WINTER 2002

SEASONAL VARIATION IN VERTICAL DISTRIBUTION OF DOUGLAS' SQUIRREL, TAMIASCIURUS DOUGLASII, IN AN OLD-GROWTH DOUGLAS-FIR AND WESTERN HEMLOCK FOREST IN THE MORNING

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Douglas' squirrel, Tamiasciurus douglasii, occurs in southwest British Columbia, western Washington, western and central Oregon, and northern California (Hall 1981), where it is a diurnally active tree squirrel in coniferous forests. Douglas' squirrel eats seeds from conifer cones, truffles and other fungi, nuts, fruits, shoots and buds of coniferous trees, and occasionally maturing pollen cones, bird eggs, and young birds (Maser 1998). Douglas' squirrel population densities are affected strongly by fluctuations in food supplies (Sullivan and Sullivan 1982), and old-growth forests appear to be higher quality habitat for the squirrels due to greater and more reliable quantities of conifer seed (Buchanan and others 1990; Carey 1991).

The requirements for food, shelter, and predator-avoidance of Douglas' squirrel influence its vertical use of the forest. However, little information exists on seasonal vertical distribution within the forest canopy by Douglas' squirrels. The objectives of this study were to compare the number of morning detections of Douglas' squirrels within 3 different forest canopy height zones of an old-growth Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) forest and to compare them among seasons. A construction crane, installed in a natural old-growth forest for canopy research and observation, provided the unique opportunity to survey the vertical patterns.

The study site was located at the Wind River Canopy Crane Research Facility in the T. T. Munger Research Natural Area, Wind River Experimental Forest, Gifford Pinchot National Forest, in the Cascade Mountains of southwestern Washington at 371 m elevation (Franklin 1972; Parker 1997). The forest is a classic oldgrowth Douglas-fir and western hemlock forest approximately 500 yr old and is described in Franklin (1972) and Franklin and DeBell (1988). The forest is characteristically tall, with Douglas-fir reaching 65 m (average height 52.2 m) and western hemlock reaching 55 m (average height 19.0 m). Stand density is 435 trees/ ha and basal area is 82 m²/ha. Cone production generally occurs above 40 m.

Squirrels were surveyed during weekly avian censuses (Shaw and Flick 1999) from March 1996 to March 1999 (n = 121 surveys). We defined the forest canopy as the forest floor (ground) up to the apex of the tallest tree where light is available for photosynthesis. The canopy was divided into 3 zones; lower (ground to 20 m), middle (20 to 40 m), and upper (40 to \geq 60 m). The construction crane lifted 2 observers into the canopy in a gondola that was lowered to 50 m, 30 m, and 10 m in sequence. At each level, squirrels were detected by sight or sound using a fixed-area point count (Manuwal and Carey 1991) in a 30-m radius, 360° plot vertically limited to that height zone and at a distance of 85 m from the center of the crane. Each plot was surveyed for 5 min for a total of 20 min at each canopy zone. Detections were summed for each zone for each survey day. Surveys began within one-half hour of dawn during March to October, and at mid-morning during November to February. We waited 3 min before beginning the 5 min observation to allow for squirrels and birds to resume activity after disturbance.

Detecting squirrels was a secondary objective in a survey protocol designed to assess small bird activity. Squirrel behavior was not quantified. Monthly survey totals for the 3-yr

124 NORTHWESTERN NATURALIST

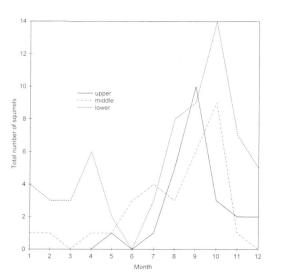
period were: January–8, February–9, March–7, April–10, May–13, June–12, July–14, August–10, September–11, October–11, November–6, and December–10. We defined 3 seasons, based on weather patterns, for comparison of squirrel vertical detection patterns: winter (December to March), early (April to July), and late (August to November).

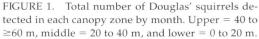
A Welch Modified *t*-test (S-Plus, 2000 Pro R3) was used to compare number of squirrel detections by month and by season to test whether means were significantly different at $P \leq 0.05$. In this procedure there is no assumption of equal variance in the distributions from which the means were calculated.

A total of 117 detections were noted during 121 surveys. Douglas' squirrels were detected most commonly during August, September, October, and November when the average for each month was >1.5 squirrels per survey day. The monthly detections averaged <1 squirrel per survey for the remainder of the year. Average number of detections was 0.5 per survey day for early and winter seasons and 2 per survey day during the late season. Douglas' squirrels were detected 23 times (20%) in the upper canopy, 30 times (26%) in the middle canopy, and 64 times (55%) in the lower canopy. However, during winter, >80% of the detections were in the lower canopy, and the animals were detected rarely in the middle and upper canopy (Fig. 1). There was a distinct shift in the number of detections to the middle and upper canopy during the early and late seasons, with most upper canopy detections occurring during the late season (Fig. 1).

The mean number of squirrel detections between the upper and lower canopy were significantly different only in April (t = 2.714, df = 9, P = 0.02) and October (t = 2.593, df = 13, P = 0.02). There were no seasonal differences in canopy use except in winter when the squirrels were rarely detected above 20 m. The mean number of detections during the winter in the lower canopy was significantly different from the mean number of detections in either the middle or upper canopy (t = 2.4205, df = 28, P< 0.003).

Our data suggest that, at this location, Douglas' squirrels occur in the upper canopy primarily during late summer and early fall, and are generally restricted to the lower canopy during winter. Douglas' squirrels may have





been detected more often in the late season because mating activity in spring increases the population size in August to November (Smith 1968; Koford 1982; Carey 1991), so that more squirrels were present during surveys in the late season. Increased activity associated with cone collection and territory defense (Smith 1968; Carey 1991) may also have increased the likelihood of detection.

The major food resources of the middle and upper canopy are conifer cones (July to November), bird nests (April to July), and young conifer shoots (June). Squirrels were detected in the upper canopy >10% of the time only during the late season when cone crops were maturing, suggesting that the use of the upper canopy may be restricted generally to food acquisition. The upper canopy at this site is open, with isolated tree crowns (Parker 1997), possibly increasing exposure to predators and therefore decreasing general use by squirrels. The major winter food resource for squirrels is cached food. Food is usually hidden in underground burrows, hollow stumps, hollow fallen trees, along streams, in moist depressions, or under moss on the ground (Carey 1991; Maser 1998); upper canopy zones offer few locations for caching. In this old-growth Douglas-fir and western hemlock forest, Douglas' squirrel is an animal of the forest floor and lower canopy, except during late summer and fall when it can

83(3)

WINTER 2002

GENERAL NOTES

be detected in the upper canopy, presumably in search of food.

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