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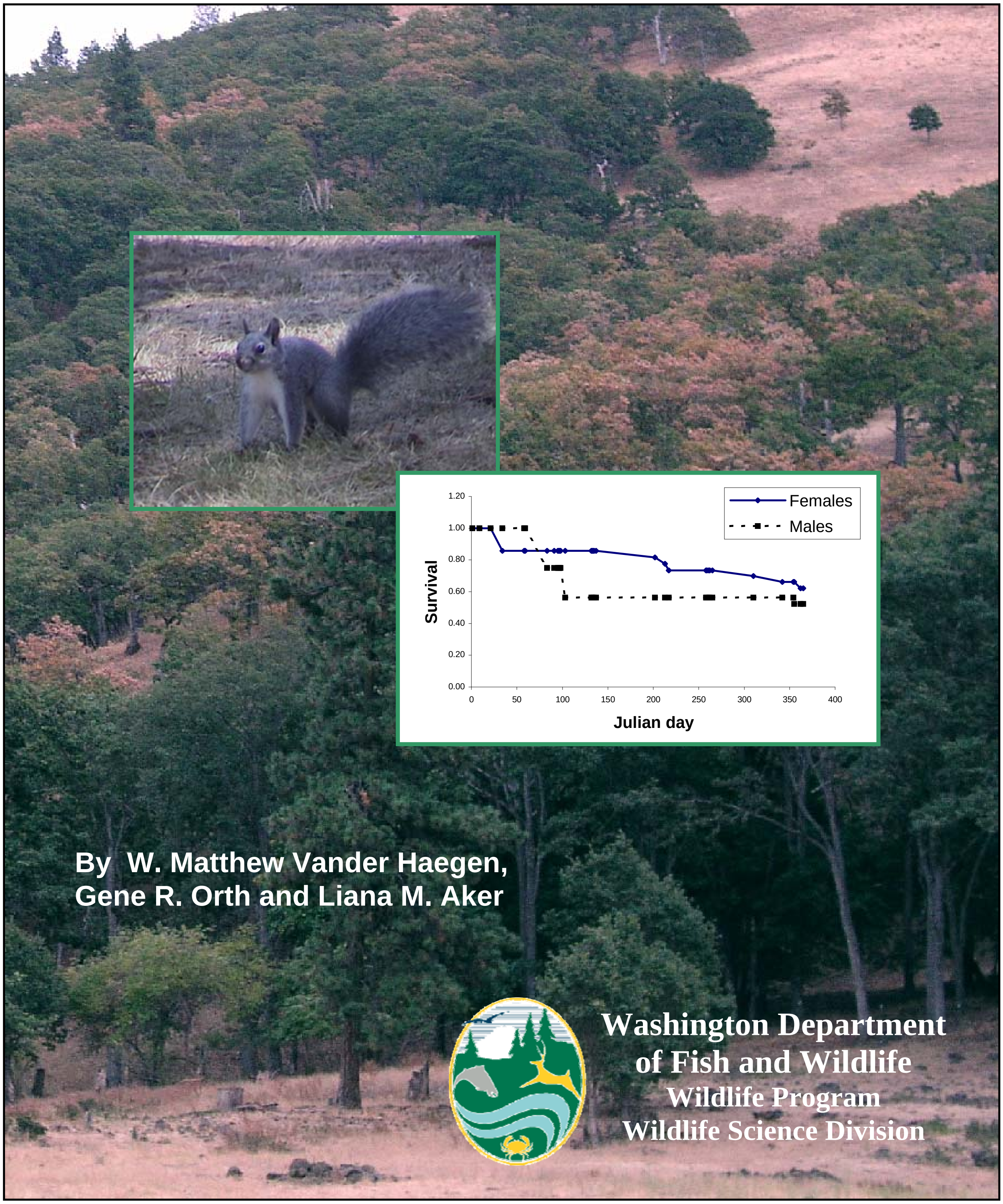
ECOLOGY OF THE WESTERN GRAY SQUIRREL IN SOUTH-CENTRAL WASHINGTON



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Progress Report

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Ecology of the western gray squirrel in south-central Washington

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ABSTRACT

We studied the ecology of the western gray squirrel (*Sciurus griseus*) in south-central Washington from 2000-2004, focusing on the parameters necessary to examine population growth and how they may be influenced by natural and human-caused events. We captured 149 individual squirrels during 17 semi-annual trapping session (651 total captures) and marked most with ear tags and radio-collars. Annual survival of adults ranged from 51 to 65% and was similar for males and for females. Mortality for males tended to occur more frequently during late winter and early spring, coinciding with the mating season. Survival of juvenile squirrels from first capture in fall through 1 March ranged from 60 to 86%. Predation was the major cause of mortality for western gray squirrels most years. Notoedric mange was present in the population all years and was most prevalent, and most severe, in winter and early spring. Mortality due to mange ranged from 10 to 40% annually and was the dominant cause of death one year. Most females attempted breeding each year, including yearlings. Litter size averaged 3.3 and ranged from 2-5 (n = 19). The number of young raised to emergence from the natal den (approx. 8 weeks of age) averaged 2.5 (n = 45). Density of squirrels on 3 study sites, as determined from mark-recapture estimates, ranged from 0.1 to 0.26/ha in spring and from 0.17 to 0.43/ha in fall. Home range (95% fixed-kernel) estimates for female western gray squirrels averaged 18.7 ha (9.9 sd, n = 49); 50% core use areas averaged 4.29 ha (2.25 sd, n = 49). Examination of core use area plots revealed little overlap among females within the same year, suggesting exclusive use of these core areas. Females demonstrated strong fidelity to core use areas from year to year although the size of these areas varied among years. Twenty percent of juvenile squirrels dispersed from the study area where they were captured. Dispersal rates for males (3 of 13) and for females (3 of 17) were similar. Mean dispersal distance was 2862 m (213 sd). Mast surveys of Oregon white oak and ponderosa pine revealed wide variation in availability of these foods from year to year, but similar trends between the 2 study sites surveyed. Plans for 2005 include continued demographic monitoring with an emphasis on survival and movements of young after leaving the natal den. Potential timber harvests on 2 of the 3 study sites also may provide an opportunity to examine how females respond to changes in the stand structure of their core areas and home range.

ACKNOWLEDGEMENTS

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INTRODUCTION

Photo: Foraging western gray squirrel

BACKGROUND

The western gray squirrel (*Sciurus griseus*) inhabits oak/conifer forests in the western United States from southern California to north-central Washington (Verts and Carraway 1998). Throughout their range, western gray squirrels are most frequently associated with pines (*Pinus* spp.) that provide nesting cover and food, and oaks (*Quercus* spp.) that provide natal den sites and acorns for food (Verts and Carraway 1998). Both tree genera also are associated with hypogeous fungi, another staple food of western gray squirrels. Populations of western gray squirrels are considered stable in much of California, where they are considered a game species (California Department of Fish and Game 2000) and where their habitat contains numerous species of both oak and pine. From mid-Oregon north through Washington, oak/pine communities are simpler, containing primarily ponderosa pine (*P. ponderosa*) and Oregon oak *(Q. garryana*). Both species are intermittent producers of mast, making food resources less reliable than in more southern parts of the species' range. Although classified as a game species in Oregon, the western gray squirrel has shown evidence of declines in its population in the north-central part of the state (Foster 1992), and the Oregon Department of Fish and Wildlife lists the squirrel as "undetermined" on the State Sensitive Species List. While once hunted in Washington, the western gray squirrel has been protected since 1944 (Washington Department of Fish and Wildlife 1993).

Western gray squirrel populations in Washington have declined over the last century and their range has diminished (Washington Department of Fish and Wildlife 1993). Western gray squirrels currently exist in only 3 locations: Puget Sound, north-central Washington (Chelan and Okanogan Counties), and south-central Washington (primarily Klickitat County). The Puget Sound population, already at a low point in the early 1990s (Ryan and Carey 1995), has declined dramatically since then and is believed to be dangerously low (Bayrakci 1999). Causes for the decline in the Puget Sound population likely include habitat loss, habitat alteration, and increased mortality related to vehicle traffic (Ryan and

Carey 1995). Relatively little is know about the north-central Washington population, although densities are believed to be low and recent surveys of nests suggest that squirrels are declining, at least locally (WDFW unpublished data). The population in Klickitat County is the largest of the three, yet continuing habitat loss suggests that it too may be declining. Land development and harvest of ponderosa pine have increased markedly in south-central Washington, reducing habitat for western gray squirrels (Washington Department of Fish and Wildlife 1993). The number of acres logged and the number of logging permits requested for Klickitat County increased dramatically in the mid-1990s due to increased lumber prices and logging of insect and drought-killed pines (Washington Department of Natural Resources 1996). This severe reduction in habitat combined with an uncertain future for the extant populations of western gray squirrels prompted the Washington Department of Fish and Wildlife to list the species as state-threatened in 1993.

Current threats to western gray squirrel habitat in Washington include; harvest of mast-producing softwoods, conversion of oak woodlands to softwood stands through silvicultural practices and fire suppression, clearing of oak woodlands for suburban and urban development, and fragmentation of oak woodlands. Biological threats to western gray squirrel populations include; loss of mast-producing softwoods to pine beetle infestations, invasion by potential competitors including the eastern gray squirrel (*S. carolinensis)* and California ground squirrel (*Spermophilus beecheyi*), and mange epidemics such as those documented in the early and mid 1900s and more recently in Klickitat County in 1998 (Cornish et al. 2001).

Timber harvest changes habitat for western gray squirrels by removing mast-producing trees, destroying nests and potential nest sites, and decreasing the interconnected tree canopy that squirrels use to travel safely through their territories. Studies of the closely related tassel-eared squirrel (*S. aberti*) in Arizona reported that recruitment of young into the population was related to continuity of the upper canopy (Dodd et al. 1998) and that both squirrel density and recruitment declined along with tree canopy cover and density following timber harvest (Patton et al 1985, Pederson et al. 1987). Findings from a study examining nesting activity on harvested and control sites in Klickitat County suggest that western gray squirrels will use some harvested stands, but frequently at reduced levels (Vander Haegen et al. 2004). How timber harvest affects population parameters of western gray squirrels has not been studied.

Relatively little is known about the ecology of the western gray squirrel and much of our existing knowledge comes from south in the species' range where habitat is very different from that in Washington and northern Oregon. Most work in Washington has focused on locating nest sites and examining the general distribution of the population (Bowles 1921, Barnum 1975, Rodrick 1986, Roderick 1999). Studies in Oregon and California have been largely descriptive, with quantitative data based largely on small sample sizes (Ingles 1947, Cross 1969, Gilman 1986, Foster 1992). A recent study funded by WDFW and conducted through the University of Washington (Linders 2000) used radio-telemetry to examine home range and movements of the western gray squirrel on the Klickitat

Wildlife Area, a protected area with no commercial tree harvest. With sample sizes over twice those of most previous studies, this research documented home ranges considerably larger than those reported in the literature (Linders et al. 2004). How this most northern population of western gray squirrels may differ in other ways from those in the species' core range is unknown.

INVESTIGATION

In spring of 2000 we began a study of the ecology of western gray squirrels in Klickitat County, focusing on the parameters necessary to examine population growth and how they may be influenced by natural and human-caused events. Parameters under investigation include: adult and juvenile survival, annual reproductive success, juvenile dispersal, adult movements and home range, and seasonal shifts in abundance. Ancillary investigations include: nest site selection, patterns of nest use, annual shifts in availability of oak and pine mast, seasonal shifts in food use, and genetic diversity.

This report presents updates on key components of the study and includes some preliminary analyses. Those wishing to cite findings presented in this progress report are requested to first contact the lead author.

Key Objectives

1. Examine the annual survival and reproductive ecology of western gray squirrels in Klickitat County.

2. Examine spatial use of the landscape by western gray squirrels in Klickitat County.

3. Investigate the effects of timber harvest on western gray squirrel populations in Klickitat County.

STUDY AREA AND GENERAL METHODS

Photo: Ponderosa pine stand in Klickitat County

STUDY AREA

Study sites were established on the Klickitat Wildlife Area (KWA) in central Klickitat County, an area known to have a resident population of western gray squirrels. The “east grid” site was established in the summer of 2000 east of Canyon Creek (Fig. 1), in the general area used by Mary Linders for her thesis work (Linders 2000) on western gray squirrel movements and habitat use. A second area was added in 2002 on the west side of Canyon Creek. The east and west grid study sites are separated by a deep canyon and are 3km apart (measured from each grid center). Both study sites are oak-pine woodlands with occasional open patches of perennial bunch grasses. Dense timber dominated by ponderosa pine and Douglas fir occurs primarily on north slopes. Neither site has been harvested for timber in the last 50 years and wildfire also has been largely absent. As a result, dense stands of young pine and oak occur sporadically across the site and mortality caused by pine bark beetles (*Dendroctonus brevicomis and D. ponderosae*) has created occasional openings. A third site was established in 2004 on commercial timberlands owned by the Campbell Group. This site is on the north rim of Dead Canyon approximately 9.5 km north of the KWA sites. Addition of the Dead Canyon site expanded the geographic scope of the study, providing an additional measure of spatial variation for the parameters of interest and the potential to examine response of squirrels to timber harvest.

On each site, we constructed a 77.4 ha study plot defined by a 12 x 12 survey grid with points separated by 80m (Fig. 2). These grids form the framework for mark-recapture trapping conducted each spring and fall, as well as providing a systematic sampling frame for measuring vegetation, mast availability, and other site characteristics. Survey grid points are marked with vinyl flagging and are identified with sequential codes beginning with A1 in the northwest corner and ending with K12 in the southeast corner.

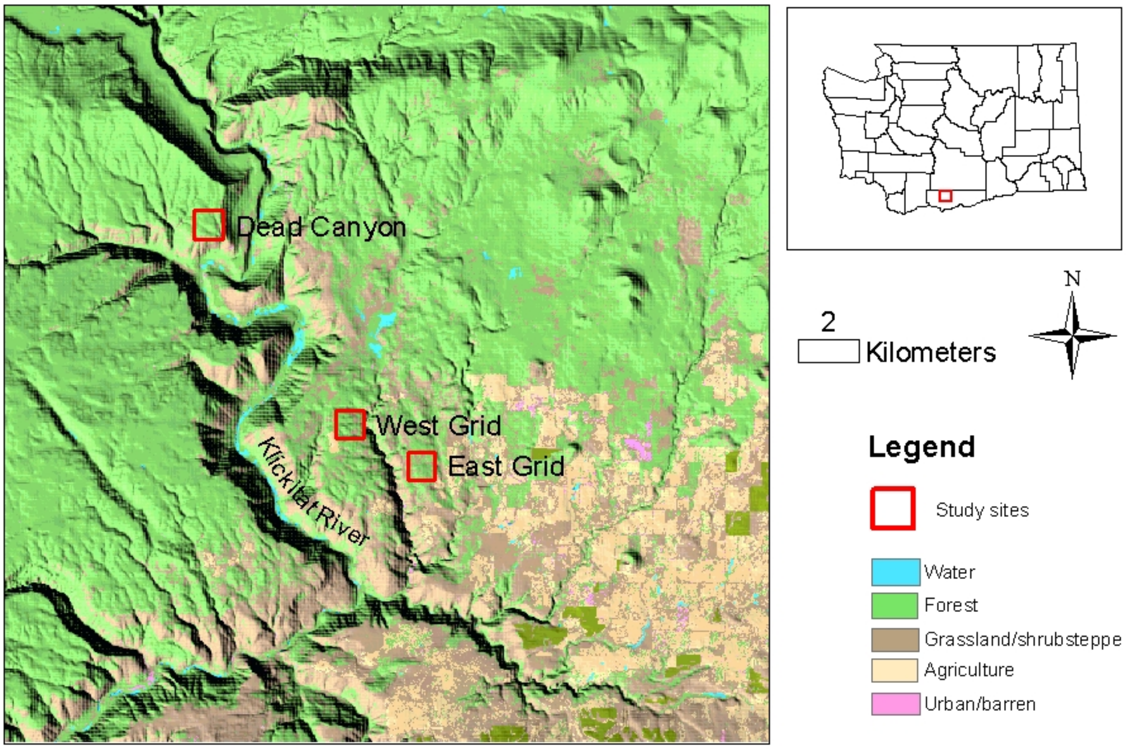

Figure 1. Location of study sites in Klickitat County, Washington.

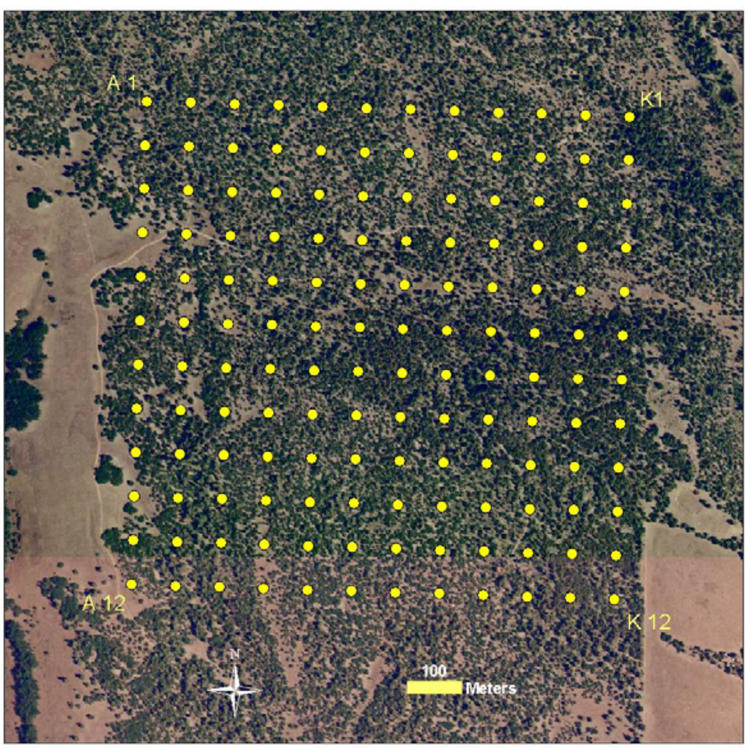

Figure 2. Layout of the 77 ha trapping grid for western gray squirrels, Klickitat Wildlife Area (east grid).

GENERAL METHODS FOR CAPTURING AND HANDLING

We live-trapped squirrels on the study grids in spring and fall. Goals of the trapping effort were to 1) check the physical condition of animals and assess their breeding status, 2) estimate the abundance of the population, and 3) attach radio collars to selected animals. We used a mix of single door, 7x7 and 9x9 inch wire mesh traps (Tomahawk Live Trap Co.). Traps were baited with whole English walnuts and were wired open for 2 weeks prior to trapping to allow animals to become familiar with the traps. Trapping took place over 8 days, with traps set at first daylight and then checked and closed beginning at 1100 hours. All traps were closed by sunset. Animals that moved off of the study grids often were target-trapped in order to replace radio-collars and check their condition.

From 2000-2002 we anesthetized captured animals with Isoflurane, an inhalation anesthetic that we administered on cotton balls that were place in a plastic bag along with the trap (3cc for a 7x7 inch trap, 4cc for a 9x9 inch trap). Once the animal ceased moving (generally 3-5 min), it was removed from the bag and anesthesia was maintained by inserting the animal's head partway into a plastic cone that supplied Isoflurane via evaporation. The cone was open at the narrow end, and a cotton ball soaked with 1cc of Isoflurane was placed inside the cone. Animals generally were down for 15-20 min during a full work-up (health check, blood draw, and attachment of ear tags and a radio collar). In fall of 2003 we began using a cloth handling cone (Koprowski 2002) in place of the anesthetic (Fig. 3). The handling cone offered several advantages including quicker handling time and less apprehension for novice workers unfamiliar with anesthetic drugs.

Figure 3. Affixing an ear tag to a western gray squirrel using a cloth handling cone

Adult animals and juveniles of sufficient size (> 600g) were fitted with radio-collars (Fig. 4) (Holohil Systems, Inc., Carp, Ontario). Transmitters weighed 15g and had a projected battery life of 18mo. From 2000-2003, collars were made of multi-strand wire coated with plastic and attached with a brass crimp; beginning in 2003, collars were made from UV-resistant plastic cable-ties. Both collar designs included an outer sheath of 3mm (inside diam.) vinyl tubing (Tygon R-3603). The tubing was cut to final length during the fitting process as the cable tie was tightened, providing a positive stop that would prevent the tie from closing further. Although squirrels occasionally chewed through the cable tie collar (probably one squirrel chewing through another's collar), this rarely occurred. Of note, the same collar design frequently was chewed through and removed by western gray squirrels in Okanogan County, Washington (Sara Gregory, pers. comm.).

All squirrels were marked with numbered, metal ear tags (National Band and Tag Co., no. 1005-3) attached to both ears (Fig. 4). From 2000-2002, animals also were marked with a passive integrated transponder (PIT tag) (Biomark, Inc.) inserted subcutaneously over the dorsal midline. PIT tags allowed positive identification of captured individuals in the event that both ear tags were lost. Animals were weighed with a spring scale at each capture and checked for general physical condition. We collected a small piece of ear tissue or a sample of blood on each animal's initial capture for DNA analysis. Blood was sampled by clipping a claw on a hind foot and collecting 70-100 μl in 1 or 2 micro-capillary tubes.

Figure 4. Anesthetized western gray squirrel sporting ear tags and a radio collar (cable tie version).

SURVIVAL

Photo: Western gray squirrel infected with notoedric mange.

METHODS

Survival Analysis

Radio-collared animals were tracked weekly through the year and their status determined either visually or by monitoring the radio signal for indications of movement. During most telemetry locations investigators attempted to see the animal, so kill sites generally were documented within days of the incident. Several animals that were suspected to have succumbed to disease were sent to wildlife disease laboratories for analysis.

Telemetry data were subjected to analysis using the Kaplan-Meier estimator using code (White and Garrot 1990) written for SAS (SAS Institute 1990). Adult survival was estimated for the period 1 January-31 December, with young produced the previous year entering the adult data pool on 1 March (approximate mean date for initiation of mating activity). Juvenile survival was estimated for the period 16 September-28 February, with most animals entering the analysis pool during fall trapping in September/October. Juveniles collared in September generally were ≥20 weeks old and weighed a minimum of 600g. Animals whose fate was unknown were censored out of the dataset on the date of their last telemetry location. In addition, several animals that were found dead and decomposed in nests during winter/spring 2003 were censored from the data set as we could not attribute cause of death to disease versus collar related mortality (see Occurrence of Mange). We tested for differences between the survival functions for males and females using the log rank test (Cox and Oakes 1984).

We examined cause-specific mortality by running Kaplan-Meier analyses for both sexes combined and censoring out animals lost from other causes. We ran separate analyses for mortality caused by predation and disease. Timing of mortality by these 2 sources was examined by plotting individual deaths, by cause, for each year.

Disease Monitoring

Condition of each animal captured was assessed during semi-annual trapping efforts on the study grids (see Study Area and General Methods). Animals were inspected for hair loss, scabbing, and lesions indicative of notoedric mange (Cornish et al. 2001) and were scored based on the proportion of the body involved: 1 = no involvement, 2 = 10% or less, 3 = more than 10%. Carcasses and /or tissue samples from several animals were sent to the Washington Animal Disease Diagnostic Laboratory in Pullman or to the Wyoming State Veterinary Lab in Laramie when the cause of death was not apparent.

RESULTS

Adult Survival

Annual survival of adult western gray squirrels ranged from 51 to 65% for the period 1999-2003 (Table 1). Sexes were combined for analysis in 1999 and 2001 to increase sample size; survival estimates and patterns of mortality were similar for both sexes in both years. Annual survival of males was lower than that for females in 2001, 2002 and 2003, but the differences were not different statistically. Patterns of mortality over the year differed between sexes in 2002 and 2003, with males exhibiting a peak in mortality during late winter/early spring and females dying sporadically over the year (Fig. 1a, b). In 1999 and 2001 both sexes showed a peak in mortality during late winter/early spring (Fig. 1c).

Table 1. Annual survival estimates for adult western gray squirrels on Klickitat Wildlife Area derived using the Kaplan-Meier estimator.

Year/Sex	n[a]	Mortalities	Survival	Lower 95%CI	Upper 95%CI
1999 Both	28	8	0.52	0.29	0.76
2000 Both[b]	13	1	--	--	--
2001 Both	21	5	0.65	0.40	0.90
2002 Male	18	4	0.52	0.15	0.89
Female	26	7	0.62	0.38	0.87
Both	44	11	0.60	0.39	0.80
2003 Male	23	8	0.39	0.13	0.65
Female	33	9	0.58	0.37	0.79
Both	57	17	0.51	0.34	0.67

[a] Number of individual animals contributing to the estimate.
[b] Sample size inadequate for analysis.

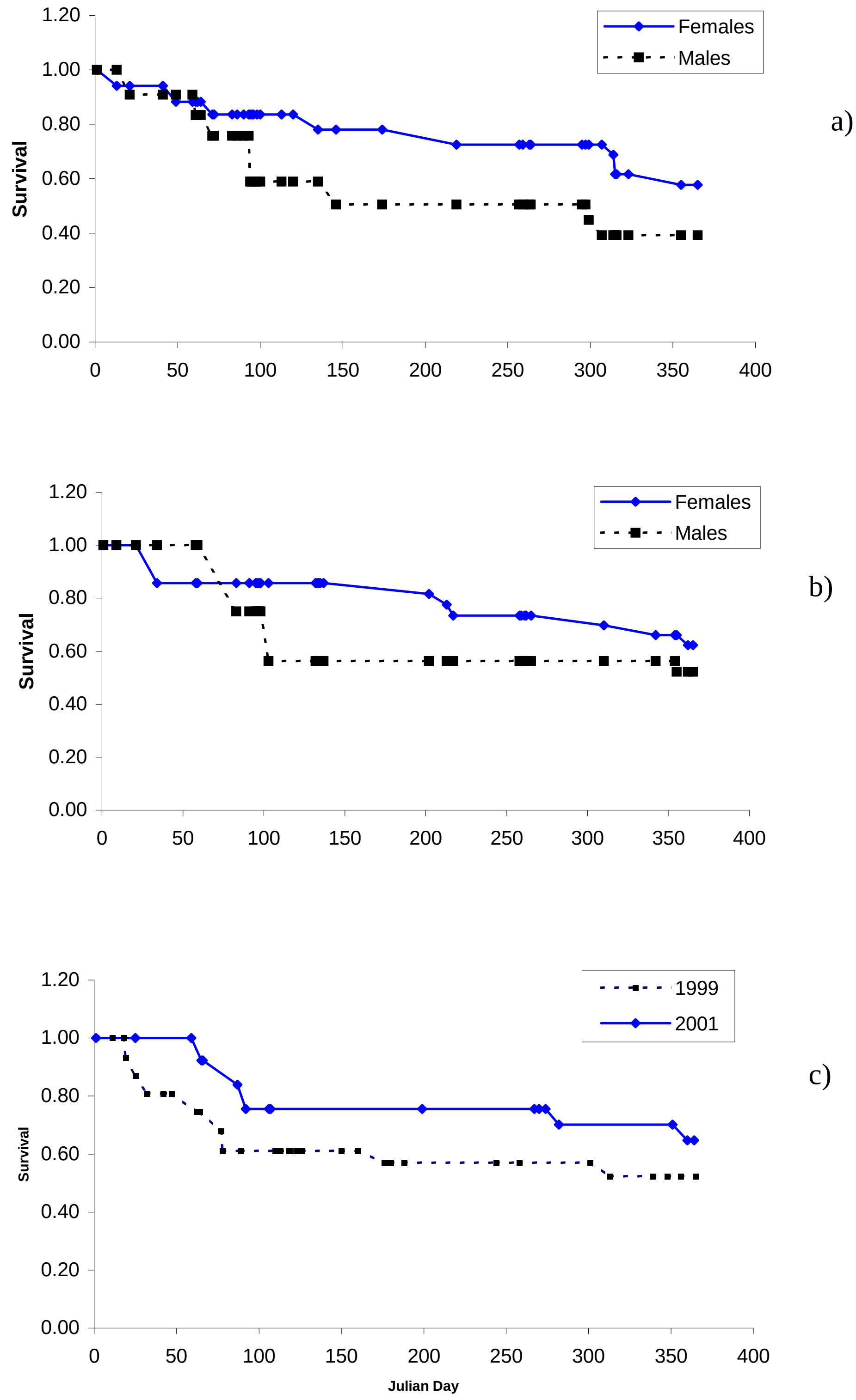

Figure 1. Kaplan-Meier survival curves for adult western gray squirrels in a) 2003, b) 2002, and c) 1999 and 2001 (sexes combined), Klickitat County, Washington.

Causes and timing of adult mortality

Predation was the major cause of mortality for adult western gray squirrels in 3 of the 4 years, with isolated cause-specific mortality rates ranging from 26 to 39% (Fig. 2). Avian and mammalian predators were implicated from sign at the kill sites; rare observations of kills identified bobcats (*Lynx rufus*) and northern goshawks (*Accipiter gentilis*) as known predators. Disease was the major source of mortality among adult squirrels in 1999 with a cause-specific mortality rate of 40% (Fig. 2). Disease was less of a factor in other years but still was responsible for mortality rates of from 9-15%. Notoedric mange was present in the population in all years and was the primary cause of disease mortalities. Whereas predation appeared to occur sporadically over the course of the year, deaths due to disease were concentrated during the late winter and early spring with 11 of 15 deaths (73%) occurring during Jan-April (Fig. 3).

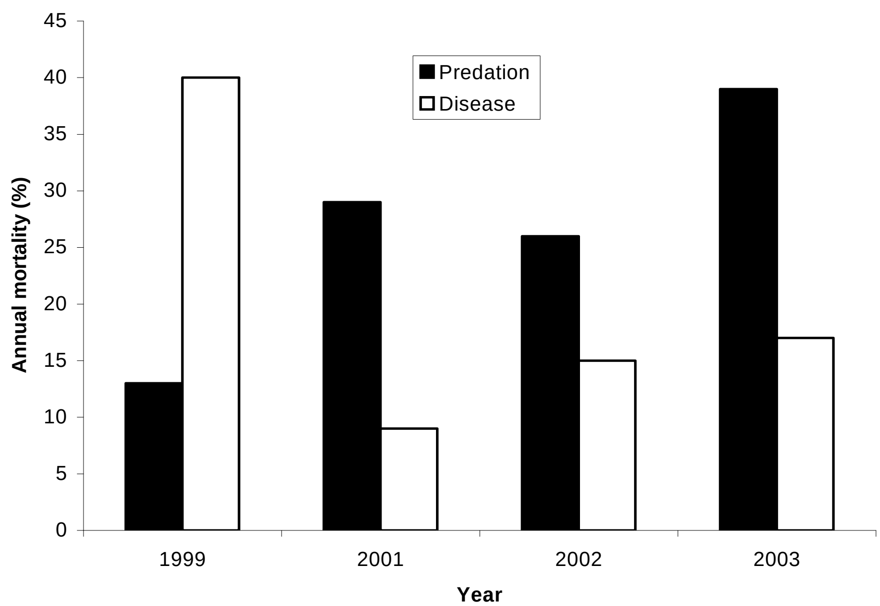

Figure 2. Causes of mortality for western gray squirrels on Klickitat Wildlife Area, derived through Kaplan-Meier analysis.

Juvenile survival

Survival rates for juveniles from early fall through entry into the breeding population ranged from 60 to 86% (Table 2). For 3 of these years estimates were based on low sample sizes and simple ratio calculations. A sufficient sample was available in 2002 to employ Kaplan-Meier methods and this may represent the most reliable estimate. Survival from Kaplan-Meier analysis was equivalent to 0.947/month or 0.52 when projected for a 12 month period. Five juveniles were killed by predators and 3 died from complications related to notoedric mange. The mange deaths occurred in late December whereas the depredations occurred throughout the analysis period.

Table 2. Survival estimates for juvenile western gray squirrels on Klickitat Wildlife Area for the period September-February.

Year	n[a]	Mortalities	Survival[b]	Lower 95%CI	Upper 95%CI
2000	5	2	0.60	--	--
2001	5	1	0.80	--	--
2002	16	4	0.72	49	96
2003	7	1	0.86	--	--

[a] Number of individual animals contributing to the estimate.
[b] Estimate for 2002 derived using the Kaplan-Meier estimator; other years derived using simple ratio of number dead/number in sample.

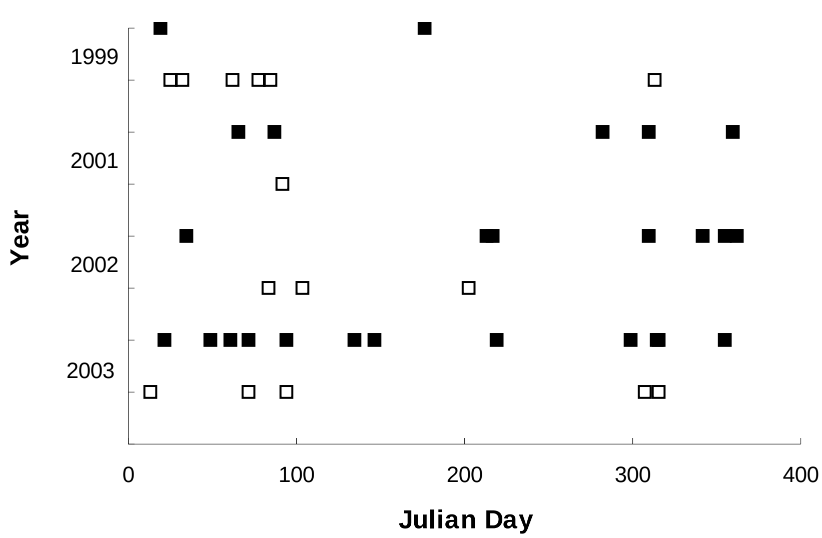

Figure 3. Timing of individual mortalities of adult western gray squirrels by cause (open squares = disease, closed squares = predation), Klickitat Wildlife Area.

Occurrence of Mange

Notoedric mange was evident in the population all years and was most prevalent in the late winter and spring (Fig. 4). Proportion of captured animals showing signs of mange averaged 19% in spring and 4% in fall. Mange reached its highest incidence in spring of 2003 (32%, n = 19). Severity of mange cases also varied by season with the most severe cases (involving >10% of the body) occurring predominantly in late winter and spring.

Analysis results from the diagnostic disease laboratories suggest that 7 of 8 animals examined died of complications caused by notoedric mange. Findings typically reported chronic hyper plastic and superficial perivascular dermatitis with severe erosion/ulceration and serocellular crusting—the thickening and cracking of infected skin typical of mange infections. In 2 cases, the mange infections were further complicated by cutaneous fungi (zygomycosis) that thrive on decaying organic matter. One animal (#2332) apparently died of complications arising from a lesion that developed on the ventral neck, beneath the radio-collar. The wound was deeply ulcerated with significant secondary infections of cocci bacteria (likely *Staphylococcus sp. or Streptococcus sp.*) and may have resulted from reaction to the radio-collar. Similar lesions were found on several other animals captured during the winter of 2003, though none as severe as this case and most appeared to be healing. Although collar-related injuries of this magnitude had not been observed previously, we modified the collar design by adding heat-shrink rubber tubing to cover all exposed metal parts.

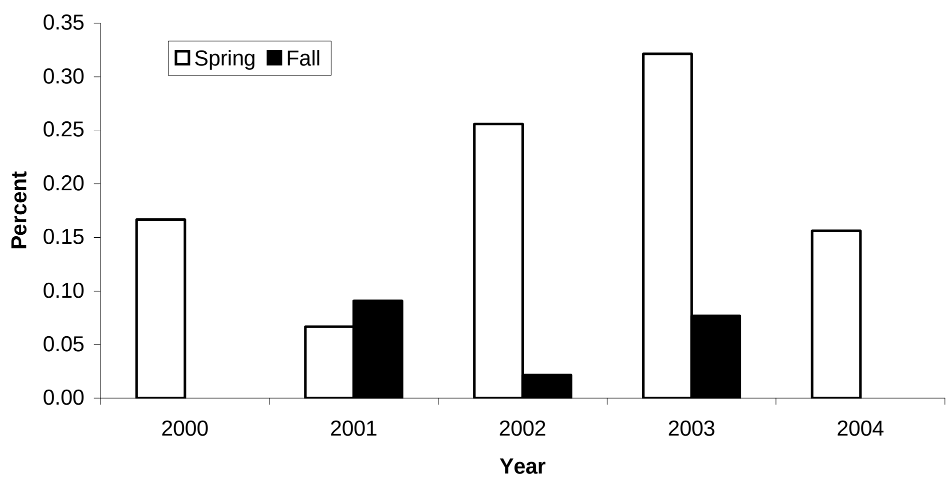

Figure 4. Occurrence of notoedric mange in western gray squirrels captured on Klickitat Wildlife Area, Klickitat County, Washington. Sample size was 29 in 2000, 34 in 2001, 77 in 2002, 55 in 2003, and 57 in 2004.

DISCUSSION

Annual survival of western gray squirrels in Klickitat County was within the range reported for tree squirrels (50-70%) by Gurnell (1987). There are no good estimates specifically for western gray squirrels in other parts of their range. The trend towards lower annual survival of males and the pattern of increased mortality of males during the breeding season in Washington suggest a cost to males for their increased movements related to breeding. Linders et al. (2004) reported greater movements by males during the breeding (versus non-breeding) season, a time when male tree squirrels typically expend considerable effort in search of females in estrus (Gurnell 1987). Survival of juvenile western gray squirrels was not dissimilar from that of adults. However, this does not include the period between emergence from the natal den and our fall trapping in September, a 2-3 month period when the young squirrels may be the most vulnerable to predation.

The levels of mange infection observed between 2000 and 2004 were substantially lower than that observed on KWA in 1998/1999 when 33 of 56 (59%) squirrels handled showed signs of mange (Cornish et al. 2001). Deaths due to mange were correspondingly higher in 1999 and then again in 2003, when occurrence of mange reached a second peak in the population. Predation rates may be linked to some degree to prevalence of mange in the population, as inflicted animals become weak as the infection progresses. This may explain the high rate of mortality due to both disease and predation in 2003. The etiology of mange infections in tree squirrels is not well understood, although food shortages and other stressors in the environment may increase the severity of outbreaks (Lavoipierre 1964, Carlson et al. 1982). Research is needed to determine potential relationships between occurrence of outbreaks and winter severity, patterns of nest use, food availability, and habitat quality.

PRODUCTIVITY

Photo: Litter of young western gray squirrels in an oak den

METHODS

Early in the study it was determined that females typically use cavities in oak trees as natal dens and begin exploring for suitable oaks early in the breeding season. Repeated locations of a female in the same oak den, particularly during April-July, were taken as an indication of reproductive activity and when use continued for a period exceeding 3 weeks the den was monitored for presence of young. In 1999, presence of young was determined using "emergence counts" wherein the den was observed from a distance (generally early in the morning) to see if young emerged onto the den tree. Females with advanced young typically leave the den for extended periods during the day and the young often leave the den to practice climbing and explore their surroundings. Typically, these activities are limited to the den tree. Several emergence counts were attempted on each den and the maximum number of young counted was used as the production estimate. In 2000 we began using a small video camera lowered into the dens to document presence of young and to obtain early litter counts when possible. These video counts were later followed up with emergence counts in order to document early (pre-emergence) mortality and to obtain final counts for production estimates. Ratios of juveniles per adult female were derived from fall trapping on 77.4 ha grids (see Abundance Estimates).

RESULTS

Thirty female western gray squirrels were monitored for reproductive success during the period 1999-2004. One female was followed for 6 years, 2 were followed for 4 years, 1 for 3 years, and the remaining 26 for 1 or 2 years. An additional 6 females were radio-tracked during this period but not with sufficient frequency to determine if they attempted to raise a litter.

Timing

Female western gray squirrels began using oak dens as early as December and frequently used a number of dens prior to parturition. The earliest date that a female began using a natal den (where presence of young was confirmed) was 25 February; the latest was 16 July.

Juvenile western gray squirrels began emerging from natal dens as early as 24 April and as late as 8 August. Median dates of emergence differed by as much as 20 days among years (Table 1); however, the majority of dens in our sample (20 of 29) had young emerging in the month of June. The median date for emergence across all years was 15 June.

Table 1. Approximate timing of emergence from natal dens for western gray squirrel young of the year.

Year	N	Median	Earliest	Latest
2000	4	22-Jun	05-Jun	08-Aug
2001	6	05-Jun	24-Apr	28-Jun
2002	5	05-Jun	01-May	24-Jun
2003	6	25-Jun	16-Jun	25-Jul
2004	8	15-Jun	03-Jun	12-Jul
All years	29	15-Jun	24-Apr	08-Aug

Annual Reproduction

Females on our study sites generally reared one litter per year. Most (5 of 6) first year females that survived to the breeding season were confirmed to give birth; the reproductive status of 2 additional yearlings was not determined. Newborn squirrels typically remained hidden in the natal dens until 6-8 weeks old when they began venturing out onto the natal tree during the female’s prolonged absences. Litters typically stayed in the natal den 1-2 weeks after the young began emerging and then moved with the female to a nearby shelter nest in a pine or fir. Once the litter moved to a shelter nest accurate counts of young no long were possible.

The number of young raised to emergence age (approx. 8 weeks old) averaged 2.5/female/year and ranged from a high of 4.0 in 2000 to a low of 1.6 in 2004 (Table 2). Low productivity in 2004 likely was caused by poor condition of some females resulting from notoedric mange. One female (2341) was determined by video to have a litter on 29 April, but apparently abandoned that litter and ultimately succumbed to the disease in early July. A second female (2282) also with severe mange was determined to have a litter on 4 May but apparently abandoned that litter before being killed by a predator in early July. Three of 11 females (27%) did not successfully raise young in 2004. Overall, the proportion of females found to successfully raise young averaged 89% over 6 years (n = 45). The mean number of young raised to emergence by 6 yearling females that were known to have litters was 2.2 (range 0-4).

Number of young in litters averaged 3.3 and ranged from 2-5 (Table 2). Values used in this analysis include only litters where a count was possible before the young emerged or, in a single case, where an emergence count revealed the maximum reported for the species (5). Most video counts of neonates were minimum counts because small young can remain hidden in the nest material; uncertain video counts were modified when emergence data were available. Partial mortality (pre-emergence) was evident in only one of 19 litters (5%).

Lifetime reproduction

Four females were tracked for 3 or more years allowing us to examine the potential contribution of longer-lived, established females to the population. Female 2253 was captured as a juvenile and raised a total of 9 young over 4 breeding seasons before her death. Female 2056 raised 13 young over 4 seasons and female 2038 raised 11 young over 3 seasons. Both were captured as adults and may have had young in years prior to capture. Female 2019 raised 15 young over 6 seasons and may survive to breed again in 2005. Over the course of this study, these 4 females raised a combined total of 48 young to the point of emergence, or 2.8 young/year/female.

Table 2. Litter size and annual productivity (young/breeding female) of western gray squirrels on Klickitat Wildlife Area.

	Litter size [a]			Young produced [b]		
Year	N	Mean	Range	N	Mean	Range
1999	--	--	--	5	2.2	1-3
2000	2	4.5	4-5	4	4.0	3-5
2001	6	3.5	3-4	8	3.1	1-4
2002	5	3.2	3-4	10	2.7	0-4
2003	5	2.6	2-3	7	2.3	0-3
2004	1	3.0	--	11	1.6	0-3
All years	19	3.3	2-5	45	2.5	0-5

[a] Includes only those females where an early indication of litter size was obtained.
[b] Includes only females where a complete count of young was achieved before the young left the natal dens or females that were determined not to have successfully reared young.

Photo: Anesthetized, lactating female western gray squirrel exhibiting enlarged teats and nuzzle marks.

Young/adult female—A general index to productivity often is derived by using the ratio of young to adult females captured in the fall. On our study area, this ratio for both KWA grids combined ranged from 0.69 to 1.67 and averaged 1.0 over 5 years (Fig. 1). These values contrast sharply with productivity values determined by monitoring radio-collared females, both in magnitude and in annual trend (Fig. 1).

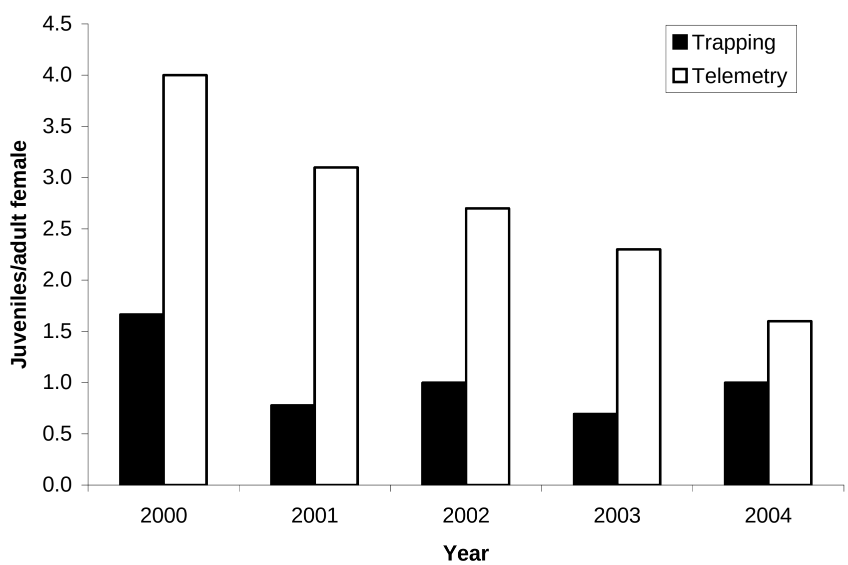

Figure 1. Ratios of juveniles/adult female in the population derived through fall trapping on Klickitat Wildlife Area (Trapping) and by documenting the reproductive success of radio-collared adult females (Telemetry).

DISCUSSION

Reproductive success of western gray squirrels in Washington was similar to that reported from studies in California. Ingles (1947) reported a mean of 2.7 (n=9) young produced per female based on observations at nest sites (presumably emergence counts) in northern California. Mean litter size reported for a study population in southern California was 3.0 (n=72), as determined from embryo counts from females collected February-August (Asserson 1974). Although the long breeding season for western gray squirrels has led some to suggest that females may raise 2 litters/year (Cross 1969), studies in California have failed to document multiple litters (Ingles 1947, Asserson 1974). One litter per year also appears to be the norm in Washington, where in several years of intense radio tracking we have not recorded a definitive case of multiple litters. However, circumstantial evidence from one female in 1999 (M. Linders, pers. comm.) and from one female in 2003 suggests that multiple litters may occur, albeit at a very low rate.

That notoedric mange not only causes mortality in squirrels but can also affect productivity was evidenced in 2004 when 2 females with severe mange abandoned their litters. The severe energetic demands on lactating females apparently were too much for these animals that also were dealing with the bacterial infections and increased thermoregulatory costs inherent with mange. However, animals may recover from mange, even from severe cases. One female that was trapped in April with a severe case of mange and low body weight recovered and successfully raised a litter later that summer.

The disparity in reproductive success derived by trapping versus telemetry presents interesting questions concerning which, if either, is a realistic expression of recruitment. There are several possible reasons why these two measures of reproductive success might differ. First, the numbers derived from tracking females over the breeding season estimate production at the point where the young leave the den sites and do not reflect loss to mortality over the 2-3 months between emergence and fall trapping. Young animals tend to be naïve and may be subjected to high rates of predation during their first months out of the den. Second, some unknown proportion of young may be dispersing off of the trapping grids between emergence and fall trapping. If the populations on our trapping grids are more productive than those in surrounding areas there may be a net loss of juveniles during such dispersal events. Third, juvenile squirrels may be less “trappable” than adults, perhaps not recognizing the walnut bait as food. Over 5 years of grid trapping in fall we have noticed a low recapture rate of juveniles within a trapping session compared to adults. The important questions of early juvenile dispersal and survival will be addressed during the 2005 field season.

ABUNDANCE ESTIMATES

Photo: western gray squirrel in ponderosa pine.

METHODS

We live-trapped squirrels on the east study grid beginning in 2000, on the west grid beginning in 2001, and at Dead Canyon beginning in 2004. Traps were set out on a 12x12 trapping grid with 80m spacing (144 traps total). Traps were baited with whole English walnuts and were wired open for 2 weeks prior to trapping to allow animals to become familiar with the traps. Trapping took place over 8 days, with traps set at first daylight and then checked and closed beginning at 1100 hours. All traps were closed by sunset. All animals were handled on their first capture and simply identified and released on subsequent captures.

We used mark-recapture techniques to estimate the abundance and density of squirrels on the study areas. Program CAPTURE (White et al. 1982) was used to derive adjusted abundance values based on recapture data. Density estimates based on log-likelihood methods generally had high variance values so we calculated simple densities by dividing adjusted abundance by study size area.

RESULTS

We handled 149 individual squirrels during 17 trapping session (651 total captures) between 2000 and 2004 (Table 1). Numbers of squirrels on individual study sites, as estimated by program CAPTURE, ranged from 8 to 17 in spring and somewhat higher, 13 to 33, in fall. Density of animals on the study sites averaged 0.23/ha (0.08 SE) and tended to be greater in fall than in spring. Abundance of squirrels on the west grid was significantly lower than on the east grid in both spring and fall of 2003 and was significantly greater than on the east grid in spring of 2004 (Fig. 1). Abundance of squirrels on the Dead Canyon site was significantly greater than that on the East Grid in spring 2004; all 3 sites had similar abundances in fall 2004.

Table 1. Abundance and density of western gray squirrels on 3 study sites in Klickitat County, Washington.

Site	Period	Year	N[a]	N_{est}[b]	SE	Density[c]
East grid	Spring	2001	12	12	0.99	0.16
		2002	17	18	1.67	0.23
		2003	14	17	3.50	0.22
		2004	10	10	0.61	0.13
	Fall	2000	12	15	3.30	0.19
		2001	18	18	0.79	0.23
		2002	18	22	4.41	0.28
		2003	18	33	7.88	0.43
		2004	12	16	4.30	0.21
West grid	Spring	2002	15	15	0.86	0.19
		2003	8	8	0.89	0.10
		2004	14	14	0.18	0.18
	Fall	2002	21	31	6.21	0.40
		2003	12	13	1.36	0.17
		2004	14	18	3.55	0.23
Dead Canyon	Spring	2004	16	20	3.70	0.26
	Fall	2004	16	17	1.30	0.22

[a] Number of animals captured during 8-day trapping period.
[b] Number of animals estimated to be using the 77.4 ha grid, derived using program CAPTURE.
[c] Estimated density of squirrels on the study area (squirrels/ha = N_{est} /77.4).

DISCUSSION

Densities of western gray squirrels on the 3 study sites were lower than those reported for populations in California (Grinnell and Storer 1924, Asserson 1974, Hall 1980). Densities in California range from 1.0/ha in Shasta County (Gilman 1986) to 4.3/ha in a Butte County park where introduced mast-producing trees provided supplemental food (Ingles 1947). Unfortunately, these studies used a variety of methods to derive density estimates, making direct comparisons difficult. The most appropriate dataset for comparison with Washington likely come from a study in northern California where densities were estimated using grid-trapping and maximum likelihood estimation (Hall 1980). Values from this study ranged from 1.37 to 2.16/ha in spring and 1.5 to 2.37 in fall (Hall 1980). Densities of western gray squirrel in Washington were closer to those reported for the closely related tassel-eared squirrel in ponderosa pine forests in northern Arizona, where values averaged 0.25/ha in January, 0.35 in April, and 0.44 in August (Dodd et al. 2003). Squirrel populations on these Arizona sites were affected by long-term drought and very low rates of recruitment (Dodd et al. 2003).

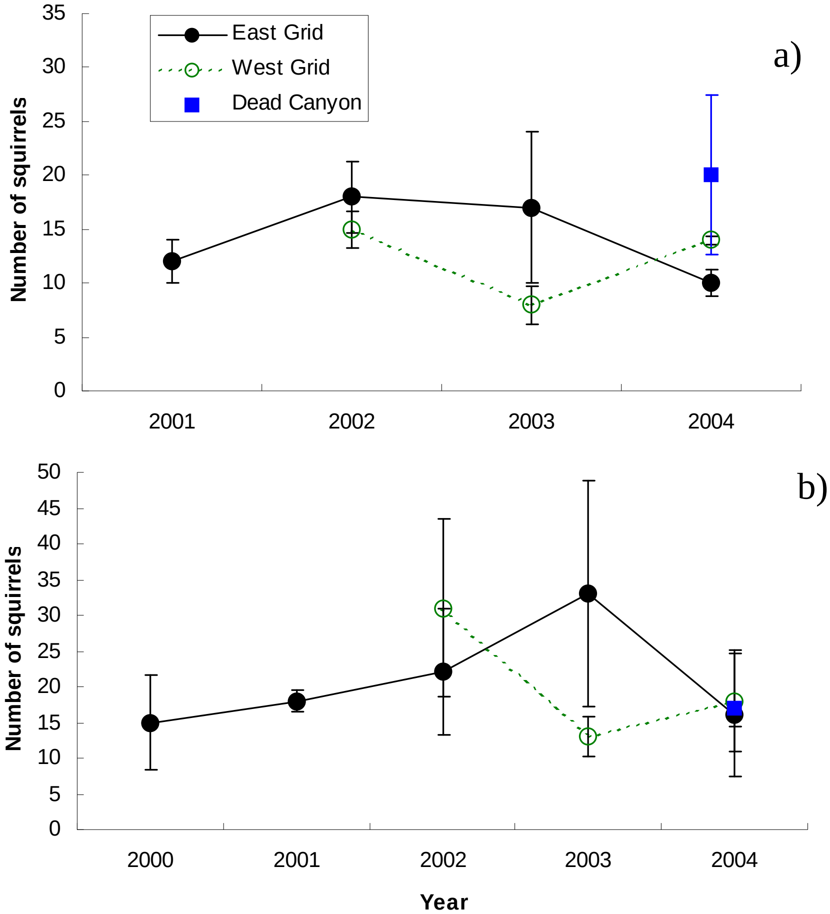

Figure 2. Spring (a) and fall (b) abundance estimates (with 95% CI) for western gray squirrels on 3 study sites in Klickitat County, Washington.

MOVEMENTS

Photo: Juvenile western gray squirrel

METHODS

Radio-collared animals were tracked 1-3 times/week through the year and locations derived by approaching them on foot using hand-held receivers and 2-element "H" antennas. When strength and direction of the radio signal indicated that the animal was nearby, binoculars were used to attempt obtaining visual confirmation and, when possible, to observe the animal's condition and behavior. Coordinates (UTM) for the location were derived via GPS and were recorded, along with characteristics of the surrounding stand and other ancillary information, using a PDA and Pendragon Forms data-logging program.

Core use areas were defined by 50% fixed-kernel utilization distributions using the Animal Movements extension in Arcview 3.2. The smoothing parameter was derived using least squares cross validation and the appropriate grid size was calculated by the program. Core use areas were determined for females with $\geq$30 locations within a calendar year. To avoid complications related to non-independence of locations, repeated locations at nest sites (including natal dens) were eliminated from female/year datasets.

Juvenile dispersal was assessed by tracking the movements of young of the year captured on the study area in the fall and followed through at least 28 February of the following year. We assumed that juveniles captured on the study grid in September and October were produced by females resident on the grid, although this remains untested. We considered a permanent movement of >1000m to represent dispersal. Dispersal distances were measured as the linear distance from the center of the capture study grid to the center of the new use area as determined from telemetry locations. Animals that died or were lost shortly after moving the requisite 1000m from the capture grid were assumed to have dispersed and distance was measured from their last telemetry location.

RESULTS

Home range (95% fixed-kernel) estimates for female western gray squirrels averaged 18.7 ha (9.9 sd; range = 1.9 - 42.4, n = 49) and included estimates for multiple years for 10 individuals. Core use areas averaged 4.29 ha (2.25 sd; range = 0.5-10.8 ha, n = 49) over 3 years. Examination of core use area plots for years 2001-2003 revealed little overlap among females within a year, suggesting exclusive use of these core areas (Figure 1). Females demonstrated strong fidelity to core use areas from year to year (Figure 2) although the size of these areas varied among years. All 10 females with sufficient locations to calculate core use areas for $\geq$2 years maintained similar core areas. In 4 separate cases core areas established by a female were "taken over", in whole or in part, by a second female following the death of the first.

Dispersal information was available for 30 juvenile squirrels captured and radio-marked on the study grids during 2000-2003. Twenty percent of the juvenile squirrels dispersed from the study grid where they were captured. Dispersal rates for males (3 of 13) and for females (3 of 17) were similar. Mean dispersal distance was 2862 m (213 SD). Maximum dispersal distance was recorded for a male that was killed by a predator 5116 m from the capture grid. Three of 6 dispersing animals died within 6 months of moving; 2 disappeared (likely due to radio failure), and one established a home range 2.7 km from the capture grid.

DISCUSSION

Female western gray squirrels established core use areas that generally were unique from those of other females. Presumably these areas contain some resources that enhance the individual's reproductive potential. Once established, these cores areas appear to be maintained by the female from year to year, possibly over her lifetime. The value of these core areas and their potential importance to the population is suggested further by the assumption of these areas by another female following the death of the resident female. Whether these animals are related is unknown. Moreover, use of core areas by females was not always exclusive: in several cases, the core use area of 2 females overlapped. These instances may represent a female sharing part of her area with a female offspring. We plan to explore these questions using genetic markers.

The majority of juvenile squirrels remained in the general area where they were originally captured and did not disperse. The dispersal rate we report may overestimate the actual value as we assumed that the animals would not have moved back to their natal area. Similarly, our estimate also may underestimate the distance that gray squirrels disperse if animals that died or were lost (5 of 6) had not completed their dispersal movements. It is possible that some dispersal may have taken place before fall capture efforts began (i.e., within 2-3 months after emerging from the den). We plan to examine this issue by marking a sample of young before they leave the natal den.

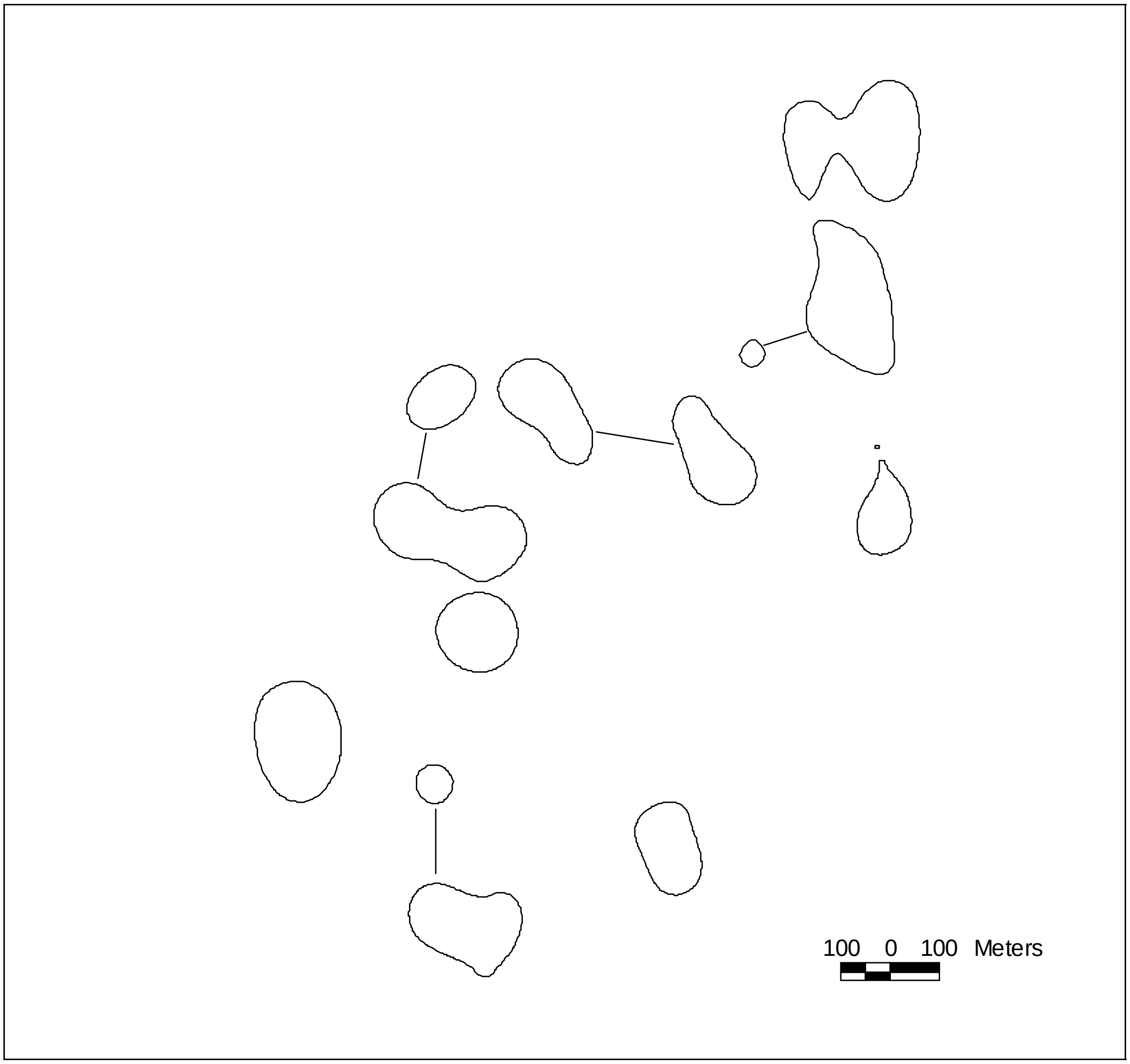

Figure 1. Core use areas (50% fixed-kernel estimates) for 9 adult female western gray squirrels on Klickitat Wildlife Area (east grid) for the year 2001. Polygons connected with lines represent disjunct areas used by the same female.

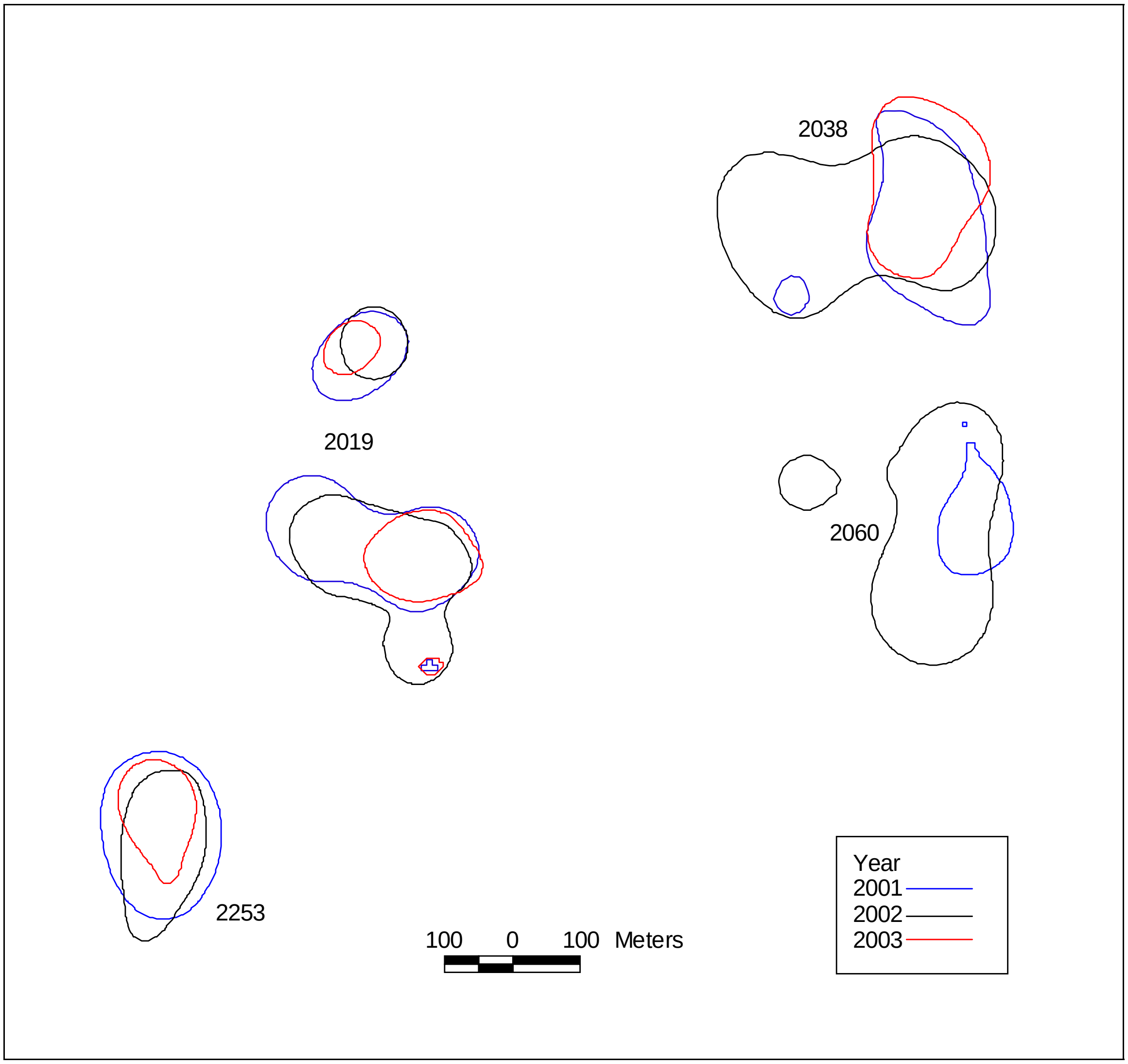

Figure 2. Core use areas (50% fixed-kernel estimates) for 4 adult female western gray squirrels on Klickitat Wildlife Area (east grid).

VEGETATION SAMPLING

Photo: Measuring vegetation on Klickitat Wildlife Area

METHODS

Characteristics of Study Areas

Vegetation of the east and west study sites on Klickitat Wildlife Area was sampled 9 August – 11 September 2004. Primary sampling occurred within nested circular plots centered on each grid point. Trees were measured within a 10.6m radius circular plot and stems >5cm dbh (diameter at breast-height) were tallied by species and measured for dbh. Closure of the uppermost tree canopy was estimated using ocular estimation with a single value recorded for the plot using the following cover classes: 1) 0-1%, 2) 2-5%, 3) 6-25%, 4) 26-50%, 5) 51-75%, 6) >75%. Samplers were first trained on sites where canopy closure had been estimated using a Moosehorn coverscope. Shrubs and saplings were sampled within a 5.6m radius plot, with stems <5cm dbh tallied by species in 2 height classes: 0.5-2m and 2-8m. "Modal" height (height of the majority of plants) was estimated by eye for each of the height classes. Closure of the canopy within each of the 2 height classes was estimate within the 5.6m radius plot using ocular estimation. Course woody debris (CWD) also was sampled within the 5.6m radius plot. Downed trees were tallied by decay class and dbh class for all logs >10cm diam (large end) that fell within the circle. Ground cover (plants <0.5m tall) was estimated within the 5.6m radius plot. Percent of the ground obscured by each of the following groups were estimated by ocular estimation: grasses, forbs, coniferous tree seedlings, deciduous tree seedlings, vines, hard-leaved shrubs, moss, litter (leaves, needles, and fallen branches <10cm in diameter), CWD (fallen branches and trees >10cm diameter), rock, and bare soil.

Connectivity of the upper canopy trees was measured for the tree (>12.5cm dbh) closest to point center. We counted the number of adjacent upper canopy trees that had canopies that touched, or were within 1m of touching, the canopy of the focal tree.

Very large trees (> 50cm DBH) are rare on the landscape and were likely to occur on few plots. We sampled for these larger trees along a 40m-wide belt transect when walking from one sample point to the next. Candidate trees were viewed with a laser rangefinder and those within the belt transect were tallied by species.

Characteristics of natal den trees

We measured the characteristics of natal den trees and their surrounding stands on the Klickitat Wildlife Area 9 August – 11 September 2004. We sampled vegetation within nested 10.6m and 5.6m radius circular plots centered on the den tree using the same methods that were used to characterize vegetation at the grid points. We also measured the height, dbh, and condition (percent live crown) of the den tree as well as the height, diameter, and position in the tree of the cavity entrance. For comparison, we collected similar data (excluding cavity entrance measurements) on a sample of random trees within each study grid. Because a subset of the natal den trees was located off of the study grids, we collected data on a random oak near each of these dens to increase the likelihood that our random sample represented potential den trees available to the squirrels. Random oaks off the study grids were selected by pacing 80m on a random bearing from the den tree and selecting the nearest oak $\geq$ 24cm dbh.

Photo: Oregon white oak den tree

RESULTS

Vegetation was characterized for 144 points on each of the east and west study grids. Forty five natal den trees were characterized, along with 112 random oaks on the study grids and 21 random oaks off the study grids. Data will be analyzed in 2005.

MAST SURVEYS

Photo: Oregon white oak

METHODS

We obtained an index to mast production for ponderosa pine and Oregon white oak at even numbered grid points (72 points/grid) in August from 2002 to 2004. The closest tree (>10cm dbh for oak, > 20cm for pine) of each species was marked with a metal tag as the focal tree for that point. If no suitable tree was found within 25m of the grid point, that species was excluded from the sample for that point. An observer then viewed each focal tree with binoculars, counting the number of cones or acorns of the current year visible on one side of the tree. Each tree was then classified into one of 4 groups base on number of acorns or cones visible: none visible, 1-10 visible, 11-25, 26-50, and >50. The same trees were sampled each year.

RESULTS AND DISCUSSION

Data were collected annually for 72 pine trees and 68 oaks on the east grid, and for 63 pines and 72 oaks on the west grid. Mast crop for both species varied widely across the 3 years (Fig. 1). Very few oaks were recorded with acorns in 2002, whereas most of the oaks sampled had acorns in 2004. The acorn crop in 2003 was intermediate. The pine crop was very low in 2003, intermediate in 2004, and greatest in 2002 when over half of the trees sampled had cones. Patterns of mast abundance were similar between study sites.

Western gray squirrels began feeding on pinecones as early as June most years; an unknown proportion of cones were consumed before our August surveys. Acorns developed later in the summer and generally were available to squirrels only briefly before our surveys began. For both species, the survey results represent a relative index of availability among years.

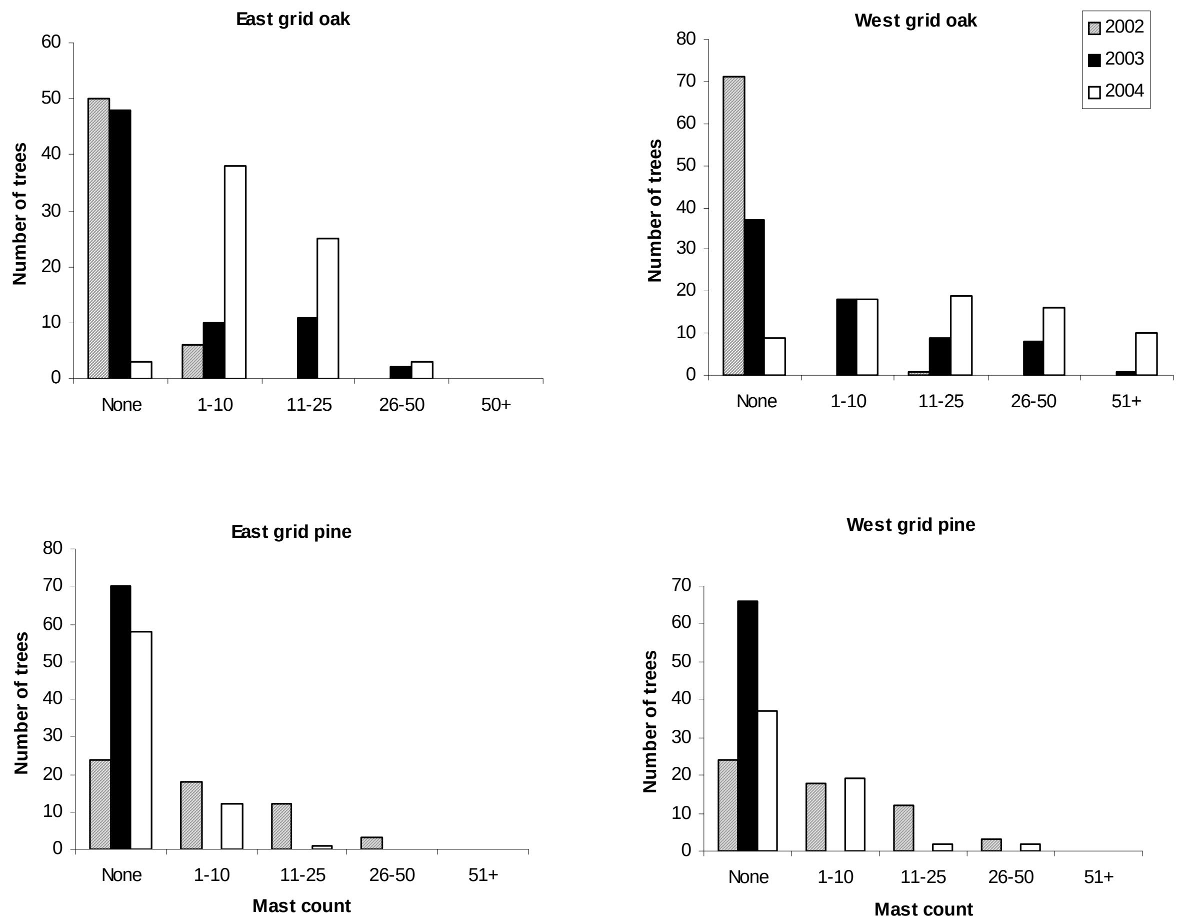

Figure 1. Number of Oregon white oak and ponderosa pine trees counted with varying mast on the Klickitat Wildlife Area, Klickitat County, Washington. Results are presented separately for the east and west study grids.

FUTURE PLANS

Photo: Ponderosa pine cone and cone cores stripped by foraging squirrels

POPULATION STUDIES

- We will continue documenting annual survival and productivity with two specific goals in mind. First, we need to examine relationships among population parameters and environmental variables; specifically, food availability, winter weather (temperature and snow depths), and the occurrence and severity of mange. Second, we need to model the population trajectory and assess which parameters play key roles in determining that trajectory. Determining the range of annual variability in population and environmental parameters is a critical part of this process and additional years of data will strengthen our ability to draw conclusions.

- The fate of juvenile squirrels between emergence from the natal den and our fall capture activities remains a black box with the potential to significantly alter the dispersal and juvenile survival data reported here. To fill this data gap, we will capture and tag a sample of young squirrels before they leave the natal den.

- We will pursue development of microsatellite markers with the goal of examining the genetic relationship among animals within and among populations in Klickitat County. Measuring relatedness of individuals among different populations will allow us to estimate the degree of dispersal and genetic transfer across the landscape.

EFFECTS OF TIMBER HARVEST

One of the goals of this project is to examine the effects of timber harvest on western gray squirrel populations. Extensive searches within Klickitat County earlier in the study failed to identify suitable sites with nesting colonies of squirrels that also were slated for timber harvest. Indeed, most sites with known colonies on commercial or state timberlands have been harvested within the last 20 years (WDFW unpublished data). Addition of the Dead Canyon site to the study in 2004 provides the opportunity to document the response of western gray squirrels to forest management; the site is scheduled for a selective harvest in 2005 or 2006. The west grid site on the KWA also may undergo a timber harvest in 2005 or 2006, as it has been identified by WDFW Lands Division staff as a suitable candidate for forest health thinning. Western gray squirrels likely would benefit from thinning the dense stands of young pine and oak on KWA; an experimental harvest on the west grid could help to determine suitable prescriptions for habitat improvement.

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