempPY)	657.7	6.454	0.008	3	359.0
S(sex + temp)	657.8	6.536	0.008	3	359.1
S(age + precip + temp)	657.8	6.602	0.007	4	357.1
S(sex + age)	658.0	6.749	0.007	3	359.3
S(tempPY)	658.1	6.892	0.006	2	361.5
S(precipPY)	658.2	6.943	0.006	2	361.5
S(age + precip)	658.3	7.047	0.006	3	359.6
S(temp)	658.3	7.068	0.006	2	361.6
S(sex × snow)	658.3	7.097	0.006	4	357.6
S(age)	658.5	7.306	0.005	2	361.9
S(age × snow)	658.8	7.576	0.004	4	358.1
S(sex × age)	658.9	7.638	0.004	4	358.2
S(age + snow + temp)	659.4	8.149	0.003	4	358.7
S(sex × temp)	659.4	8.221	0.003	4	358.8
S(age + snow)	659.5	8.242	0.003	3	360.8
S(age × temp)	659.7	8.494	0.003	4	359.0
S(age + temp)	660.3	9.065	0.002	3	361.6

[a] Time = biological year (Apr–Mar); sex = male or female; season = breeding or non-breeding; age = juvenile or adult; precip = total winter precipitation (Nov–Mar); temp = number of winter days with mean air temperature < 0°C; snow = number of winter days with >10 cm snow depth; precipPY = precip for the previous biological year; tempPY = temp for the previous biological year.

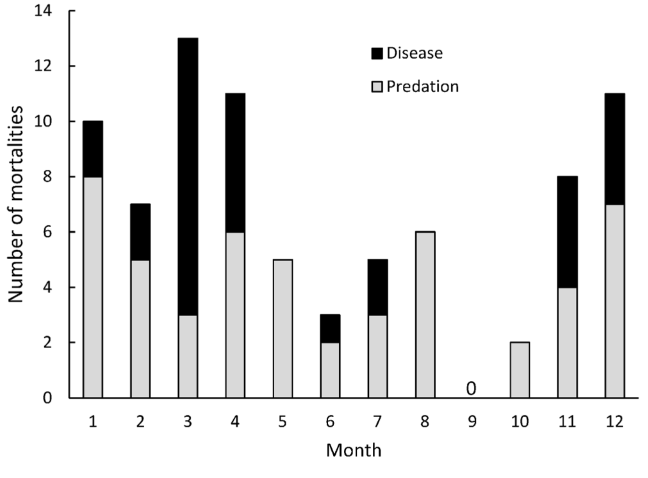

Figure 2. Timing of mortality from disease and predation for western gray squirrels in south-central Washington, USA, 1998–2004.

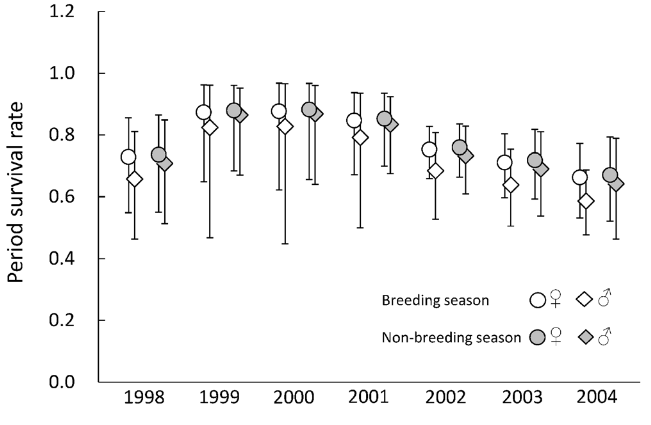

Figure 3. Period survival rates (6-month) for western gray squirrels during the breeding (Mar–Aug) and non-breeding (Sep–Feb) seasons based on model-averaged parameter estimates and their 95% confidence intervals (bars), south-central Washington, USA.

contained the parameter for sex, and examination of parameter estimates indicated lower survival for males compared to females (Fig. 3). The third-ranked model contained the interaction of sex and season, providing evidence for variation of survival within the year; specifically, lower survival of males during the breeding season (Fig. 3).

Four additional models were within 4 $\Delta\mathrm{AIC}_c$ units of the top-ranked model, but we discounted 3 of them for the following reasons. Model $\mathrm{S}_{(\mathrm{age+time})}$ differed from the top model by the addition of 1 parameter (age) and we found virtually no change in the log likelihood, indicating a spurious effect of the added variable (Burnham and Anderson 2002). The fourth- and fifth-ranked models both contained season, and the higher ranked model $\mathrm{S}_{(\mathrm{sex}\times\mathrm{season})}$ indicated an interaction with sex that was not accounted for in these 2 models. The seventh-ranked model included weather parameters (precipitation and T_{air}) along with sex; the β estimate for precipitation (0.091, SE = 0.043, 95% CI = 0.007–0.174) was positive with a confidence interval that did not include zero, suggesting a positive effect of winter precipitation on survival. The β estimate for T_{air} (0.031, SE = 0.020, 95% CI = −0.009–0.071) also was positive suggesting a positive effect of warmer temperatures on annual survival; however, a confidence interval that included zero indicated a weak effect for temperature. Overall, we found little evidence for weather having a significant effect on survival as models with weather parameters had relatively low weight (<0.03). We also found little evidence for an effect of acorn crop size on survival for the years 2000–2004; models containing the mast parameter all ranked lower than the same models without the parameter (Table 2).

Annual survival of female squirrels ($\bar{x} = 0.62$, SD = 0.13) was greater than that of males ($\bar{x} = 0.55$, SD = 0.14). Survival of females over the breeding season ranged from 0.66 to 0.88 among years and averaged 0.78 (SD = 0.09), whereas that of males ranged from 0.59 to 0.83 ($\bar{x} = 0.72$, SD = 0.10). Survival of females over the non-breeding season ranged from 0.67 to 0.88 ($\bar{x} = 0.79$, SD = 0.09) and was similar to that of males during this period ($\bar{x} = 0.76$, SD = 0.09, range 0.64–0.87). Models that included a parameter for age all ranked very low (Akaike weights < 0.08; Table 1), indicating that survival of juvenile squirrels from early fall through March of the following year was similar to that of adult squirrels. In a separate model including only the 39 squirrels marked as juveniles, survival through March when they entered the adult population was 0.62 (SE = 0.09) when calculated equivalent to a 12-month period.

Table 2. Ranking of top models for survival (*S*) of western gray squirrels in south-central Washington, 2000–2004, with and without a parameter for acorn availability (mast) showing second-order Akaike's Information Criterion (AIC_c), differences in AIC_c values from the top model ($\Delta\mathrm{AIC}_c$), model weight (w_i), number of parameters (*K*), and model deviance.

Model[a]	AIC_c	$\Delta\mathrm{AIC}_c$	w_i	*K*	Deviance
S(sex + time)	570.6	0	0.251	6	290.7
S(sex × season)	571.0	0.4288	0.203	4	295.1
S(time)	571.2	0.5329	0.192	5	293.2
S(sex × season + mast)	571.2	0.5600	0.190	5	293.2
S(sex + time + mast)	572.6	2.0201	0.091	7	290.7
S(time + mast)	573.2	2.5500	0.070	6	293.2

[a] Sex = male or female; time = biological year (Apr–Mar); season = breeding or non-breeding; mast = acorn abundance.

DISCUSSION

Our investigation of this threatened tree squirrel revealed relatively high annual survival rates and yet found patterns of mortality that may put it at further risk. Survival rates for western gray squirrels in south-central Washington were within the range presented by Gurnell (1987) as typical of adult tree squirrels and were greater than those for the Abert's squirrel in Arizona (Dodd et al. 2003, 2006), another large arboreal squirrel of western conifer forests and perhaps the most ecologically similar species to the western gray squirrel. Along with relatively high annual survival, we found persistent notoedric mange, a disease that caused mortality in all years and has the potential for catastrophic population declines (Bryant 1926). Our results also suggest a link between winter weather, nesting behavior, and outbreaks of mange in this population and that maintaining quality habitat may be the most effective way to reduce the likelihood of future epizootics.

We found no evidence for lower survival of juvenile western gray squirrels compared to adults. Juveniles entered our radio-marked sample in the fall at 5–8 months-old (spring litters vs. summer litters) and represented that portion of the annual cohort that had survived the post-weaning period, a time of relatively high mortality documented for several species of tree squirrel (Thompson 1978, Steele and Koprowski 2001, Kerr et al. 2007) and typical of young mammals in general (Caughley 1966). Western gray squirrels likely experience their lowest survival during this naïve period of learning, 2–4 months after emerging from their natal nest. In addition to the potential for increased predation, juvenile squirrels during late-spring and early summer are more susceptible than adults to food shortages (Koprowski 1991).

Female western gray squirrels are in estrus for only 1 day, requiring males to expand their daily movements and increase their energy expenditure during the breeding season to actively track the reproductive status of potential mates (Steele and Koprowski 2001). Males on our study area had larger home ranges than females and moved considerably longer distances that females during the breeding season (Linders et al. 2004), a pattern documented for other tree squirrels (Koford 1982, Edelman and Koprowski 2006, Pasch and Koprowski 2006). Extensive movements of male squirrels may have the dual effects of increasing the animals' exposure to predation and depleting stored energy reserves. Reduced body condition may explain the greater incidence of mange in spring-captured males in our study; these physical factors combined with intense activity and large movements typical of this period likely contributed to the lower survival of males during the breeding season.

Mange was a significant and annually-recurring mortality factor for western gray squirrels in this population. Anecdotal reports provide evidence of earlier epizootics in this species in south-central Washington during the 1930s and 1940s (Linders and Stinson 2007). High incidence of mange in fall 1998 through spring 1999 and high mortality of squirrels during this period (Cornish et al. 2001) identify this event as the most significant outbreak over the course of our 7-year study. Bryant (1921, 1926) documented what was likely a more severe epizootic in western gray squirrel populations in California, with significant mortality. Five years after this mange outbreak in California, squirrel numbers had not recovered in the Yosemite Valley where they previously were abundant (Bryant 1926). Population estimates on our study site suggest that squirrel numbers were increasing following the 1998–1999 epizootic only to decline again after a second, smaller peak of mange occurrence in 2003 (Vander Haegen et al. 2005). Western gray squirrels recovered from this event and were once again abundant on the Klickitat Wildlife Area in the fall of 2009 (WDFW, unpublished data).

Predation and disease both influence abundance of squirrel populations, but their relative importance (Steele and Koprowski 2001) and degree of interaction (Scott 1988) is unknown. Allen (1942) reported mange as the most influential agent of natural mortality during his 2-year study of fox squirrels in Michigan, with significant mortality and a propensity for occurrence in winter. Predation was the greatest cause of mortality most years in our study, with similar losses to avian and mammalian predators. Complicating any analysis of this type is the fact that the ultimate cause of death for animals retrieved from the field does not necessarily reflect all contributing factors; parasites and disease may increase susceptibility of the host to predation (Errington 1933, Scott 1988). Most animals captured with mange in our spring trapping and ultimately killed by predators were depredated within 1 month of capture when the animals likely still had the disease. Scabbing around the eyes, emaciation, and secondary bacterial infections concurrent with mange lead to debilitation (Sweatman 1971) and likely compromise the animals' vigilance and its ability to detect and evade predators (Errington 1933, Cornish et al. 2001).

Susceptibility of a population to infection by parasites is a function of density of infective life-stages in the environment, rate of contact between potential hosts and infective stages, and susceptibility of the host once contact is made (Scott 1988). What causes mite numbers to increase to the point where the mange disease is manifested on individual animals is unclear, but likely is related to the host's ability to mount an effective immune response (Scott 1988). Individuals suffering from poor nutrition or stress may be more susceptible to parasite infection (Lavoipierre 1964, Carlson et al. 1982, Scott 1988). The propensity for mange to occur in winter and spring suggests that winter severity might be a contributing factor (Allen 1942, Scott 1988); however, we found no evidence for this in our study. To the contrary, winters with milder temperatures and with more precipitation were correlated with increased incidence of mange in Washington. We also found no correlation between intensity of mange in spring and size of acorn crops the preceding fall, although acorns are only 1 of several fall-winter foods for this population and a more complete test would include assessment of pine and fir seed crops. Although physical stress in squirrel populations may be a trigger for the disease, environmental conditions that benefit survival and spread of mites are likely strong contributing factors.

Mites can be passed from host to host by direct contact of infected and uninfected animals or indirectly via nest material that harbors adult or immature mites (Sweatman 1971). Gordon et al. (1943) studied the development of notoedric mange in captive rats (*Rattus norvegicus*) and concluded that the motile, immature life stages (larvae and nymphs) were more effective at transferring among hosts than the adult forms. Greater host densities lead to greater transmission rates of parasites (Scott 1988, Altizer et al. 2003); however, western gray squirrels in our study population had the largest home ranges reported for the species (Linders et al. 2004) suggesting that densities were not unusually high. Direct contact among hosts may be facilitated by communal nesting, but this also was minimal in our study population. Whereas adult eastern gray squirrels frequently share nests (Steele and Koprowski 2001), western gray squirrels are largely solitary with the exception of females rearing young. We found that synchronous sharing of nests among western gray squirrels was uncommon and exclusively a winter phenomenon (Linders 2000; WDFW, unpublished data). Occasional nest-sharing during winter would facilitate spread of mange during this season, but the rarity of this behavior suggests a minor role in causing epizootics.

Western gray squirrels build multiple nests in their territories and individual nests may be used sequentially by several squirrels (Linders 2000). Asynchronous nest-use by individual squirrels likely contributes to spread of mites, and this in turn may be facilitated by winter weather. Our telemetry studies revealed that squirrels in winter spent more time in nests during wet weather (WDFW, unpublished data), a behavior that likely increased their contact with infective stages of the mite. Potential for nests to be primary vectors of mite transfer is suggested by a study of white-footed mice (*Peromyscus leucopus*) where infestations of *Notoedres* spp. in a captive population cleared when bedding was changed regularly (Telford 1998). Mites are sensitive to environmental conditions of temperature and relative humidity and likely survive off the host for only a few days (Arlian 1989); Gordon et al. (1943) reported that free-living *Notoedres* larvae survived <48 hours on a host. Survival and infestive behavior of *Sarcoptes* spp. mites while off the host were found to be temperature dependent; some adult female mites held at cold temperatures (−25° C) for 1 hour died and survivors were not infestive when introduced to hosts, whereas all females held at more moderate temperatures (10–25° C) survived and successfully burrowed into hosts (Arlian 1989). If free-living *Notoedres* mites (particularly the immature stages) also are sensitive to cold temperatures, milder winters may increase their survival in squirrel nests;

winters with more precipitation may put squirrels in contact with infective mites for longer periods.

MANAGEMENT IMPLICATIONS

Our results suggest that *Notoedres* mites are endemic in this western gray squirrel population with disease cycling facilitated by suitable environmental conditions in some years. Sequential use of nests by individual squirrels during mild winters with temperatures conducive to survival of ephemeral, free-living mites may partially explain the periodic epizootics of notoedric mange in this western gray squirrel population. The most effective strategy for managers for limiting future epizootics may be to maintain quality habitat and thereby reduce environmental stressors that may be triggers for the disease. Shrinking habitat availability can not only elevate environmental stress, but can increase host densities and result in greater transmission rates of parasites and greater individual parasite loads (Scott 1988, Altizer et al. 2003). Continued deterioration of suitable habitat will place additional stressors on western gray squirrel populations and may compound the effects of mange on this threatened species.

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