



Research Article

Endemic Diseases Affect Population Dynamics of Tree Squirrels in Contrasting Landscapes

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ABSTRACT Habitat loss and fragmentation can have detrimental effects on wildlife populations and where pervasive can create population isolates that may experience reduced genetic diversity and lower persistence. Diseases that cause epizootics also can reduce wildlife populations and may have disproportionate effects on small populations. We studied survival of radio-marked western gray squirrels (*Sciurus griseus*) using known-fate models in Program MARK and we quantified annual reproductive success by following females through the breeding season and counting young at natal nests. We used data on survival and productivity to model population growth rate and associated parameters using deterministic and stochastic approaches. Populations of western gray squirrels that we studied in an extensive, forested landscape and in a highly fragmented, urbanizing landscape in Washington, USA differed in their modeled growth rate. Adult survival was similar between populations although both were strongly affected by different endemic diseases with high epizootic potential. The demographic parameters that differed most between these 2 populations were related to productivity; litter size was marginally smaller and reproductive success was significantly lower in the urbanizing Puget Trough compared to rural Klickitat County. Results of our demographic modeling suggest that the larger Klickitat population is robust to immediate threats, whereas the smaller Puget Trough population is at risk because of its small size and low fecundity. Periodic outbreaks of notoedric mange in the Klickitat population reduce adult survival, although our models suggest that these epizootics would need to occur more frequently than observed to be of significant risk to the population. Continued degradation and fragmentation of western gray squirrel habitat in the Klickitat region along with mild winters resulting from climate change could increase the frequency and severity of mange epizootics and further threaten this population. Actions to retain and improve habitat resources may help ameliorate the effects of future mange epizootics and maintaining quality habitat should be a management priority in this region. The insular Puget Trough population experienced mortality due to tularemia each year of our study with infection rates $\geq 14\%$. Lack of characteristic histological indications in some affected squirrels may lead to underreporting of tularemia in animals submitted for routine necropsy and could complicate assessment of mortality risks in wildlife population studies. Given its small size and isolation, the Puget Trough population should be monitored closely for indications of decline in number or occupancy; this small population may need periodic augmentation to maintain genetic diversity. Increasing suitable habitat and maintaining connectivity between currently occupied range and potential habitat in the surrounding landscape will be crucial to the long-term viability of this population but will be challenging in the urbanizing landscape of the Puget Trough. © 2017 The Wildlife Society.

KEY WORDS landscape, notoedric mange, productivity, *Sciurus griseus*, survival, tularemia, western gray squirrel, Washington State.

Fragmentation of ecological systems by anthropogenic land conversion is one of the most pervasive factors affecting wildlife populations worldwide (Fahrig 2003, Fischer and Lindenmayer 2007). Loss of habitat causes population

declines (Fahrig 2003) and isolation of remaining patches can lead to reduced genetic diversity and loss of demographic function that can further exacerbate declines in small populations (Gilpin and Soule 1986, Montgelard et al. 2014). Small and meso-sized mammals may live in spatially structured populations occupying discrete patches of suitable habitat with dispersing animals forming connections that maintain genetic flow and allow for rescue of declining populations (Levins 1969, Hanski 1991, Fronhofer et al. 2012); fragmentation can disrupt these connections and in

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extreme cases may create population isolates (Bolger et al. 1997). Such insular populations, whether natural or the result of anthropogenic habitat loss, are more likely to have reduced genetic diversity (Frankham 1998) and can have reduced productivity, adult survival, and persistence (Bolger et al. 1997, Rushton et al. 2006, Goldstein et al. 2017). Identifying the status of insular populations and the factors impinging on their growth and survival is central to establishing conservation actions to increase their likelihood of persistence.

The largest native tree squirrel in western North America, western gray squirrels (*Sciurus griseus*) occur along the west coast of the United States from Baja California to Washington State (Carraway and Verts 1994). Their range is limited to pine (*Pinus* spp.) and oak (*Quercus* spp.) forests and woodlands of the West Coast Mountains and adjacent foothills. Their somewhat limited range is a characteristic shared with other native sciurids in western North America such as the Abert's squirrel (*Sciurus aberti*; Nash and Seaman 1977) and Mexican fox squirrel (*Sciurus nayaritensis*; Best 1995) and contrasts with the expansive ranges of the eastern gray squirrel (*Sciurus carolinensis*; Koprowski 1994a) and fox squirrel (*Sciurus niger*; Koprowski 1994b) of eastern North America (Steele and Koprowski 2001). Although eastern gray squirrels and fox squirrels have exhibited tolerance to anthropogenic land use and have established populations in urbanizing environments (Steele and Koprowski 2001), western gray squirrels have proven less adaptable and contract their range as forests are replaced by urban and suburban development (Rodrick 1986, King 2004, Linders and Stinson 2007, Cooper and Muchlinski 2015). The range of western gray squirrels in Washington has contracted largely as a result of land use changes; the species is listed as threatened in Washington and a recovery plan has been implemented (Linders and Stinson 2007, Vander Haegen et al. 2007).

Diseases that cause epizootics also can reduce wildlife populations and may extirpate or depress populations for decades (Daszak et al. 2000, Skerratt et al. 2007). Perhaps the most prevalent disease documented to cause population declines in tree squirrels is mange (Bryant 1921, Ingles 1947, Cornish et al. 2001, Steele and Koprowski 2001). Mange is caused by species of burrowing, sarcoptid mites that remain with the host through successive generations (Sweatman 1971). High mortality rates of western gray squirrels in Klickitat County, Washington, attributed to mange in 1998–1999 (Cornish et al. 2001) likely constituted an epizootic where 53% of adult squirrels captured in spring were infested (Vander Haegen et al. 2013); anecdotal reports provide evidence of an earlier epizootic in south-central Washington during the 1930s (Rodrick 1986, Linders and Stinson 2007). Although factors important to the epidemiology of the disease in tree squirrels are not known, Vander Haegen et al. (2013) reported a correlation between incidence of mange and mild winter temperatures that may promote survival of mites. Others have hypothesized that epizootics result from changes in the susceptibility of the host population, either through environmental stress leading to weakened individu-

als (Lavoipierre 1964, Carlson et al. 1982, Cornish et al. 2001) or through changes in virulence of the mite population (Pence et al. 1983, Soulsbury et al. 2007).

Rodents are highly susceptible to infection with tularemia and tree squirrels can be locally important hosts for the disease (Friend 2006). Caused by an infectious bacteria (*Francisella tularensis*), tularemia can cause epizootics resulting in high rates of mortality in rodent and lagomorph populations (Friend 2006). Species with high susceptibility and high sensitivity to tularemia (e.g., lagomorphs) may die within 2–10 days of infection and exhibit few clinical indications (Morner and Addison 2008). Rodents in general are susceptible to tularemia, but not highly sensitive, allowing the disease to progress for a longer period resulting in development of characteristic lesions and necrosis in the lymph nodes, liver, and spleen (Friend 2006, Morner and Addison 2008). From a wildlife conservation perspective, chronic diseases such as mange and tularemia 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 population dynamics of western gray squirrels in 2 contrasting landscapes in Washington State, USA: Klickitat County (1998–2005) in the southern Cascade Mountains, where forests and woodlands are extensive and the primary land use is commercial timberland; and the southern Puget Trough (2007–2012) where urbanization is rampant and suitable habitat persists mainly on a 348-km² military base. Our goals were to measure vital rates and model population growth for each of these populations, and evaluate factors influencing population growth or decline. We predicted that the population in the highly fragmented Puget Trough would have lower persistence because of small population size, isolation, and potentially lower genetic diversity. We also predicted that the larger Klickitat population would have high persistence but that periodic epizootics of mange would put that population at risk.

STUDY AREA

At the northern terminus of the species' range in Washington State the western gray squirrel occurs primarily along the eastern slope of the Cascade Mountains with discrete populations at the northern and southern extents and tenuous connection between (Fig. 1). A third, isolated population occurs on the west side of the Cascades in the southern Puget Trough. Estimates of historical range for the species in Washington are based largely on suitable habitat (Linders and Stinson 2007) and there are no occurrence records that would connect the Puget Trough population to either Cascade population (Wildlife System Data Management database, Washington Department of Fish and Wildlife [WDFW], Olympia, WA, USA), suggesting that the Puget Trough population has been isolated since at least the late 1800s.

Our southern study population was located on the Klickitat Wildlife Area, a 5,260-ha state-managed conservation and

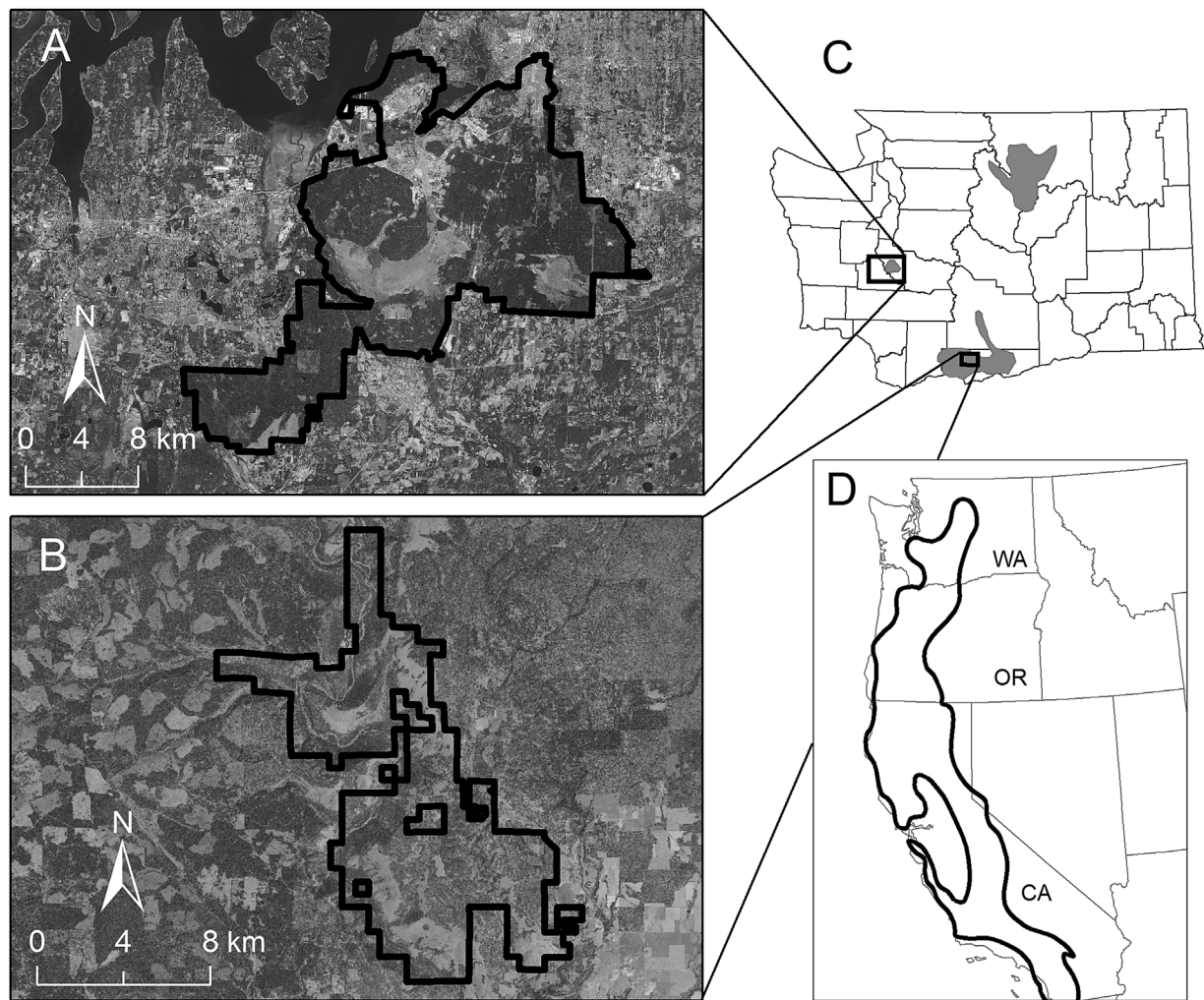


Figure 1. Study areas for research on the western gray squirrel in Washington, USA: (A) Joint Base Lewis-McChord (black polygon) in the urbanizing landscape of the south Puget Trough, and (B) Klickitat Wildlife Area (black polygon) in the industrial forest landscape of southcentral Washington. Inset maps show (C) the current range of the western gray squirrel in Washington State (gray polygons) as depicted in the species recovery plan (Linders and Stinson 2007) and (D) the general range of the species in North America, occurring almost exclusively in the states of Washington, Oregon, and California (adapted from Carraway and Verts 1994).

recreation area in south-central Washington (Klickitat population). 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 1909–2011. 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 to 176 cm (Western Regional Climate Center 2011). The breeding season for western gray squirrels in Washington begins in January with females entering estrus and extends through August when most litters have weaned (WDFW, unpublished data).

Most of the Klickitat County 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 dry forest and shrubsteppe 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*). Land use surrounding the study area was primarily industrial timberlands along with livestock ranching and small-woodlot forestry.

Our northern study population in a highly fragmented landscape occurred on Joint Base Lewis-McChord (JBLM), a 34,800-ha United States Department of Defense military base located in the southern Puget Trough (Puget Trough population). Extensive training areas on the base have been protected from development since its establishment in 1917 and support native prairie, Oregon oak woodland, and ponderosa pine woodlands that have been largely eliminated

from the surrounding landscape. Western gray squirrels once ranged throughout the Puget Trough region but contracted to JBLM as urban development and rural land use changes greatly reduced acreage of oak woodland and pine forest (Linders and Stinson 2007). At the time of our study there was no reliable estimate of the extant population on JBLM, but surveys conducted by the Pacific Northwest Research Station indicated severely declining numbers (Ryan and Carey 1995, Bayrakci et al. 2001). Mean daily temperature in winter averaged 4.0°C and ranged from 0.1°C to 7.9°C for 1948–2011. Mean daily temperature in summer averaged 16.6°C and ranged from 9.2°C to 23.9°C. Annual precipitation averaged 100 cm with most of that falling during winter. Annual snowfall averaged 18 cm and ranged from 0 to 60 cm (Western Regional Climate Center 2012).

Most of the Puget Trough study area was forested, with Douglas fir the most common overstory tree and areas of Oregon oak woodland and ponderosa pine woodland and savanna. Common trees in riparian areas included bigleaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*), and Oregon ash (*Fraxinus latifolia*). Common understory species included common snowberry (*Symphoricarpos albus*), beaked hazel (*Corylus cornuta*), oceanspray (*Holodiscus discolor*), Indian plum (*Oemleria cerasiformis*), and western swordfern (*Polystichum munitum*). Land use surrounding JBLM was primarily urban and suburban development with some industrial forestlands and small-woodlot forestry.

We studied western gray squirrels in Klickitat County from 1998–2005 and in the Puget Trough from 2007–2012. Resources available to squirrels were similar on the 2 areas with regard to dominant mast-producing tree species (Oregon oak, Douglas fir, and ponderosa pine) although we have data on annual mast production only for Oregon oak. The index of acorn production measured annually by the United States Forest Service was similar between areas during the years of study and averaged 1.8 (range = 1.4–2.2) in the sampling region that encompassed the Klickitat study area and 1.7 (1.2–2.2) for study plots on JBLM (Peter and Harrington 2009; D. Peter, Pacific Northwest Research Station, personal communication). The major disease issues differed between populations with mange prominent in the Klickitat population but apparently absent in the Puget Trough, whereas tularemia was an annual mortality factor in the Puget Trough but never was detected in the Klickitat population. The suite of potential predators of western gray squirrels was similar on both study areas and included bobcats (*Lynx rufus*), coyotes (*Canis latrans*), cougars (*Puma concolor*), red-tailed hawks (*Buteo jamaicensis*), northern goshawks (*Accipiter gentilis*), barred owls (*Strix varia*), and great horned owls (*Bubo virginianus*).

METHODS

Survival

We captured squirrels on both study areas using box traps (Models 105 and 106, Tomahawk Live Traps, Hazelhurst, WI, USA) baited with whole walnuts. We trapped squirrels primarily during spring and fall but also sporadically

throughout the year when targeting individuals. We handled animals using a cloth handling cone (Koprowski 2002) or with the aid of isoflurane anesthesia (Vander Haegen et al. 2005). 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, and attached numbered metal ear tags (No. 1005, National Band and Tag, Newport, KY, USA). We fitted most adult animals and juveniles of sufficient size (>600 g) with radio-collars (Model SC-2, Holohil Systems, Carp, Ontario, Canada) that weighed 15 g and had a projected battery life of 18 months. We handled all animals in accordance with guidelines developed by the American Society of Mammalogists (Sikes et al. 2011).

We tracked radio-collared animals via homing (White and Garrott 1990) 1–3 times/week throughout the year and determined their status either visually or by monitoring the radio signal for indications of movement (transmitters lacked a mortality mode). We determined location of the animal with a global positioning system receiver (Trimble Navigation, Sunnyvale, CA, USA) and recorded information on behavior of the animal including foraging and nest use. During most telemetry locations, investigators attempted to see the animal, so kill sites generally were documented 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 animals suspected to have succumbed to disease to the veterinary diagnostic laboratories at Washington State University or the University of Wyoming for necropsy and ancillary testing. Dead animals submitted from JBLM were tested for the causative agent of tularemia (*Francisella tularensis*; Morner and Addison 2008, Nelson et al. 2014) using real time polymerase chain reaction (PCR) assay following the Laboratory Response Network algorithm (Nelson et al. 2014). Tissue samples that were positive for *F. tularensis* via PCR were sent to Washington Department of Health Public Health Laboratory or to the United States Centers for Disease Control and Prevention for confirmatory testing.

Productivity

We assessed annual productivity of western gray squirrels on both study areas by following radio-marked females through the breeding season, supplemented with periodic captures to document physical evidence of breeding such as enlarged teats indicating nursing of young. When females began sustained use of a single nest, we climbed the tree (when the female was away) to inspect the nest for young and to obtain an initial litter count. We counted litters in shallow, cavity nests visually with the aid of a flashlight and counted litters in deep cavity nests or in stick nests with the aid of a video probe (Sony Corporation, New York, NY, USA). Once we determined a female had young, we revisited the nest when the young were estimated to be 7–8 weeks old to conduct emergence counts, visual observation of young exiting the nest (Rushton et al. 2006). Female western gray squirrels with advanced young typically leave the den for extended periods during the day and the young often leave

the den to climb on the nest tree (Vander Haegen et al. 2005). We conducted emergence counts either using binoculars while hidden from the nest or by securing a video camera (Sandpiper Technologies, Manteca, CA, USA; Sony Corporation, New York, NY, USA) to a nearby tree to record activity at the nest and immediate surroundings. We attempted several emergence counts on each nest and used the maximum number of young observed on ≥ 2 counts where young were seen as our estimate of production. Western gray squirrels typically abandon the natal nest when young are 8–10 weeks old, precluding further accurate counts. We tested for differences between study populations in mean litter size and number of young produced using t -tests after first confirming homogeneity of variance.

We estimated reproductive rate as the proportion of females documented to have litters out of all females tracked each year. We determined females had litters either by documenting young in nests or by observing the presence of enlarged teats during inspection at captures; females determined not to have produced young showed no indication of teat enlargement and no sustained use of a single nest. We estimated production rate as the mean number of young reared to emergence age among females determined to have given birth and tracked sufficiently to derive an accurate count. We derived an estimate of fecundity for each population by multiplying the reproductive rate \times production rate $\times 0.5$ (assuming a 1:1 sex ratio at birth).

Analysis

We estimated survival within the Puget Trough population 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–30 Mar) 2007–2011. 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 right-censored radio-marked animals when we suspected failure of the transmitter ($n = 3$), when the animal apparently slipped the collar ($n = 2$), or when we removed the collar ($n = 1$). We classified animals captured in the summer or fall of their birth year as juveniles and 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 scrotal (testes apparent outside of the body cavity) in their first spring (WDFW, unpublished data). We derived survival estimates for the Klickitat population using similar methods (Vander Haegen et al. 2013).

We developed a set of candidate models to explore alternative hypotheses for factors related to adult survival. This *a priori* model set included single parameter models for year, season (breeding, Mar–Aug; non-breeding, Sep–Feb), sex, mast crop, and measures of winter severity; 2-parameter models that included combinations of winter severity and

mast crop, and models where sex was combined additively or as an interaction with each other parameter; and 3-parameter models where sex or mast crop were combined with measures of winter severity. We used model averaging (Burnham and Anderson 2002) in Program MARK to estimate survival rates and 95% confidence intervals from a set of top-ranked models. We used Akaike's Information Criterion for small samples (AIC_c) to compare models and we considered models ≤ 2 AIC_c units of the top model as our top model set. We considered models with similar deviance values (within 2 units) and that differed only by the addition of a single parameter as not representing an improvement over the more parsimonious model of the pair. We used a second set of models to test the effect of age on female survival that included all adult females and 15 juvenile females (we tracked only 1 juvenile male). We compared the top-ranked adult model with a model including a parameter for age (adult, juvenile) and used AIC_c to assess the effect of the added parameter.

We generated weather variables from data obtained for the Gray Army Airfield weather station located on JBLM. We considered 2 metrics of winter severity derived for November–March: number of days with snow depth > 10 cm, and number of days with mean air temperature (T_{air}) $< 5^\circ\text{C}$. 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, USA (Stephenson and Brown 1980, Dodd et al. 2003). 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). Lacking published thresholds for T_{air} as an influence on squirrel energy needs, we used the long-term mean for winter T_{air} on our study areas. We used data from annual surveys of Oregon white oak acorn production on JBLM (Peter and Harrington 2009) as an index of mast availability for our study area (D. Peter, personal communication).

Population Models

We used data on survival and productivity to model population growth rate (λ) and associated parameters using deterministic and stochastic approaches. Deterministic models use parameter mean values and do not account for annual variation (Caswell 2001). Although estimates of λ from these models tend to be biased high, deterministic models may provide better estimates than stochastic models when sampling duration is low and variation in vital rate parameters is high (Doak et al. 2005). Stochastic models generally are considered more realistic because they incorporate annual variability in vital rates; however, the need to estimate additional parameters requires greater sampling intensity and duration to achieve reasonable accuracy (Doak et al. 2005). Using simulation analysis, Doak et al. (2005) concluded that 5 years of data may be a reasonable minimum for building stochastic models that provide useful results; our sampling effort in the Puget

Trough straddled this threshold so we followed their recommendations to conduct deterministic and stochastic modeling and consider results from both.

Deterministic models.—We built a 2-stage matrix model (Caswell 2001) and used mean values for age-specific survival (juvenile and adult) and fecundity (adult) to estimate λ using the POPBIO package (Stubben and Milligan 2007) in the R programming language (R Development Core Team 2011).

We defined a matrix, $A = \begin{pmatrix} F_0 & F_1 \\ S_0 & S_1 \end{pmatrix}$, where F_0 is fecundity of first-year females and set equal to fecundity of adult females (F_1), and S_0 and S_1 are annual survival of juveniles and adults, respectively. We lacked empirical data for survival of young juveniles from emergence to when they were first radio-marked in early fall; there are few estimates in the literature for survival of tree squirrels during this period and none for western gray squirrels. We estimated survival during this period as 50% of the empirical value for older juveniles (measured Sep through Mar of the following year), which resulted in a period survival rate of 0.73–0.74, similar to the empirical rate reported for red squirrels (*Tamiasciurus hudsonicus*) during this period (Boutin and Larsen 1993). We used life-stage simulation analysis (Wisdom et al. 2000) to examine the relative influence of key vital rates on λ and to model uncertainty in estimates in λ . We generated 1,000 bootstrap simulations using empirical means and standard deviations (SD) for adult and juvenile survival and annual fecundity using a β -distribution for survival and a log-normal distribution for fecundity (Wisdom et al. 2000). We allowed for correlation between adult survival and fecundity using an inverse continuous probability distribution and empirical estimates. Because juvenile survival rates were a product of period rates and sample sizes were small we set SD equal to that of adult survival. Using these bootstrap estimates of λ , we calculated the proportion of simulations where $\lambda > 1$ indicating a growing population. To compare rates of population growth between the 2 study areas, we calculated the difference between λ values generated after each simulation and examined the frequency of these delta values against a hypothetical value of zero (indicating no difference between populations).

Stochastic models.—We created stochastic models for both populations in Program VORTEX (version 10.0.7.5; Lacy and Pollak 2014). Vortex uses observed variability in reproductive parameters and survival rates to project population growth as a series of discrete sequential events that occur according to defined probabilities (Lacy et al. 2014). Our models used the following parameters: percentage of females rearing young, number of young produced from successful litters (as frequencies), and annual survival rates for adult females, adult males, and young <1 year old. Within model runs we allowed for concordance of survival and reproductive rates, assuming that environmental variation would have similar effects (positive or negative) on both. We chose to use observed measures of variance (SD) to approximate annual variability given the relatively short

duration of our studies and therefore our measures included both process and sampling variance (White 2000).

Each model run of 1,000 simulations began with a population of 100 individuals, our estimate for an approximate population size for the Klickitat Wildlife Area based on mark-recapture studies (WDFW, unpublished data). We set carrying capacity for each run at 1,000 to minimize its effect on population growth because we know little about how density dependence affects these populations. We chose to minimize the number of assumptions in the models, allowing the empirical data to have the most strength in model outcomes. We parameterized models for both populations with identical initial population size and carrying capacity to more directly compare effects of differing vital rates on λ . We ran additional models for the smaller, Puget Trough population using a lower initial population size of 50 and lower carrying capacity of 250 to evaluate the influence of these 2 parameters on model outcomes. The program calculated a stable age distribution based on birth and death rates and the initial population size (Lacy et al. 2014). We examined sensitivity of projected population growth rates to key parameters by varying each parameter independently by $\pm 10\%$ and 20% .

We built a set of catastrophe models to simulate severe outbreaks of mange in the Klickitat population and examined the effects of periodicity of outbreaks on λ and on extant population size at year 100. The catastrophe models reduced survival rates (adult and juvenile) based on empirical data from the study area (Vander Haegen et al. 2013) and reduced reproductive rate by a similar magnitude. We modeled 2 scenarios: a moderate effect of mange where survival was equal to the mean value observed during the epizootic in 1998–1999 (survival = 0.54 for F and 0.47 for M), and a severe effect with survival set equal to the lower 95%

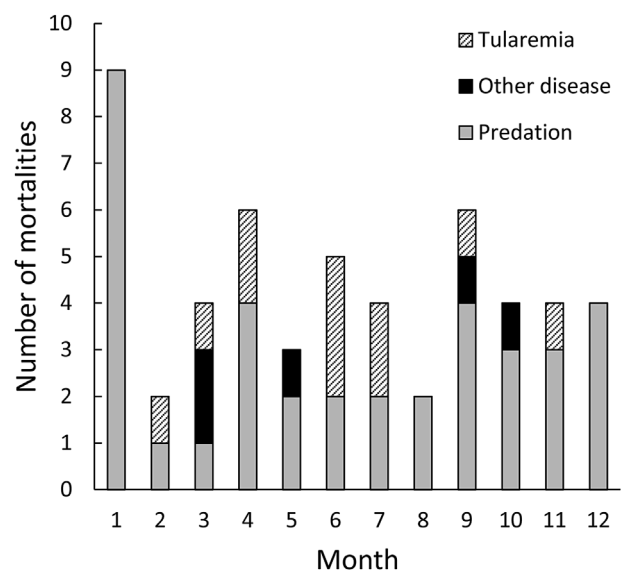


Figure 2. Timing of mortality from disease and predation for western gray squirrels in the south Puget Trough, Washington, USA, 2007–2011. Other disease category includes 3 animals where necropsy found no apparent cause of death.

confidence interval value for survival during that same period (survival = 0.30 for F and 0.24 for M). Each scenario included a model where vital rates were depressed only for the year of outbreak and a second model where effects of mange extended a 2nd year with vital rates reduced to half the magnitude used in the first year to simulate a gradual recovery. We did not develop comparable models for tularemia in the Puget Trough population because we lacked data on periodicity of epizootics and mortality rates associated with severe epizootics.

Climate statistics.—We examined historical winter temperatures for our Klickitat County study area to test for patterns correlating mild winters with mange epizootics proposed by Vander Haegen et al. (2013). We use daily records for the Goldendale weather station (no. 453222) located 14 km from the study area for the period 1910–2010, supplemented with 70 days of data from the Bickleton weather station (no. 450668; 50 km) to fill in missing days for the years 1938 and 1947 (Western Regional Climate Center 2011). We used daily mean temperature values to calculate a measure of winter mildness for comparison with temperatures associated with the mange epizootic documented in 1998–1999 (Vander Haegen et al. 2013). We calculated winter mildness as the number of days where mean air temperature exceeded 0°C for the period 1 November through 31 March (Vander Haegen et al. 2013)

RESULTS

Survival Analysis

Puget Trough population.—We radio-marked 78 western gray squirrels on JBLM between October 2006 and December 2011 that contributed to our estimates of annual survival. Sixty-two were marked as adults (42 F, 20 M) and 16 were marked as juveniles (15 F, 1 M). Six juveniles survived with working radio-collars to enter the adult population in April and were included in models of adult survival. The oldest animals monitored were 2 females (1 captured as an adult, 1 as a juvenile) that survived ≥ 5 years; 6 additional animals (4 F, 2 M) captured as adults survived for ≥ 4 years.

We were able to determine the likely proximate cause of death for 60 animals; 67% were killed by predators, 28% succumbed to disease, and 5% died from accidents (2 were struck by vehicles and 1 nursing female was found dead with >40 porcupine quills embedded in the head and neck). There was no clear pattern to mortality by cause over the year, although over twice as many animals were depredated in January than in any other month (Fig. 2). We could attribute only 44% of predations to specific predator groups based on sign at the kill site; 3 squirrels were likely killed by raptors and 11 were likely killed by mammals. In one case we observed a red-tailed hawk consuming a freshly killed adult. Three animals died as a result of trauma, possibly inflicted by a predator or resulting from a fall. One adult female died from pyometra and a second died from septicemia but was PCR-negative for *F. tularensis*. We found 3 other animals intact with no outward indications of trauma; analysis at the

Table 1. Model selection results for survival (*S*) of western gray squirrels in the South Puget Trough, Washington, USA, 2007–2011, showing Akaike's Information Criterion (AIC_c), differences in AIC_c values from the top model (Δ AIC_c), model weight (w_i), number of parameters (*K*), and deviance (*D*).

Model ^a	AIC _c	Δ AIC _c	w_i	<i>K</i>	<i>D</i>
Adults only					
<i>S</i> (null)	427.8	0.000	0.198	1	187.6
<i>S</i> (snow)	428.6	0.756	0.135	2	186.4
<i>S</i> (temp)	429.5	1.647	0.086	2	187.3
<i>S</i> (season)	429.7	1.912	0.076	2	187.5
<i>S</i> (mast)	429.8	2.005	0.072	2	187.6
<i>S</i> (sex)	429.8	2.006	0.072	2	187.6
<i>S</i> (snow + mast)	430.7	2.655	0.052	3	186.3
<i>S</i> (snow + temp)	430.6	2.739	0.050	3	186.4
<i>S</i> (temp + mast)	431.3	3.446	0.035	3	187.1
<i>S</i> (time)	431.4	3.586	0.032	5	183.2
<i>S</i> (sex + temp)	431.5	3.657	0.031	3	187.3
<i>S</i> (sex + season)	431.7	3.921	0.027	3	187.7
<i>S</i> (sex × temp)	431.8	4.010	0.026	4	185.6
<i>S</i> (sex + mast)	431.8	4.014	0.026	3	187.6
<i>S</i> (mast + snow + temp)	432.5	4.668	0.019	4	186.3
<i>S</i> (sex + snow + temp)	432.6	4.752	0.018	4	186.4
<i>S</i> (sex + time)	433.3	5.512	0.012	6	183.1
<i>S</i> (sex × mast)	433.3	5.523	0.012	4	187.1
<i>S</i> (sex × season)	433.7	5.875	0.010	4	187.5
<i>S</i> (global)	441.4	13.600	0.000	10	183.1
Females only					
<i>S</i> (age)	361.6	0.000	0.500	2	165.8
<i>S</i> (null)	361.6	0.009	0.500	1	167.8

^a Snow = number of winter days with >10 cm snow depth; temp = number of winter days with mean air temperature <5°C; season = breeding or non-breeding; mast = index of acorn abundance; sex = male or female; time = biological year (Apr–Mar); age = juvenile or adult.

diagnostic lab found no obvious cause of death and we attributed these mortalities to unknown cause.

Ten of the 16 animals succumbing to disease died as a result of infection with *F. tularensis*. Genetic typing confirmed the organism in all cases was *F. tularensis holarctica*, the less virulent type B of the bacteria (Nelson et al. 2014). An adult female that was killed by a predator but not consumed also tested positive for tularemia. We observed 1 adult female behaving abnormally 2 days before she died from tularemia, exhibiting loss of physical coordination, and reduced avoidance of humans. We documented tularemia in the population in each year of the study and April, June, and July were the only months with ≥ 2 mortalities from this disease (Fig. 2). Histopathology revealed characteristic degeneration of liver and spleen tissue in most individuals that died of tularemia; findings are detailed in Nelson et al. (2014). In all

Table 2. Model parameters (\bar{x} and SD^a) used in stochastic population models of western gray squirrels in Klickitat County and in the South Puget Trough, Washington, USA.

Parameter	Puget Trough	Klickitat
Female survival	0.62 (0.10)	0.64 (0.15)
Male survival	0.62 (0.10)	0.55 (0.17)
Juvenile survival	0.53 (0.13)	0.56 (0.12)
Reproduction ^b	0.76 (0.11)	0.90 (0.07)

^a Standard deviations reflect variance among annual values.

^b Proportion of females successfully rearing young.

cases tularemia was confirmed through PCR-detection of *F. tularensis* using standard protocols (Nelson et al. 2014). Although we did not test for prevalence of the bacteria in the population, 11 mortalities tested positive via PCR from 78 radio-marked animals, suggesting an infection rate $\geq 14\%$. Two eastern gray squirrels that died on the study area and that were part of related research (Johnston 2013) also tested positive for tularemia (Nelson et al. 2014).

Model results.—Five models of annual survival were within 2 AIC_c units of the top-ranked model and each contained only 1 parameter (Table 1). Within this top model set only the null model and the model containing a parameter for total snowfall had support; the remaining models had deviance values similar to the top model (Burnham and Anderson 2002). Adult survival had a negative relationship with total snowfall with a beta estimate of -0.036 (SE = 0.035, CI = -0.099 to 0.027) although the confidence interval contained zero suggesting a weak effect. Our estimate of annual survival of adult western gray squirrels was 0.61 ± 0.04 (SE) based on the top 2 models; we found little evidence for differences between males and females or between breeding and non-breeding seasons (Table 1). Models that included a parameter for year also ranked low, suggesting no strong annual variation during the 5 years of our study.

With only 16 animals available in the juvenile dataset (15 F, 1 M), we chose to combine age groups in an all-female model set to evaluate the effect of age. The addition of a parameter for age made little improvement to the top-ranked model for adult females (Table 1); values for AIC_c were identical and deviance values were similar, indicating that older juvenile females survived at rates similar to adults (Burnham and Anderson 2002). Further, confidence intervals for the parameter estimate for age included zero, indicating that any effect of age in female survival was weak. The survival rate from the top-ranked female model (0.58 ± 0.05) provided an estimate of juvenile survival for the period beginning September (when most young were collared) through April, when they were reclassified as adults. We used this estimate of juvenile survival in our population models (survival data were available for only 1 juvenile male).

Table 3. Reproductive parameters from western gray squirrels monitored with telemetry at 2 sites in Washington, USA: Klickitat County (1999–2005) and the South Puget Trough (2008–2011).

Parameter	Puget Trough			Klickitat		
	<i>n</i>	\bar{x} or %	SE	<i>n</i>	\bar{x} or %	SE
Reproductive rate ^a	72	91	6	53	93	3
Adults	61	96	2	45	98	2
Yearlings	11	55		8	75	
Initial litter size ^b	15	3.07	0.21	12	3.67	0.25
Production rate ^c	39	2.08	0.22	39	2.76	0.18
Fecundity ^d		0.94			1.30	

^a Females known to have litters or exhibiting enlarged teats. Annual sample size for yearlings insufficient to calculate variability.

^b Number of young counted within 2 weeks of parturition.

^c Number of young reared to emergence from the den (includes only females known to have given birth).

^d Reproductive rate \times production rate \times 0.5 (assuming a 1:1 sex ratio).

Klickitat population.—Survival estimates for the Klickitat population were published previously (Vander Haegen et al. 2013). For both age groups, survival estimates were similar to those for the Puget Trough population (Table 2).

Reproductive Success

Klickitat population.—We documented reproductive rate for 35 female western gray squirrels between 1999 and 2005. Some females contributed data in >1 year resulting in reproductive assessments for 53 female-years. Data were available for 8 females as yearlings, 30 females known to be at least 2 years old, 7 females ≥ 3 years old, 4 females ≥ 4 years old, 2 females ≥ 5 years old, and 1 female each known to be ≥ 6 and ≥ 7 years old. Twenty-five females contributed 1 year of data; 5 females contributed 2 years of data; 3 females contributed 3 years of data; and 1 female each contributed 4 and 5 years of data.

Most females attempted to breed each year ($\bar{x} = 93\%$) with annual effort ranging from 86% to 100% (Table 3). All adult females but 1 (98%) showed evidence of breeding during the 7 years of the study, whereas 5 of 7 first-year females showed evidence of breeding. The adult female that did not attempt to breed had a severe case of mange and died in July in an emaciated condition. We tracked 2 additional adult females with severe mange during the breeding season; 1 lost a litter when she was depredated and the second recovered sufficiently to raise a litter later in the year. We were able to document initial litter sizes (pre-emergence young counts) for 12 litters. Litter size varied from 2 to 5 and averaged 3.67 (Table 3). We found no evidence of in-nest mortality of young; we counted young litters and later documented the number of emerging young for 11 females and in all cases the numbers matched.

We determined the number of young produced for females that attempted to breed (survival of litter to emergence) for 25 females (39 female-years). Annual production rate varied from 1.9 to 4.0 and averaged 2.76 ± 0.18 (Table 3). This value reflects survival of litters through emergence from the natal nest at 7–8 weeks of age. Our estimate of annual fecundity for the Klickitat population was 1.3 females produced per female in the population (Table 3). This value includes 3 females that did not attempt to breed and 1 female infected with mange that was depredated with a young litter in the nest.

We tracked 4 females for ≥ 3 years, allowing us to examine the potential contribution of longer-lived, established females to the population. We captured female 2253 as a juvenile and she raised 9 young over 4 breeding seasons. Female 2056 raised 13 young over 4 seasons and female 2038 raised 11 young over 3 seasons; we captured both as adults and they may have produced young in years prior to capture. Female 2019 raised 15 young over 6 seasons. Over the course of our study these 4 females raised 48 young to emergence age, or 2.8 young/female/year.

Puget Trough population.—We documented reproductive rate for 44 female western gray squirrels between 2008 and 2011. Some females contributed data in >1 year, resulting in reproductive assessments for 73 female-years. Data were available for 11 females as yearlings, 39 females known to be at least 2 years old, and 25 females ≥ 3 years old. Twenty-five

females contributed 1 year of data; 12 females contributed 2 years of data; 4 females contributed 3 years of data; and 3 females contributed 4 years of data.

Most females attempted to breed each year ($\bar{x} = 91\%$) with annual effort ranging from 74% to 100% (Table 3). The low breeding rate in 2010 (74%) was caused by low yearling effort (only 1 of 6 yearlings attempted); all 5 yearlings tracked in other years attempted to breed. We were able to document initial litter sizes for 15 litters. Litter size ranged from 2 to 4 and averaged 3.07 (Table 3), marginally lower than the mean litter size for Klickitat County ($t = 1.85, P = 0.076, n = 25$). This value likely reflects the litter size at parturition because we found no evidence for partial loss of litters in the nest. We counted young litters and later documented the number of emerging young for 4 females and in all cases the numbers matched, similar to our results for Klickitat County.

We determined the number of young produced for females that attempted to breed for 25 females (39 female-years). Annual production rate ranged from 1.6 to 2.5 and averaged 2.08 ± 0.22 , significantly lower than the value for Klickitat County ($t = 2.48, P = 0.015, n = 38$; Table 3). Our estimate of annual fecundity for the Puget Trough population was 0.94 females produced per female in the population (Table 3). This value reflects zero values for 7 females that were not observed to attempt a litter, 3 females that appeared pregnant but who never were documented with a litter, 4 females that died with young litters in the nest, and 1 female whose litter was depredated in the nest. Of 5 females determined to have died from tularemia during the breeding season, 1 had a young litter in the nest, 3 were yearlings that exhibited no indications of breeding, and 1 female reared 2 young to emergence, succumbing to the disease 3 weeks later. In 2010, 2 females (both ≥ 2 years old) attempted a second litter after successfully rearing young to emergence; this finding represents the first documentation of 2 litters in a single year for this species. Both females had small first litters (1 and 2 young) and both raised 2 young to emergence age in their second attempts. Both females had early first litters with young emerging in late-April or early-May; young from both second litters emerged in late-July.

We tracked 3 females for 3 years allowing us to examine the potential contribution of longer-lived, established females to the population. Females 2556 and 2560 each raised 9 young over the 3 years they were monitored and female 2560 raised 7 young over 3 seasons; we captured all

Table 4. Elasticity of lower-level parameters from matrix models and life-stage simulation analysis of western gray squirrel populations in Klickitat County and in the South Puget Trough, Washington, USA. Elasticity represents the median value and rank represents the proportion of times the parameter held the highest value over 1,000 simulations.

Parameter	Puget Trough		Klickitat	
	Elasticity	Rank	Elasticity	Rank
Juvenile fecundity	0.193	0.00	0.304	0.00
Adult fecundity	0.245	0.00	0.244	0.00
Juvenile survival	0.440	0.18	0.542	0.72
Adult survival	0.560	0.82	0.457	0.28

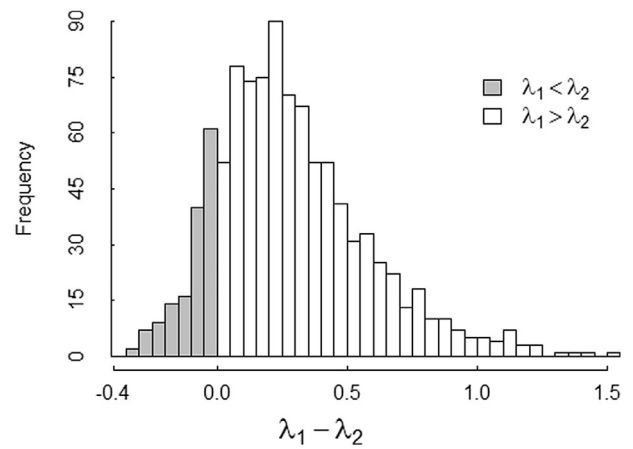


Figure 3. Population growth rate for western gray squirrels in Klickitat County, Washington, USA (λ_1) was greater than that for the population in the south Puget Trough (λ_2) in 85% of bootstrap samples ($n = 1,000$) generated from empirical estimates of survival and productivity. Values on the horizontal axis represent the difference between lambda estimates derived from each simulation run ($\lambda_1 - \lambda_2$).

as adults and they may have produced young in years prior to capture. The median number of young reared to emergence was 3 in the Klickitat population and 2 in the Puget Trough population; 23% of females reared >3 young

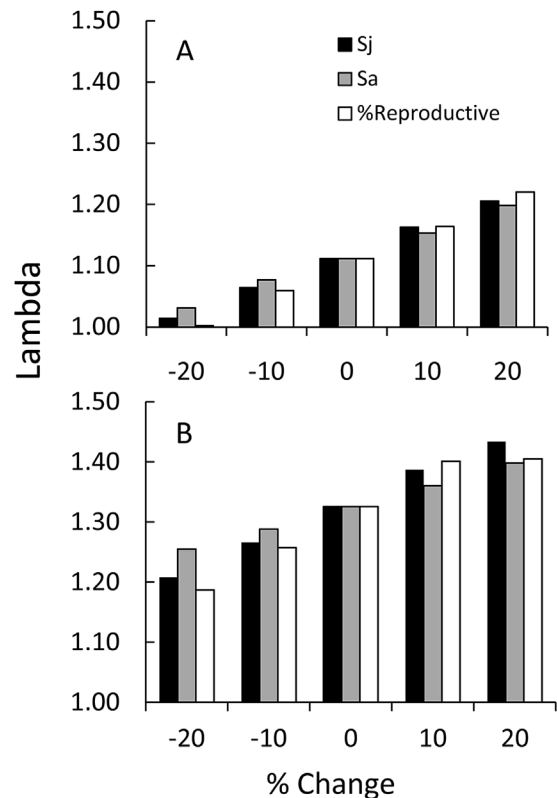


Figure 4. Sensitivity of stochastic population growth rate (lambda) to changes in juvenile survival (Sj), adult survival (Sa) and proportion of females successfully rearing young (% Reproductive) from the base model (0% change) for western gray squirrel populations in (A) the south Puget Trough and in (B) Klickitat County, Washington, USA.

in Klickitat compared to 13% in the Puget Trough. Only 3% of females in Klickitat reared zero young compared to 21% in the Puget Trough.

Population Models

Deterministic analysis.—Matrix model analysis for the Klickitat population estimated λ as 1.34 with a stable age distribution biased toward the younger age class (0.57 juvenile, 0.43 adult). Estimates of population growth rate from life-stage simulation analysis were positive ($\lambda > 1$) in 83% of simulations. Elasticity of lower-level parameters (separating fecundity into its productivity and survival components) was greatest for survival of juveniles and this parameter was greatest in 72% of the simulations (Table 4). Population growth rate for the Puget Trough population was estimated at 1.11 with a stable age distribution biased slightly toward adults (0.48 juvenile, 0.52 adult). Estimates of population growth rate from life-stage simulation analysis were positive ($\lambda > 1$) in 70% of simulations. Elasticity of lower-level parameters was greatest for survival of adults and this parameter was greatest in 82% of the simulations (Table 4). When we compared the simultaneous bootstrap estimates of λ for the 2 populations, we found greater values for the Klickitat population compared to the Puget Trough population in 85% of simulations (median difference = 0.25; Fig. 3).

Stochastic analysis.—Population growth rate estimated for the Klickitat population using the stochastic model was 1.33, similar to the deterministic rate. Estimated population size after 100 years was 943, 5% below the modeled carrying capacity of 1,000. Simulations that increased or decreased vital rates revealed a population robust to small changes in vital rates; λ was most sensitive to proportion of females successfully rearing young (Fig. 4). Reducing vital rates by

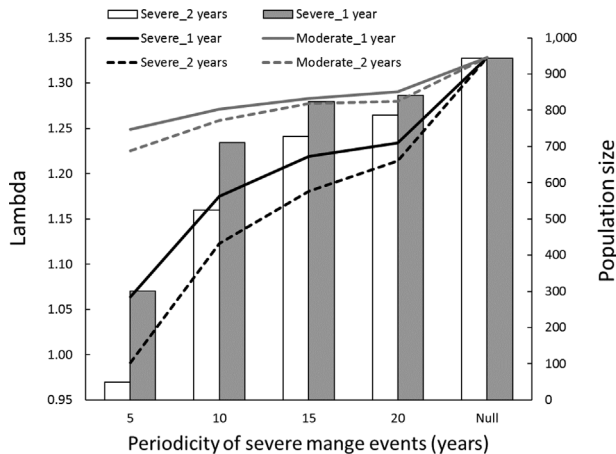


Figure 5. Predicted population size (bars) and population growth rate (λ ; lines) of western gray squirrels in Klickitat County, Washington, USA with varying periodicity of management epizootics and in the absence of epizootics (null model). We conducted simulations in VORTEX (Lacy and Pollak 2014) and modeled populations over 100 years with a starting population size of 100 and a carrying capacity of 1,000. Survival and productivity were reduced in epizootic years at either moderate (15%) or severe (51%) levels with effects lasting 1 year or 2 years, the second year simulating a gradual recovery with declines in survival rates and in proportion of females breeding set at half of that applied in the first year.

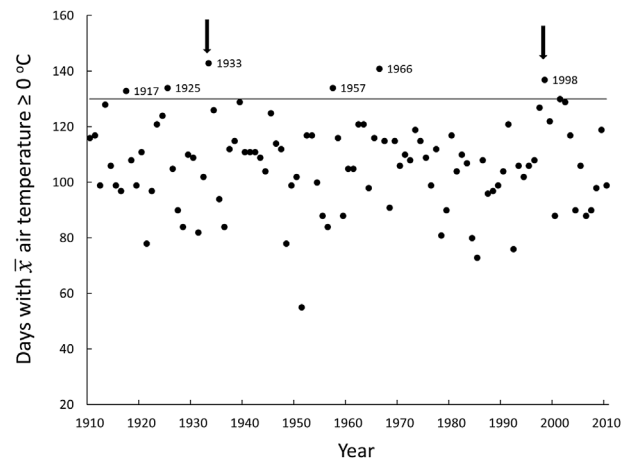


Figure 6. Index of winter mildness (no. days with \bar{x} air temperature $\geq 0^\circ\text{C}$) for the Klickitat County study area, Washington, USA. Arrows indicate periods of documented mange epizootic in southcentral Washington. Horizontal line represents 130 days, an apparent threshold we observed for severe mange in Klickitat County (Vander Haegen et al. 2013). We obtained data from weather stations in Goldendale and Bickleton, Washington (Western Regional Climate Center 2011).

20% resulted in values for λ as low as 1.18 and population sizes >850 (Fig. 4).

Models simulating periodic outbreaks of notoedric mange in the Klickitat population severe enough to reduce survival and reproduction by 15% and by 51% revealed population growth rates robust to events as frequent as every 10 years (Fig. 5). The models indicated potentially severe declines in λ and extant population size when periodicity approached 5 years. When we modeled mange to occur at maximum severity every 10 years, λ was 1.12 and the population declined to 525; increasing frequency of mange to every 5 years reduced λ to <1.0 and resulted in a population with 50 individuals remaining in year 100 (Fig. 5).

Population growth rate estimated for the Puget Trough population from the stochastic model was 1.11, similar to the deterministic rate. Estimated population size after 100 years was 858, 14% below the modeled carrying capacity of 1,000. Simulations that increased or decreased vital rates revealed a population sensitive to small changes in survival and proportion of females successfully rearing young (Fig. 4), a result of an initially low λ . Reducing vital rates by 20% resulted in values for λ near 1.0 and population size <400 (Fig. 4). Similar to results from the Klickitat population model, λ was most sensitive to variation in proportion of females successfully rearing young. When we reduced the initial population size used in the model to 50, there was essentially no change in either λ or the extant population size. Lowering the initial population size to 50 and the carrying capacity to 250 resulted in a similar value for λ and a reduction in extant population size of 22% (250 to 197), compared to 14% (1,000 to 838) for the base model.

Mange and climate.—Our analysis of temperature patterns for the Klickitat study area indicated infrequent occurrence of mild winters of the type associated with a recent outbreak of mange in 1998–1999. In our Klickitat study, mange

prevalence peaked in spring of 1999 following a winter where 137 days had mean air temperature $\geq 0^{\circ}\text{C}$ (Vander Haegen et al. 2013). Between 1910 and 2010, the number of winter days with mean temperature $\geq 0^{\circ}\text{C}$ exceeded 130 in only 6 years (Fig. 6); these mild winters occurred with a frequency ranging from 8 to 30 years ($\bar{x}=16.2$, $\text{SD}=11.1$). Mild winter temperatures in 1933 correspond with the only previous mange epizootic documented in Klickitat County.

DISCUSSION

Populations of western gray squirrels that we studied in contrasting landscapes in Washington State differed in their modeled growth rate. Adult survival was similar between populations although both experienced persistent mortality from diseases caused by endemic organisms. Squirrels succumbed to notoedric mange in the Klickitat Population all years of the study (Vander Haegen et al. 2013) and to tularemia each year of our study in the Puget Trough. Although both diseases can cause severe declines in wildlife populations (Bryant 1921, 1926; Friend 2006) annual survival rates most years were within the typical range for tree squirrels (Gurnell 1987) and periodic population estimates on the Klickitat study area detected no sustained decline in numbers (Vander Haegen et al. 2013). The demographic parameters that differed most strongly between these 2 populations were related to productivity; litter size was marginally smaller and number of young produced by breeding females significantly lower in the Puget Trough compared to Klickitat County. These lower rates were reflected in results from the stochastic models for the Puget Trough population where declines in ≥ 1 key parameters resulted in projected lambda values at or near 1. Based on these findings we believe that the Klickitat population is robust to immediate threats, whereas the smaller Puget Trough population is potentially at risk.

Annual survival rates of adult western gray squirrels in the Puget Trough were similar to those reported for the Klickitat population (Vander Haegen et al. 2013) and varied little between seasons and among years. Survival of adults in both populations was similar to rates reported for fox squirrels (Conner 2001, McCleery et al. 2008) and eastern gray squirrels (Mosby 1969, Barkalow et al. 1970, Thompson 1978) in the eastern United States and greater than those for Abert's squirrel in Arizona (Dodd et al. 2003, 2006). The western gray squirrel is a relatively long-lived species for a meso-size mammal; numerous females in our radioed populations survived ≥ 4 years and 1 female in Klickitat County lived for ≥ 8 years (Vander Haegen et al. 2013). Survival of older juveniles in the Puget Trough also followed a pattern similar to the Klickitat population with no strong indication of survival rates lower than those of adults, although sample size was small. Western gray squirrels likely experience their highest mortality in the weeks after leaving the den, a period of relatively high mortality documented for several species of tree squirrel (Thompson 1978, Steele and Koprowski 2001, Kerr et al. 2007). In our models we used an estimate of survival for this period equivalent to 50% of older juvenile survival and similar to empirical estimates from

another intensively studied tree squirrel in western North America; however, mortality rates for juvenile western gray squirrels from 8–16 weeks of age was the only parameter in our models that lacked empirical data and represents a research need.

Western gray squirrels died from notoedric mange each year of our study in Klickitat County although the infection rate varied among years (Vander Haegen et al. 2013). The species identified as causing mange in western gray squirrels in Klickitat County was *Notoedres centrifera* (Cornish et al. 2001). *Notoedres* spp. mites have caused mange in eastern gray squirrels in Massachusetts (Carlson et al. 1982) and severe outbreaks of mange causing significant mortality have been documented in fox squirrels in Michigan (Allen 1942) and western gray squirrels in California (Bryant 1921, 1926; Ingles 1947; Stephenson et al. 2013). Periodicity of mange epizootics in tree squirrels is largely unknown. Mange has been studied more thoroughly in wild canids where the disease is caused by a different genus of mite (*Sarcoptes* spp.; Sweatman 1971). Sarcoptic mange has been documented to cause epizootics in foxes (*Vulpes vulpes*) lasting from 2 to 10 years (Lindstrom et al. 1994, Soulsbury et al. 2007) and up to 7 years in coyotes (*Canis latrans*; Pence et al. 1983); in both species the disease may persist at low levels (enzootic phase) for decades (Soulsbury et al. 2007, Wilson 2012). Epizootics of Sarcoptic mange in canids had various population effects including decreased population size (Soulsbury et al. 2007), reduced survival (Pence et al. 1983, Soulsbury et al. 2007), and reduced proportion of females breeding (Soulsbury et al. 2007).

Our base models for the Klickitat population represent population growth of western gray squirrels primarily during an enzootic phase and included survival and productivity rates for a population with varying incidence of mange over 7 years (Vander Haegen et al. 2013). These models suggest that the Klickitat population is maintaining a positive growth rate even with incidence of mange in the spring breeding population that ranged from 7% to 53% (Vander Haegen et al. 2013). Our catastrophe models of population growth under varying scenarios of mange indicate that epizootics with a periodicity of < 10 years would be necessary to significantly affect long-term population growth. We have no evidence for an outbreak of mange in this population subsequent to the 1999 epizootic (a period of 15 years) nor during the intervening years back to the 1930s, although there is mention in the literature of an outbreak in nearby Yakima County in the 1950s (Linders and Stinson 2007).

Analysis of winter temperatures over the 100 years preceding our study demonstrates that mild winters that may promote mange occurred infrequently in Klickitat County. Concurrency of mild winters with known epizootics in the 1930s and in 1998 offers limited support to the findings of Vander Haegen et al. (2013) that environmental conditions may facilitate survival of mites, increasing the opportunity for the disease. We know little about the epidemiology of mange in tree squirrels and there likely are multiple factors, such as reduced availability of food (Lavoipierre 1964, Carlson et al. 1982), that interact to facilitate epizootics. The 1998 epizootic corresponded with a mild winter that was preceded by failure of

the mast crop on our study site (Cornish et al. 2001); peaks in winter mildness not associated with known epizootics may not have occurred concurrently with reduced availability of food. The low frequency of mange epizootics documented in Washington and low frequency of winters with mild temperatures, combined with the high frequency of epizootics required to severely threaten the population indicated by our catastrophe models suggest that mange is not an immediate threat to the persistence of this population.

Mange epizootics can depress wildlife populations by reducing survival of adults and lowering reproductive success of infected females (Pence et al. 1983, Soulsbury et al. 2007). Mites typically are passed between individuals by direct contact or indirectly through nesting material harboring adult or immature life stages (Sweatman 1971). Free-living mites are sensitive to environmental conditions of temperature and relative humidity (Arlian 1989); free-living *Notoedres* larvae were found to survive off the host for <48 hours (Gordon et al. 1943) and adult female *Sarcoptes* mites survived shorter periods and were less infestive at low temperatures (-25°C ; Arlian 1989). Increasing winter temperatures resulting from climate change could increase infection rates of wildlife that share nests or, like western gray squirrels, that use nests asynchronously (Vander Haegen et al. 2013). Similarly, habitat fragmentation caused by land development, wildfire, or clear-cut timber harvest can increase host densities and result in higher transmission rates of parasites and greater individual parasite loads for affected species (Scott 1988, Altizer et al. 2003).

The disease affecting western gray squirrels in the Puget Trough population was the less virulent type B tularemia that is more generally associated with true rodents (Friend 2006). Most western gray squirrels determined to have died from tularemia exhibited histological signs consistent with acute infection but were in good body condition, indicating that this species is sensitive enough that most individuals succumbed early in its progression (Morner and Addison 2008). Because of their sensitivity, it is unlikely that tree squirrels serve as reservoirs for the disease and positive cases are likely to be found primarily during epizootics (Gyuranecz et al. 2011). This suggests that tularemia was epizootic on JBLM during the years of our study with an infection rate of $\geq 14\%$. Serologic surveys of other rodents and lagomorphs using PCR and blood agglutination tests indicate potentially higher infection rates during epizootics. In an endemic area in Hungary, prevalence of type B tularemia in European brown hare (*Lepus europaeus*) ranged from 5–7% but elevated to 12–37% in epizootic years (Gyuranecz et al. 2011). Infection rate among small rodent populations averaged 22% in an endemic area in Bulgaria and ranged from 5–8% during epizootics elsewhere in Europe (Gyuranecz et al. 2011). There are no comparable published data for tree squirrels.

Species that succumb quickly to tularemia have little opportunity to spread the disease and are not considered reservoir hosts (Friend 2006). Although most western gray squirrels that apparently succumbed to the disease in our study exhibited histologic indications, several lacked detectable lesions and presence of the bacteria was identified only through

PCR (Nelson et al. 2014). Lack of characteristic histological indications may lead to underreporting of this disease in animals submitted for routine necropsy and could complicate assessment of mortality risks in wildlife population studies. Moreover, lack of septicemia in some individuals in this study raises the possibility of subclinical infection that may lead to longer retention of the bacteria and potential shedding of the organism into the environment as a source of disease transmission (Nelson et al. 2014). Among rodents, chronic infection with type B tularemia has been reported in water voles (*Arvicola amphibius*; Friend 2006). More detailed research on diseases of wildlife that makes use of advanced genetic techniques such as real-time quantitative PCR will expand our understanding of disease epidemiology and the potential risks to wildlife populations (Blanchong et al. 2016).

The bacterium that causes tularemia typically is spread by arthropods including tick species known to infest tree squirrels (Friend 2006). Ticks may serve both as hosts of the bacteria and as primary reservoirs between epizootics where the bacteria can exist in their digestive tract for years (Friend 2006). Ticks, mosquitos, and other blood-feeding arthropods also are potential transmission vectors for humans (Morner and Addison 2008). Research on the prevalence of tularemia in native western and introduced eastern gray squirrels and the frequency of individuals with subclinical indications would provide important information on the role of the disease as a mortality factor and the potential role of tree squirrels in zoonosis.

Reproductive rates of female western gray squirrels on our study sites were similar to those reported for other sciurids in North America; most adult female tree squirrels breed annually and the proportion of first-year females breeding typically is lower (Nixon and McClain 1975, Steele and Koprowski 2001, Descamps et al. 2007). What little published information exists for western gray squirrels is based on counts of fetuses, corpora lutea, and uterine scars from females collected in California and reported mean litter sizes ranging from 2.2 to 3.0 (Fletcher 1963, Asserson 1974, Swift 1977). Mean litter size in the Klickitat population (3.7) exceeded these estimates and also was greater than that in the Puget Trough. Western gray squirrels were reported to have only 1 litter per year (Ingles 1947, Fletcher 1963, Asserson 1974) although previous reports indicated the potential for second litters based on length of the breeding season, occurrence of 2 peaks in ovarian activity, and large, maturing follicles in the ovaries of several females that had reared young (Fletcher 1963, Swift 1977). Our observations of females successfully raising 2 litters in 2010 represent the first documentation of multiple litters for this species; however, the low frequency over 11 years of study indicates that multiple litters are uncommon in Washington.

Mammals differ concerning which vital rates have proportionally greater effect on population growth and these differences have been aligned both with increasing body size (Emlen and Pritchard 1989) and along a fast-slow continuum described by fecundity, age at first breeding, and generation time (Promislow and Harvey 1990). Typically, population growth for smaller, fast mammals is affected more by fecundity,

whereas larger, slow mammals are influenced more by adult and juvenile survival (Emlen and Pikitch 1989, Heppell et al. 2000). Modeling the effects of vital rates on both population size and likelihood of extinction, Emlen and Pikitch (1989) showed that meso-sized mammals are affected more strongly by survival, with similar response to changes in juvenile and adult survival. Western gray squirrels are meso-sized mammals with relatively low annual fecundity, reproduce first at 1–2 years old, and may breed for many years positioning them midway along the speed continuum. Elasticity analyses of vital rates for both of our study populations revealed greater effect of survival over fecundity with similar values for juvenile and adult survival, similar to predictions from size-based models (Emlen and Pikitch 1989).

Our stochastic models suggest that population growth also was sensitive to proportion of females breeding, a finding similar to that reported by Goldstein et al. (2016) for an introduced population of eastern gray squirrels. Failure to reproduce is not uncommon among female tree squirrels, particularly in years when food resources are low (Steele and Koprowski 2001). Low reproductive rate in the Puget Trough population was most evident in 2010 when we documented only 1 of 6 yearlings attempting to breed. This was the same year that 2 adult females successfully raised multiple litters, suggesting that lack of resources was not the cause. Moreover, the acorn crop was the highest recorded during this study in the fall of 2009 (D. Peter, personal communication), also indicating resources were available. Apparent aborted litters documented for several females on JBLM also reduced estimated reproductive rate. Swift (1977) examined 31 reproductive tracts of western gray squirrels collected in California and found evidence of resorbed fetuses (≤ 25 mm long) in 2 females, a phenomenon that has been attributed to severe environmental stress or reduced resource availability (Conaway et al. 1960, Owusu et al. 2010). Although resource availability and its influence on reproductive energetics are key influences on productivity in mammals (Bronson 1985, Speakman 2008), low productivity in the Puget Trough population also may have been related to genetic issues including inbreeding forced by small population size.

There is strong evidence that inbreeding depression can affect reproduction and survival and may reduce the time to extinction in small populations (Lande 1988, Frankham 2005, O'Grady et al. 2006). Possible evidence for this in tree squirrels was reported for the Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*), an endangered species that occurs on a single mountain in southeastern Arizona. This insular population has both low genetic diversity and low productivity resulting from depressed reproductive rate and lower number of young produced per female compared with core populations (Rushton et al. 2006, Fitak et al. 2013). The Mt. Graham red squirrel population also occurs at the southern edge of the species' range and has lower adult female survival compared to core populations; reduced productivity observed in this population may be related to an altered age structure of breeding females and have more to do with demographics than genetics (Goldstein et al. 2017). In the Puget Trough, a tendency toward smaller litters, fewer

young produced per female known to breed, and overall lower fecundity of western gray squirrels are findings consistent with inbreeding effects possible in a small and isolated population, although we cannot isolate this as the cause. With numbers likely < 100 (Ryan and Cary 1995, Linders and Stinson 2007) the Puget Trough population falls in the critically low range both for genetic and for demographic effects (Reed et al. 2003, O'Grady et al. 2006).

We studied 2 discrete western gray squirrel populations during different years and cannot rule out factors in addition to population size and isolation that might explain the observed differences in reproductive success and modeled population growth. Available food resources can differ spatially and temporally, although they appeared similar on our 2 study areas. Tree squirrels depend on tree seeds for a significant portion of their diet (Gurnell 1987) and the major mast-producing species were the same on both areas. Indices of acorn production measured each year were similar for both study areas, suggesting that this key food was available to squirrels at similar levels (Peter and Harrington 2009; D. Peter, personal communication); we had no comparable data for conifer seeds. Hypogeous fungi also are an important food of western gray squirrels (Steinecker and Browning 1970, Byrne 1979) and both fungal diversity and abundance can vary with the forest community (Carey et al. 2002, Lehmkuhl et al. 2004). Fecal analysis of our study squirrels on JBLM indicated regular consumption of hypogeous fungi by almost all individuals throughout the year, suggesting that this key food source was readily available (Johnston 2013). Our 2 study populations were affected by different diseases although we had little direct evidence that disease affected reproduction beyond death of females before they attempted to breed. Most females with severe mange in spring died without giving birth (Vander Haegen et al. 2013), although 1 diseased female recovered sufficiently to reproduce later in the year. Because of the cryptic nature of tularemia, we had no information on disease risk until a female died; however, 1 female succumbed to tularemia while nursing young and a second female died soon after her young were independent. The ultimate impact of tularemia on reproduction of western gray squirrels in the Puget Trough population is unknown and should be investigated.

In addition to demographic and genetic constraints, the small size and insular nature of the Puget Trough population put it at risk for extirpation caused by stochastic events such as disease epizootics and wildfire (Gilpin and Soule 1986, Lande 1988, Sinclair 1996). Although documented cases where disease has eliminated wild animal populations are few, there is increasing realization of the potential for disease to endanger small populations (Holmes 1996, Frick et al. 2010, MacPhee and Greenwood 2013). Wildfire that removes most or all of the forest canopy eliminates habitat for tree squirrels for decades or longer and the dry-forest communities of the Pacific Northwest are experiencing an increasing trend in large-scale fires (Westerling 2016). In 2014 and 2015 alone, $> 300,000$ ha of forest burned in Washington's North Cascades (Northwest Interagency Coordination Center 2014, 2015), 1 of 3 western gray squirrel recovery zones in the state (Linders and Stinson

2007). Longer-term, deterministic changes resulting from forest succession and climate change also can reduce availability of suitable habitat, whereas shifts in land management priorities away from those favorable to western gray squirrels could have devastating effects on a small population limited to a single ownership. Retaining or increasing connectivity between occupied habitat on JBLM and potential habitat in the surrounding landscape will be crucial to the long term viability of this population but will be challenging in the urbanizing landscape of the south Puget Trough.

MANAGEMENT IMPLICATIONS

The Klickitat and Puget Trough western gray squirrel populations exist with endemic diseases with high epizootic potential; however, our data indicate that the potential threat to the Puget Trough population is the more critical given its small size and lower reproductive success coupled with the cryptic nature of tularemia that makes epizootics more likely to go undetected. Small, insular populations like that in the Puget Trough should be monitored closely for indications of decline in number or occupancy and may need periodic augmentation to maintain genetic diversity. Habitat improvements should be pursued on JBLM and in the surrounding landscape to promote expansion of the population to a larger area, providing increased protection from localized events such as wildfire and disease epizootics. Although the larger size of the Klickitat population provides a buffer to stochastic events and the observed incidence of mange epizootics appears insufficiently frequent to endanger the population at present, actions to retain and improve habitat resources may help ameliorate the effects of future epizootics. Continued degradation and fragmentation of western gray squirrel habitat in the Klickitat region along with mild winters resulting from climate change could increase the frequency and severity of mange epizootics and further threaten this population.

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