But They Breed Like Rabbits, Don't They? Plight of the Western Gray Squirrel in Washington

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Extended Abstract: An icon of oak-conifer woodlands along the west coast of the United States, the native western gray squirrel (*Sciurus griseus*) struggles to maintain its foothold in Washington State. Hunting seasons were closed in 1950, but population levels have failed to rebound. Klickitat County, in south central Washington, has long been considered the core of Washington's western gray squirrel population, yet population densities of 0.1–0.2 squirrels/ha are among the lowest reported for any tree squirrel in North America. Research on radio-collared squirrels indicates that females occupy large home ranges and nearly exclusive core areas centered on stands of large ponderosa pine (*Pinus ponderosa*). Site fidelity is high for reproductive females, and newcomers readily occupy core areas vacated when a resident female dies. These observations are consistent with the assumptions of Moffat's equilibrium, which are (1) breeding sites are limited and defended from potential conspecific competitors (i.e., breeders), and (2) all available breeding sites are occupied (Moffat 1903; Hunt 1998). Moffat worked with breeding birds and found that individuals maximize their lifetime reproductive fitness by delaying breeding until a site of sufficient quality becomes available. These potential breeders are termed floaters, and their presence is indicative of a population at equilibrium.

We used Moffat's test to determine whether western gray squirrels in Klickitat County exist in a state of population equilibrium. A Microsoft Excel workbook programmed with Moffat's equations (Hunt and Law 2000) was run with the following parameters: (1) adult survival averages 0.61 ± 0.19 SD (n = 31 for 1999, n = 13 for 2000, n = 22 for 2001, and n = 44 for 2002 [measured]), (2) reproductive rate averages 3.0 ± 0.9 young per litter (n = 30 [measured]), (3) a 1:1 sex ratio for adults and juveniles, (4) subadult survival is 0.60 (assumed for a good food year [Gurnell 1987]), (5) juvenile survival is 0.50 (assumed for a good food year [Gurnell 1987]), (6) squirrels live for 9 years, (7) squirrels are subadults for 1 year, and (8) reproductive rates are the same for adults and subadults. Population size was set arbitrarily, beginning with 100 breeding females and 100 territories.

Western gray squirrels in Klickitat County failed Moffat's test, showing a lack of floaters (-86) and appearing to be in decline. We then ran a model of unconstrained population growth (λ) to determine what rates of survival and reproduction are required to reverse current trends

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and move toward recovery. We tested survival rates for juveniles and adults at increments of 0.1, and adult survival at 0.61. We tested subadult survival at 0.5 and 0.6, and fecundity at 1.5 based on the 5-year average, and at 1.95, one standard deviation above the mean. Assumptions about life span, reproductive rate, and subadulthood also apply to the model of unrestricted growth, however, no constraints regarding use of space apply. Resulting values for λ were tabled by reproductive rate and subadult survival (Table 1). The standard deviation for measured survival (0.61 ± 0.19) was used to narrow the range of potential growth that can be expected based on existing knowledge.

The tabled values for unrestricted population growth indicate that given current reproductive rates, juvenile survival would need to exceed 0.6–0.7 (depending on subadult survival) to reach equilibrium, assuming that adult survival could be increased to 0.80, one standard deviation above the current average. Western gray squirrel recovery efforts will focus on increasing habitat quality through active management of the two primary mast-producing species, Oregon white oak (*Quercus garryana*) and ponderosa pine. Stabilizing and increasing mast production will likely also stabilize population fluctuations by increasing survival rates for squirrels of all ages.

Table 1. Potential values for unrestricted population growth (λ [lambda]) for western gray squirrels in Klickitat County, Washington.

Adult Survival

Juvenile Survival

	0.55	0.65	0.75	0.85	0.95	0.61
0.30	0.64	0.74	0.82	0.89	0.95	0.70
0.40	0.72	0.80	0.88	0.94	1.00	0.77
0.50	0.77	0.85	0.92	0.98	1.04	0.82
0.60	0.82	0.89	0.96	1.02	1.07	0.87
0.70	0.86	0.93	0.99	1.04	1.09	0.90
0.80	0.90	0.96	1.02	1.07	1.11	0.93
0.90	0.93	0.98	1.04	1.09	1.13	0.96
1.00	0.95	1.01	1.06	1.11	1.15	0.99

Subadult survival = 0.50
 # females/female = 1.50

	0.55	0.65	0.75	0.85	0.95	0.61
0.30	0.69	0.78	0.86	0.92	0.98	0.74
0.40	0.76	0.84	0.91	0.98	1.03	0.81
0.50	0.82	0.89	0.96	1.01	1.07	0.87
0.60	0.87	0.93	0.99	1.05	1.10	0.91
0.70	0.91	0.97	1.02	1.08	1.12	0.95
0.80	0.94	1.00	1.05	1.1	1.14	0.98
0.90	0.97	1.03	1.07	1.12	1.16	1.00
1.00	1.00	1.05	1.10	1.14	1.18	1.03

Subadult survival = 0.60
 # female offspring/female = 1.50

	0.55	0.65	0.75	0.85	0.95	0.61
0.30	0.71	0.80	0.87	0.94	1.00	0.76
0.40	0.78	0.86	0.93	0.99	1.05	0.83
0.50	0.84	0.91	0.97	1.03	1.08	0.88
0.60	0.89	0.95	1.01	1.06	1.11	0.93
0.70	0.93	0.99	1.04	1.09	1.14	0.96
0.80	0.96	1.02	1.07	1.11	1.16	1.00
0.90	0.99	1.04	1.09	1.13	1.18	1.02
1.00	1.02	1.07	1.11	1.15	1.19	1.05

Subadult survival = 0.50
 # females/female = 1.95

	0.55	0.65	0.75	0.85	0.95	0.61
0.30	0.76	0.84	0.91	0.97	1.03	0.81
0.40	0.83	0.90	0.97	1.02	1.07	0.87
0.50	0.89	0.95	1.01	1.06	1.11	0.93
0.60	0.94	0.99	1.05	1.09	1.14	0.97
0.70	0.97	1.03	1.08	1.12	1.16	1.01
0.80	1.01	1.06	1.10	1.15	1.19	1.04
0.90	1.04	1.08	1.13	1.17	1.2	1.07
1.00	1.06	1.11	1.15	1.18	1.22	1.09

Subadult survival = 0.60
 # females/female = 1.95

Yellow-shaded cell values are < λ = 1.0 and indicate population decline (Hunt 1998). Parameters listed below tables indicate the variable altered during modeling; additional assumptions in text. Adult survival = 0.61 was calculated from data on radio-tracked western gray squirrels (n = 31 for 1999, 13 for 2000, 22 for 2001, and 44 for 2002) on the Klickitat Wildlife Area in Klickitat County, Washington during 1999–2002. Number of female offspring per female was calculated using reproductive data from the same site (n = 25 litters and 70 young). The vertical black line at adult survival = 0.80 indicates one standard error above the mean survival rate (0.61); the lower bound is off the left end of the table.

References

Gurnell, J. 1987. The natural history of squirrels. Facts on file publications, Oxford, England.

Hunt, W.G. 1998. Raptor floaters at Moffat's equilibrium. Oikos **82**:191–197.

Hunt, W.G., and P.R. Law. 2000. Site-dependent regulation of population size: comment. Ecology **81**:1162–1165.

Moffat, C.B. 1903. The spring rivalry of birds: some views on the limit to multiplication. Irish Naturalist **12**:152–166.