Maturation and Reproduction of Northern Flying Squirrels in Pacific Northwest Forests

Lisa J. Villa, Andrew B. Carey, Todd M. Wilson, and Karma E. Glos

Authors

LISA J. VILLA is a wildlife biologist, ANDREW B. CAREY is a principal research biologist, TODD M. WILSON is a wildlife biologist, and KARMA E. GLOS is a biological technician, Pacific Northwest Research Station, 3625 93d Ave. SW., Olympia, WA 98512-9193.

Abstract

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Northern flying squirrels are the primary prey of northern spotted owls and are important dispersers of fungal spores in Pacific Northwest forests. Despite the importance of these squirrels in forest ecosystems, information is lacking on life history and methods for determining age and reproductive condition. In the laboratory, we measured epiphyseal notch, femur length, rostrum length, least interorbital breadth, rump pelage length and color, and tail width of dead squirrels. We analyzed weight, pelage color, and reproduction for field-collected data from live squirrels. We also described age-class differences in facial features and tail size and shape in the Puget Trough. A birth-year-based age-class system had several advantages over the traditional juvenile-subadult-adult class system. Three age classes can be distinguished in the field, each with varying degrees of accuracy. Reproduction of northern flying squirrels can be reliably determined in live-trapping studies. Enlargement, turgidity, and redness of genitalia are detectable signs of reproductive activity, whereas reduction, flaccidity, and paleness signal inactivity for both males and females. Nipple length is the best indicator for distinguishing sexual maturity of inactive females. The most effective way to avoid mistakes and ambiguity about age and reproductive status in the field is to take descriptive notes. Maturation and reproductive patterns were similar among the Puget Trough, Olympic Peninsula, and northern Cascade studies in Washington. Squirrels in the Coast Range of Oregon, however, displayed different patterns. Regional populations differed in proportion of females reproductively active, the reproductive maturity of yearling females, and survivorship across age classes. Regional variations suggest accurate assessment of age and reproduction is a prerequisite for understanding flying squirrel ecology.

Keywords: Northern flying squirrel, maturation, reproductive biology, Oregon, Washington, live-trapping, necropsy.

Preface

There has been substantial research on old-growth Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) forests and wildlife that depend on them (Ruggiero and others 1991). Northern flying squirrels (*Glaucomys sabrinus* [Shaw 1801]) have been of particular interest because they seem to be keystone species in late-seral forests—a main prey of strigids and mustelids on one trophic level, and a consumer and disseminator of fungal spores on another. Through its mission to develop forest management practices that steward biodiversity, the Ecological Foundations of Biodiversity Research Team has focused research on the relation between northern flying squirrels and forest health.

Despite the importance of northern flying squirrels in Pacific Northwest forest ecosystems, information is lacking on life history and methods for determining age and reproductive condition. We began studying flying squirrel populations in 1985 in Douglas-fir forests of the Coast Ranges physiographic province in southwestern Oregon (Franklin and Dyrness 1973). At that time, there was limited guidance for determining age and reproduction of flying squirrels in the field (Davis 1963, Wells-Gosling 1985). Since then, we have studied flying squirrels in the interior valleys and Klamath Mountains of Oregon, and the Olympic Peninsula, northern Cascades, and Puget Trough of Washington. We combined the skills of field biologists and laboratory technicians to assemble and refine laboratory and field methods for determining age and reproduction.

This report is one in a series of method and biology papers that provide biologists with tools for designing and implementing research and monitoring efforts for Pacific Northwest forests (appendix 1).

Contents

Introduction
World Status of Flying Squirrels

Throughout the world, flying squirrels (Sciuridae: Rodentia) and their habitat are threatened by human activities. Flying squirrels, in various genera, seem to be declining; 11 species and subspecies of flying squirrels are currently considered threatened due to forest depletion (Nowak 1991; table 1). These squirrels are becoming rare, and some species may become extinct before they are even partly understood. Thorough studies of flying squirrels and the forests they inhabit are essential to our understanding of forest ecosystems. Rapid habitat alteration worldwide makes this work urgent.

Ecology in the Pacific Northwest

The northern flying squirrel (*Glaucomys sabrinus* [Shaw 1801])[1] is an important member of the arboreal rodent community of Pacific Northwest Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and mixed-coniferous/deciduous forests. This nocturnal squirrel shares habitats with the diurnal Douglas' squirrel (*Tamiasciurus douglasii* [Bachman 1839]) and semiarboreal diurnal Townsend's chipmunk (*Tamias townsendii* [Bachman 1839]) in the Pacific Northwest (Carey 1991). Northern flying squirrels are the primary prey of northern spotted owls (*Strix occidentalis caurina* [Xántus de Vesey 1860]) west of the Cascade crest (Carey and others 1992, Forsman 1984) and are preyed on by weasels (*Mustela* spp.), marten (*Martes americana* [Turton 1806]), and other carnivores (Wells-Gosling and Heaney 1984, Wilson and Carey 1996). Flying squirrels consume sporocarps of ectomycorrhizal fungi that live symbiotically with forest plants, in particular with conifers in the family Pineaceae (Carey 1995; Maser and others 1985, 1986). Soil is inoculated with fungal spores from squirrel feces. The fungi enhance root systems of Douglas-fir and other conifers, improving water and nutrient uptake (Maser and Maser 1988). Studying flying squirrels will enhance our knowledge of aboveground and belowground processes that can be used to improve forest health and enhance biological diversity (Carey and others 1996).

Importance of Age and Reproduction

Age structure indicates whether populations are increasing, decreasing, or stable (Hutchinson 1978). Fertility and mortality differ by age for many species, and population models can be developed with age-dependent birth and death rates (Johnson 1994). Age structure combined with reproductive development can help determine specific factors that regulate populations. For example, data on reproductive rates, sex ratios, and age structures can be used to calculate gross natality (Harder and Kirkpatrick 1994). Age structure and reproduction are also good indicators of habitat quality (Maguire 1973), whereas density could be misleading as a measure of habitat quality by failing to distinguish between ecological sources and sinks (Van Horn 1983). In addition, reproductive potential and carrying capacity of prey determine the amount of predation a population can sustain and, thus, carrying capacity for predators (Maguire 1973).

Techniques that measure continuous morphological development are commonly used to determine age and reproductive characteristics. These techniques are based on skeletal features, pelage, and genitalia that progressively change from birth to death and provide a permanent record of attained age and reproduction (Larson and Taber 1980). Criteria for ideal age-determination techniques include

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[1] Scientific names for animals are from Banks and others 1987.

Table 1—List of threatened and endangered flying squirrels worldwide

Area	Species	Common name
China (Beijing)	*Aeretes melanopterus*	Grove-toothed flying squirrel
China (Yunnan)	*Trogopterus xanthipes*	Complex-toothed flying squirrel
Finland	*Pteromys volans*	European flying squirrel
Himalayas	*Belomys pearsoni*	Hairy-footed flying squirrel
Nepal	*Hylopetes alboniger*	Arrow-tailed flying squirrel
Pakistan	*Eupetaurus cinereus*	Woolly flying squirrel (Zahler 1996)
Sumatra	*Petinomys* spp.	Dwarf flying squirrels
Thailand, Malaysia	*Pteromyscus pulverulentus*	Smoky flying squirrel
U.S. (Southeast)	*Glaucomys sabrinus fuscus*	Northern flying squirrel (Federal Register 50:126)
U.S. (Southeast)	*Glaucomys sabrinus coloratus*	Carolina Northern flying squirrel (USDI FWS 1992)
U.S. (West)	*Glaucomys sabrinus californicus*	Northern flying squirrel (USDI FWS 1994)

Source: Nowak (1991) except where otherwise noted.

(1) independence from irregular nutritional and physiological variations, (2) clear separations into age classes or year classes without subjective judgment, (3) suitability for living animals of all ages, and (4) ease of application by semiskilled technicians (Larson and Taber 1980).

Research on flying squirrel age and reproduction is limited. Wells-Gosling and Heaney (1984) provide an overview of flying squirrel habits and biology. Carey (1991, 1995) summarizes information on arboreal rodents specific to the Pacific Northwest. Carey and others (1991) describe methods for assessing flying squirrel populations. Davis (1963) describes the reproductive biology of northern flying squirrels in Saskatchewan and methods for aging. Muul (1969b) and Sollberger (1943) describe the reproductive biology of southern flying squirrels (*Glaucomys volans* [Linnaeus 1758]). McCravy and Rose (1992) analyze external features that may be used as predictors of reproductive status of small mammals in the field. Morris (1972) reviews aging methods used to assess both relative and absolute age in mammals.

Goals of This Study

Our goal is to provide information on the life history of northern flying squirrels in Pacific Northwest forests, emphasizing maturation and reproductive development. Our objectives are to (1) describe methods and data used to determine age and reproductive class in the laboratory and field; (2) evaluate field techniques based on laboratory findings and suggest criteria for determining age and reproductive status of live flying squirrels; (3) summarize the reproductive biology of flying squirrels with an emphasis on reproductive cycle, breeding season, and ratios of reproductively active animals; and (4) summarize population characteristics of flying squirrels in the Pacific Northwest.

Table 2—Pacific Northwest forests studied by the Ecological Foundations of Biodiversity Team, Oregon and Washington, 1985-97

Province[a]	Location	Years	No. of grids	Grid size	Elevation	Forest age	Forest type
				Ha	m		
Coast Ranges[b]	Roseburg, OR	1985-90	19	16	79-610	Old-growth, young stands w/ old-growth legacies, young	Douglas-fir, western hemlock, mixed conifer
Olympic Peninsula	Olympic Peninsula, WA	1987-89	14	16	85-610	Old-growth, young	Western hemlock, Douglas-fir, Pacific silver fir
Northern Cascades	Baker Lake, WA	1991	3	16	475-610	Old-growth	Western hemlock, Pacific silver fir, Douglas-fir
	Darrington, WA	1992, 1996	2	16		Young	
Puget Trough	Fort Lewis, WA	1991-97	16	13	116-146	Young	Douglas-fir

[a] From Franklin and Dyrness (1973).
[b] And adjunct interior valleys and Klamath Mountains.

Study Areas

We studied flying squirrels in nineteen 16-ha stands (eight old growth, three mixed aged, and eight young) in the transition from the Western Hemlock Zone to the Mixed-Conifer/Mixed Evergreen Zone (Franklin and Dyrness 1973) in the Coast Range of southwestern Oregon (1985-90; table 2). We examined fourteen 16-ha stands (six old growth, two mixed age, and six young) on the Olympic Peninsula during 1987-89. In the Puget Trough, we studied sixteen 13-ha stands in two second-growth Douglas-fir forests in Thurston County during 1991-97. In the northern Cascades, we studied three 16-ha old-growth stands in Whatcom County in 1991, and two 16-ha young Douglas-fir stands in Skagit County in 1992 and 1996. Most of our data come from the Coast Range and Puget Trough.

Sampling Method

Most squirrels were captured, marked, and released during spring and fall trapping sessions (April-June, September-November). Trapping efforts are most successful in these seasons presumably due to rainfall, which stimulates the fruiting of hypogeous fungi and a concomitant increase in ground foraging by squirrels (Carey and others 1991). Summer trapping efforts in the Coast Range and Olympic Peninsula yielded low captures; we subsequently stopped trapping during this period. Rosenberg and Anthony (1992) trapped for flying squirrels in the western Cascades of Oregon in late summer and also had low captures.

Live-trapping grids usually were trapped for six to eight nights within a 2-week period. When many grids were trapped, trapping sessions lasted up to 6 weeks. We found 2-week trapping periods adequate for sampling flying squirrel populations in most years. Rosenberg and others (1995) had low capture rates and recommended trapping for 3 weeks. We do not recommend this as we believe it violates assumptions of closure (the size of the population is constant over the

period of investigation—no recruitment or losses occur; White and others 1982). Instead we recommend following procedures that result in high probabilities of capture (Carey and others 1991):

- Carefully set traps so that they are rigid, stable, and immovable with moderate hand pressure.
- Trap during spring or fall rains.
- Carefully adjust traps to release crisply and completely with light pressure.
- Check adjustment and add bait (peanut butter, oats, and molasses) daily.
- Use large 10 by 10 grids with 30- to 40-m spacing and two traps per station (200 per grid).

Squirrels were live-trapped in the Puget Trough from 1991-95. Additional data were collected from squirrels found in nest boxes (part of an experimental study) in the Puget Trough from 1993-97. Nest boxes were examined during August to collect information on reproductive success. All squirrels (including young) were eartagged and released.

Sample Sizes

Our studies occurred over a 13-year span (and continue still). Sampling efforts differed for each technique we examined depending on time of analysis and specimen condition and availability; sample sizes are listed for each technique. Overall, we captured 1,386 individual northern flying squirrels 4,971 times. Squirrels were eartagged, weighed, and carefully examined for age and repro-ductive condition; 208 squirrels died and were necropsied. These animals were intentionally removed for necropsy during 1987-88 in the Coast Range or died in live traps (usually from hypothermia or predation). All reproductive tissues were preserved. Most Coast Range specimens were prepared as study skins and skeletons by the Burke Museum at the University of Washington.

Statistics

Descriptive statistics and probability plots were calculated for data sets and assessed for normal distribution. Parametric techniques were used for all variables that were normally distributed. For comparisons of two groups, we used Student's-t test. For comparisons of more than two groups, we used one-way ANOVA with Duncan's multiple comparison test. All comparisons were evalu-ated at $\alpha = 0.05$.

Technique Development— Determining Age

Here we will discuss the development of techniques for determining age and reproduction in northern flying squirrels. For each technique, we provide a brief background on its use, the specific process we used, and the results of our application.

When mammals are caught in traps, it is often difficult to assign an accurate age to individuals unless a long capture history or date of birth is available. Relative age, however, can be assigned based on comparison with other individuals in the sample, and age classes can be approximated (DeBlase and Martin 1981, Morris 1972). As many features as possible should be assessed to enhance accuracy (Dimmick and Pelton 1994, Morris 1972). Here we review use of epiphyseal notch, femur length, cranial measurements, body mass, pelage, and reproductive status as measures of age.

Age Classification

Field determination of age for small mammals is usually limited to two classes: juvenile and adult. Squirrels (Sciuridae), however, often can be classified into three age classes: adult, subadult, and juvenile (Dimmick and Pelton 1994). Adults are the large, breeding members of a population. Subadults are adult size or slightly smaller, may or may not be in breeding condition, but do not breed. Often subadults are yearlings. Juveniles are smaller than subadults or adults, often have a distinct pelage (DeBlase and Martin 1981), and most are young of the year.

We used three categories to age flying squirrels in the Coast Range and Olympic Peninsula based on relative size, appearance, and evidence of reproductive maturity—juveniles were defined as small with uniform grey pelage and with no reproductive development, subadults were animals at or near adult size with no sign of reproductive activity, and adults were defined as full-grown animals in breeding condition or with evidence of past reproductive activity. Weight classes for each category were developed from early data sets and incorporated into aging guidelines.

Over time, however, we noticed subtle external differences among individuals and suspected that additional external characteristics might be used to determine relative age. We also sought to separate age classification from reproduction and weight. In the Puget Trough, therefore, we developed a birth-year-based age class system. This classification is commonly used with animals that live for several years and have no more than one reproductive cycle per year, such as flying squirrels. Birth-year class is similar to "year-class," which is the actual chronological age in years (Larson and Taber 1980). Each age class represents a cohort born in a given calendar year (January 1-December 31). We labeled classes numerically: class I individuals were born in the current calendar year in which they were examined (trapped), class II individuals were born the previous year, class III the year before class II, and so forth. We attempted to age individuals as far back as possible by using external characteristics.

Epiphyseal Notch

The most reliable reported measure of age for northern flying squirrels is closure of the epiphyseal notch (Davis 1963). Bone growth and development can be measured by the thickness and ossification of the cartilage plate adjoining the epiphysis and diaphysis of leg bones. Thickness of the epiphyseal cartilage is reduced as an animal grows older and gradually disappears until complete ossification of the cartilage has occurred (Carson 1961). Unfused epiphyses are therefore an indication of continuing growth and may serve as an index of age (Morris 1972). This growth can be determined by x-ray. In addition, if cartilage is removed by boiling or with chemicals, the epiphyseal notch is exposed (Davis 1963). The presence or absence of the epiphyseal notch can then be determined without x-rays (fig. 1).

Examining the condition of epiphyseal cartilage was originally proposed by Thomsen and Mortensen (1946) for classifying the age of cottontail rabbits (*Sylvilagus floridanus* [J.A. Allen 1890]; Hale 1949). Petrides (1951) used x-rays of gray squirrels (*Sciurus carolinensis* [Gmelin 1788]) to examine the degree of
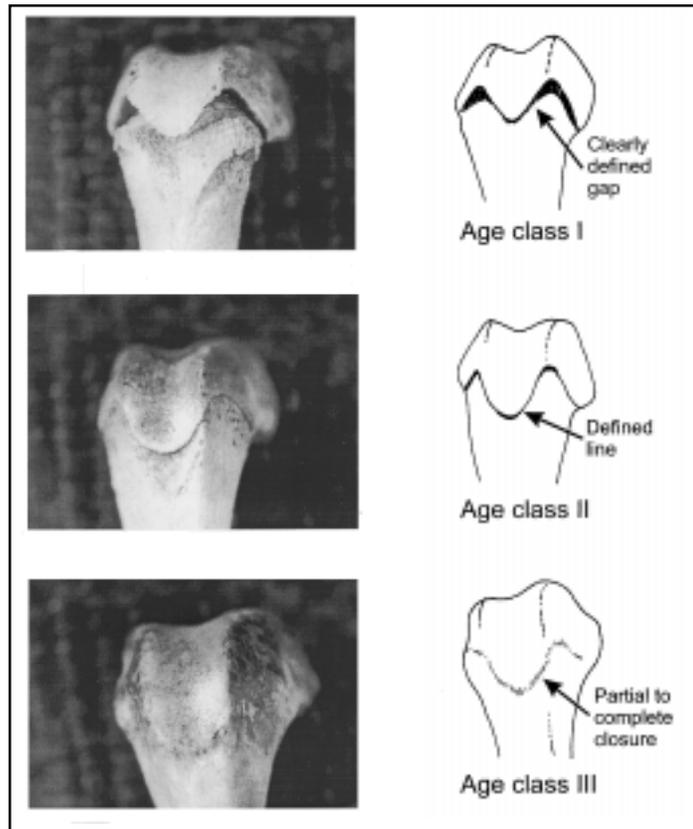
Figure 1—Epiphyseal notch condition of the distal end of the northern flying squirrel femur by age class. The notch is wide in an age class I animal (A), becomes a line at age class II (B), and nearly disappears by age class III (C).

fusion of the epiphyses of the radius and ulna at the wrist to distinguish young from adults. Carson (1961) extended use of x-rays in gray and fox squirrels (*S. niger* [Linnaeus 1758]) by developing a reference set of x-rays from known-age, captive squirrels. Expanding Petrides's (1951) designation of young and adult, Carson (1961) found that, within certain limits, squirrels could be placed in three age classes (juvenile, subadult, and adult) based on condition of the epiphyseal cartilage of the radius and ulna. The epiphyseal cartilage had three distinct thicknesses during the longitudinal growth of these bones. In both fox squirrels and gray squirrels, however, multiple litters and extended breeding seasons made placing individuals into three distinct groups difficult.

Northern flying squirrels are believed to produce only one litter per year (Wells-Gosling and Heaney 1984), and thus epiphyseal cartilage development likely would exhibit less overlap among cohorts than observed in other sciurids. Davis (1963) was the first to use epiphyseal notch to assess age in flying squirrels. Following Kirkpatrick and Barnett (1957), Davis (1963) examined the thickness of the epiphyseal cartilage not only by radiograph but also by direct observation of cleaned and dried epiphyseal notches of flying squirrels. Davis's age classification of juvenile, subadult, and adult was based on presence and degree of

ossification and closure of the epiphyseal notch and was similar to that used by Carson (1961). More recently, epiphyseal notch and femur length were used by Forsman and others (1994) to determine the age of flying squirrels from remains found in owl pellets on the Olympic Peninsula.

Method—We examined the epiphyseal notches from the proximal end of femurs from 140 Coast Range and 35 Puget Trough flying squirrels. Bones were first boiled, then examined under a dissecting microscope at 10X magnification. Femurs were sorted into three groups: little or no ossification, moderate to mostly ossified, and completely ossified (fig. 1). We assumed complete ossification occurred around 16 to 17 months, during late fall (Davis 1963).

Results—Epiphyseal notches of animals that died during spring and fall were easily sorted into three groups. During spring, two notch groups could be found—animals born the previous year (8 to 12 months old) were placed in notch group 2 (moderately ossified), and notch group 3 consisted of animals > 24 months (completely ossified). All three notch groups could be found in fall. Assuming that young of the year are born from May through August, the first notch group (little or no ossification) consisted of juveniles 2 to 5 months old, the second group (mostly ossified) were squirrels 14 to 17 months old, and the third notch group (completely ossified) were animals > 26 months.

Comparison of epiphyseal notch aging with field aging—In the Coast Range, aging was heavily dependent on reproductive condition and less emphasis was placed on chronological age. As a result, direct comparisons between epiphyseal notch classes and field age classes (using external characteristics of live animals) were difficult. Notch group 1 individuals (n = 6), with the least amount of ossification, were identified as subadults (n = 6 captures) and juveniles (n = 3 captures) in the field. Notch group 2 individuals (n = 48), with moderate ossification, were called juveniles, subadults, and adults in the field, depending on weight and reproduction. In spring, notch group 2 females were identified as subadults (34 of 57 observations) more often than adults (22 of 57 observations) or juveniles (1 observation). This was likely due to no signs of past reproduction, and they could thus be more easily distinguished from older adults. Notch group 2 males, however, were already scrotal by spring trapping and thus were called adults (41 of 50 observations) rather than young. In fall, when three age classes were present (with the addition of young of the year) males in notch group 2 were identified as adults (12 of 19 observations), young (7 of 19 observations), and juveniles (2 of 19 observations). Notch group 2 females were called adults (four of five observations) and young (one observation). In both seasons, animals in notch group 3, with complete ossification, usually were called adults in the field (females = 29 of 29 observations in spring and 3 of 4 observations in fall; males = 18 of 24 observations in spring and 16 of 16 observations in fall).

The birth-year-based age system used in the Puget Trough more closely followed that of epiphyseal notch groups. Notch group 1 individuals (n = 15), with little or no ossification, were aged by trappers as class I in the field 28 of 36 times during October and November. Fourteen of these fifteen individuals (93 percent)

were aged as class I after routine laboratory review of data, which took into consideration technician experience, multiple records, and detailed notes (appendix 2). The one misidentified squirrel was captured in early October and was unusually large (148 g); it is likely that weight biased technician decisions. Notch group 3 individuals were aged as class III 100 percent of the time (26 captures) in spring and 83 percent (18 captures) in fall (October to mid-November). All of these individuals (n = 13) were identified as age class III after data review.

We had a sample of only three individuals aged as class II by epiphyseal notch. This was insufficient to evaluate the ability of technicians to identify class II squirrels in the field. We therefore examined 79 live-capture records from 32 squirrels; 3 aged by epiphyseal notch and 29 aged as class I the previous fall (determined by multiple external characteristics or found in nest boxes as weanlings). During January and February, when class II squirrels were 7 to 9 months old, age class was accurately assessed in the field 92 percent of the time (11 of 12 captures). By May, technicians correctly aged 77 percent (n = 52 captures) of the squirrels; 58 percent of the incorrect observations in spring were made by inexperienced technicians. In fall, 47 percent (n = 15 captures) of the squirrels were correctly aged. All incorrect observations in fall were of technicians misidentifying class II squirrels as class III; none of the squirrels were misidentified as class I squirrels.

Epiphyseal notch age corresponds with birth-year age during most of the year. However, the change from little ossification to moderate ossification and the change from moderate ossification to full ossification both occur during late fall (and not on January 1 as calendar aging does). Four specimens we collected in late November, and December could not be grouped by age class without knowing the months in which they were collected. This does not present problems for trapping studies in spring and fall, but it could affect winter trapping studies or studies where mortality dates are unknown.

Epiphyseal notch seems to be the most reliable and objective technique for assigning age to flying squirrels (Davis 1963); however, methods based on annuli of tooth cementum have not been explored. For field studies of live flying squirrels, epiphyseal notch is most useful for providing known-age references from specimens. These specimens then can be used to develop external characteristic standards for each age class to account for regional differences. Also, use of a known-age reference set is helpful in providing external criteria for separating class II from class III squirrels as both can be similar in maturation and size.

For clarity and ease of comparison, subsequent sections in this report use only data from epiphyseal notch-aged flying squirrels for the Coast Range and Olympic Peninsula, except where otherwise noted. This allowed us to convert the age of these squirrels to a birth-year class system for more direct comparisons with the Puget Trough.

Femur Length

Method—Femurs from 87 Coast Range and 19 Puget Trough squirrels were cleaned and examined according to Davis (1963). Femur length was measured from head to medial condyle on the anterior surface.

Results—In the Coast Range, there were significant differences among all three age classes (F = 32.25, df = 2, p < 0.01; table 3). Femurs from Puget Trough class II squirrels were not represented. Femurs from class I Puget Trough squirrels, however, were not significantly larger (t = 1.59, df = 12, p = 0.14) than Coast Range class I squirrels. Femurs were longer in class III Puget Trough squirrels than in class III Coast Range squirrels (t = 2.56, df = 42, p = 0.01).

Femur length can be used to separate age classes; regions with large-bodied squirrels, such as the Puget Trough, may show even larger separation of age classes. Femur length also provides a quantifiable measure that supports epiphyseal notch classes. The entire bone (including epiphyseal notch), however, must be present to measure femur length. Femur length would not be a substitute measurement when the epiphyseal notch was absent or for broken bones (e.g., as may occur in owl pellets).

Skull Characteristics

Cranial characteristics of many mammals may be used to identify immature animals (DeBlase and Martin 1981). Accurate and consistent skull measurements can be taken, which are not normally influenced by large seasonal variations or nutritional status (Morris 1972). Measurements can include subjective evaluation of cranial suture closure, number and condition of teeth, cementum annuli in teeth, and measure of skull width and length. We explored the latter.

In the field, we noticed that class I flying squirrels had small, pointed heads with close-set eyes, whereas class II and older animals tended to exhibit a thickened snout, broader, more angular or blocky forehead, and widely spaced eyes (fig. 2). Class II and III physiognomy appeared robust; class I individuals appeared delicate. Field notes also suggested that adults might be separated further, with older adults having even blockier and broader faces.

Method—We used two cranial measurements to determine if facial features observed in the field could be quantified in the laboratory. We measured least interorbital breadth and rostrum length of intact skulls from 62 Coast Range squirrels aged by epiphyseal notch (study skulls were not prepared from Puget Trough specimens).

Results—Both interorbital breadth and rostrum length increased as squirrels aged. There was a significant increase (F = 5.44, df = 2, p < 0.01) in interorbital breadth between class I and older animals; overall, breadth increased 11 percent from class I to class III. There was no significant difference between class II (spring and fall) and class III individuals. Rostrum length differed significantly (F = 3.17, df = 2, p = 0.049) between class I and fall class II (and older) individuals. Length, however, increased by only 5 percent between class I and class III.

Table 3—External and internal characteristics for determining age in northern flying squirrels (Coast Range and Puget Trough, 1985-94)

Characteristic	Age class I	Age class II	Age class III
	External		
Pelage color and condition	Generally grey and short, tail narrow and pointed, face cream and grey, fur thin and drab	More gold-tipped hair, tail golden and thicker, face golden orange, fur lustrous and thick	Gold-tipped hair, tail golden and square, face golden orange, fur lustrous and very thick
Munsell soil color	Dorsal 5/6 (4-6/4-6)	Dorsal 6/7 (4-8/4-8)	Dorsal 6/7 (4-7/3-8)
Chart 10YR	Ventral 8/3 (7-8/2-4)	Ventral 7/6 (5-8/3-8)	Ventral 7/6 (7-8/4-8)
Value/chroma	Tail tip 3/1 (3-4/1)	Tail tip 3/1 (2-4/1)	Tail tip 3/1 (2-4/1)
Tail width (mm)			
Mean ± S.E.	CR [a] 37.30 ± 1.84 n = 6	CR 38.85 ± 0.68 n = 43	CR 45.24 ± 0.94 n = 24
Pelage length (mm)			
Mean ± S.E.	CR 10.78 ± 0.36 n = 6	CR 13.21 ± 0.17 n = 44	CR 13.88 ± 0.18 n = 27
	PT 10.50 ± 0.34 n = 8	—	PT 13.70 ± 0.29 n = 11
Facial features	Small, delicate features, face pointed and narrow	Less delicate features, face slightly pointed	Mature, blunt features, face blocky and wide
Body weight (g)			
Mean ± S.E. (range)	CR [b] 84.2 ± 3.6 n = 17 (51-111)	CR 115.8 ± 1.6 n = 46 (83-149)	CR 132.4 ± 1.8 n = 22 (120-149)
	PT [c] 100.3 ± 1.8 n = 58 (62-148)	PT 129.0 ± 2.5 n = 28 (108-155)	PT 141.8 ± 1.7 n = 97 (110-185)
	Internal		
Interorbital breadth (mm)			
Mean ± S.E.	CR 7.04 ± 0.23 n = 5	CR 7.65 ± 0.08 n = 38	CR 7.81 ± 0.10 n = 19
Rostrum length			
Mean ± S.E.	CR 12.14 ± 0.23 n = 5	CR 12.56 ± 0.08 n = 38	CR 12.77 ± 0.13 n = 19
Femur length (mm)			
Mean ± S.E.	CR 34.45 ± 0.82 n = 6	CR 38.24 ± 0.19 n = 48	CR 39.02 ± 0.19 n = 33
	PT 35.99 ± 0.57 n = 8	—	PT 39.99 ± 0.33 n = 11
Epiphyseal notch condition	Notch present and wide, epiphyseal cartilage thick, sandwiched, head of femur poorly developed	Notch reduced to a crack or line, epiphyseal cartilage reduced to thin disk, head of femur developed	Notch absent, bone smooth, epiphyseal cartilage completely ossified, head of femur well developed

— = no data available

[a] CR = Coast Range, PT = Puget Trough.

[b] Coast Range field body weights from epiphyseal notch-aged animals only.

[c] Puget Trough field body weights from epiphyseal notch-aged animals, animals captured originally as weanlings, animals with >2 years of trapping records, or animals described as reproductively active the previous year.

These cranial measurements suggest that, in live animals, as the breadth of the face increases, the snout does not increase proportionately. This creates a wide, blocky-appearing head in older squirrels and supported our field observations. This difference is most noticeable between class I and older individuals. With experienced personnel, class II squirrels can be separated from class III squirrels in spring; it appears that this separation between class II and III cannot be reliably made by fall however. We also noticed a difference in facial hair between age groups that may account for perception of age; a mixture of golden and dark pelage provides more contrast and definition in adult facial appearance than dark gray pelage gives to juvenile facial appearance.
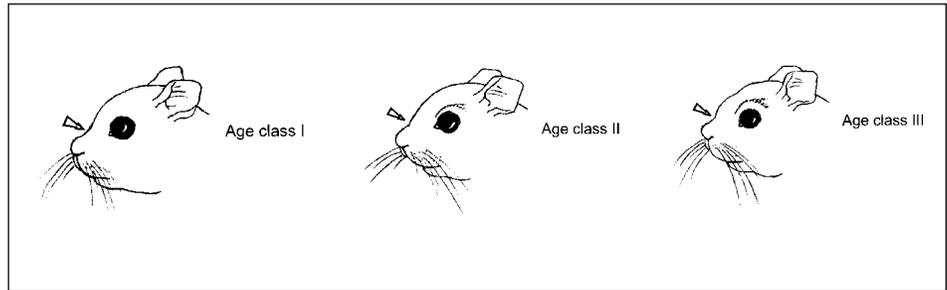
Figure 2—Northern flying squirrel facial features in profile by age class. Note the narrow, pointed features of an age class I animal (A), the broadening of an age class II head (B), and the wide, blocky head of age class III (C).

Body Mass

Mass can be used with other factors to assess age (Uhlig 1955). Mass is a measure of size and, if increase in size is directly correlated with increasing age, then mass may be used as an age index (Morris 1972). This is likely during initial development, when growth in mammals is continuous, providing a means for separating the youngest individuals from adult members of a population (DeBlase and Martin 1981). Once animals reach adult size, mass is not a reliable indicator of age because weight will differ with seasonal and year-to-year physical condition.

In Saskatchewan, flying squirrel young weighed 3.5 g at 2 days old. They rapidly increased in weight to 6 weeks old, then grew slowly until reaching adult weight (130 to 212 g) (Davis 1963). Davis (1963) reported that class I squirrels could be separated from older animals by body weight alone only until mid-September.

Methods—We analyzed body weight for each age class. In the Coast Range, only squirrels aged by epiphyseal notch were included in the sample. For Puget Trough squirrels, we included all field-determined or epiphyseal-notched class I individuals, class II individuals aged by juvenile records or epiphyseal notch, and class III individuals aged by epiphyseal notch, > 2 years of trapping records, or trapping records showing reproductive activity during the previous year. For Olympic Peninsula and northern Cascade squirrels, we summarized weights for juveniles and older animals (combining subadults and adults) because birth-year age class was not used, and we had few mortalities to obtain epiphyseal notches. Weights from first-captures in each trapping session were used in analyses. Trappers used 300-g Pesola[2] scales and took weights to the nearest gram. Scales were tested for accuracy before each trapping session.

Results—Eighty-five Coast Range, 183 Puget Trough, 102 Olympic Peninsula, and 29 northern Cascade squirrels were examined from captures in spring (April-June) and fall (October-November). There were significant differences between sexes, among seasons, and among age classes (tables 3 and 4).

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[2] The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

Table 4—Northern flying squirrel weights (grams), Oregon and Washington, 1985-95

Study area	Sex	Age class I	Age class II		Age class III	
		Fall	Spring	Fall	Spring	Fall
		------------------------------- *Mean ± SE (range)* -------------------------------				
Coast Range[a]	♂	82.3 ± 5.8 (51-101) n = 7	113.7 ± 2.5 (83-130) n = 20	122.2 ± 5.8 (110-149) n = 6	134.3 ± 3.3 (121-149) n = 8	128.5 ± 3.2 (123-137) n = 4
	♀	85.6 ± 4.7 (71-111) n = 10	114.9 ± 2.3 (104-147) n = 18	126.0 ± 1.0 (125-127) n = 2	132.5 ± 2.8 (120-145) n = 10	NA
Puget Trough[b]	♂	98.9 ± 2.4 (73-123) n = 26	122.9 ± 3.9 (108-147) n = 10	131.0 ± 1.0 (130-132) n = 2	132.2 ± 2.2 (110-172) n = 28	140.8 ± 2.5 (118-161) n = 26
	♀	101.4 ± 2.7 (62-148) n = 32	129.1 ± 3.3 (109-147) n = 12	143.3 ± 8.0 (120-155) n = 4	152.8 ± 3.4 (120-185) n = 24	146.5 ± 3.1 (114-170) n = 19
Olympic Mountains	♂	98.0 ± 4.7 (52-126) n = 16		Fall only 135.9 ± 3.1[c] (100-173) n = 32		
	♀	97.9 ± 4.9 (63-127) n = 14		Fall only 140.8 ± 3.4[c] (94-194) n = 40		
North Cascades	♂	88.0 ± 4.5 (74-98) n = 5		Fall only 128.1 ± 5.1[c] (110-150) n = 9		
	♀	72.0 ± 0.0 (72) n = 2		Fall only 133.2 ± 5.1[c] (105-174) n = 13		

NA = not applicable
[a] First-capture (live) body weights from epiphyseal notch-aged animals only.
[b] Puget Trough first-capture (live) body weights from epiphyseal notch aged animals, animals captured originally as weanlings, animals with >2 years of trapping records, or animals described as reproductively active the previous year.
[c] Age class II and III are combined.

Coast Range—During spring, age class III females were significantly heavier (t = -4.77, df = 26, p < 0.01) than class II females. Class III males were also significantly heavier (t = -4.53, df = 26, p < 0.01) than age class II males. There were no significant differences in weight between males and females for class II (t = -0.38, df = 36, p = 0.71) or class III (t = 0.41, df = 16, p = 0.69).

In fall, class I males were significantly lighter (f = 20.51, df = 2, p < 0.01) than class II and III males; there was no significant difference between class II and III males (t = -0.82, df = 8, p = 0.43). There were also no significant differences between males and females for class I (t = -0.45, df = 15, p = 0.66). There were no differences in weights between spring and fall for class II males (t = -1.52, df = 24, p = 0.14) or class III males (t = 1.10, df = 10, p = 0.30). Sample sizes for class II and III females in fall were insufficient to evaluate statistically.

Puget Trough—In spring, class II females were significantly smaller than class III females (t = -4.39, df = 34, p < 0.01); there was no significant difference between class II and III males (t = -2.44, df = 36, p = 0.16). During fall, class I females were lighter than class II or III females (F = 62.51, df = 2, p < 0.01); there was no difference between class II and III individuals.

In most seasons, weights between sexes were similar. Class III females, however, were significantly heavier than class III males in spring (t = -5.27, df = 50, p < 0.01), but not in fall (t = -1.43, df = 43, p = 0.16). Across seasons, there were

two major differences in weight; class III males were lighter in spring than in fall (t = -2.91, df = 52, p < 0.01), and class II females were smaller in spring than in fall (t = -1.97, df = 14, p = 0.07).

Olympic Peninsula and northern Cascades—There were no objective methods to retrospectively separate age classes in the Olympic Peninsula and northern Cascades, so we did not make statistical comparisons. General weight ranges, however, were similar to those of Puget Trough squirrels, and likely there are differences among age classes in these provinces as observed in the Coast Range and Puget Trough.

In the field, body weight is useful in distinguishing class I from class II and III squirrels in early fall. We found that class I squirrels in the Puget Trough generally could be distinguished from adults through October. Weight can be used as a general guide to separate age classes in spring, although there is some weight overlap between age classes, particularly for males. Weight, by itself, should not be used to distinguish ages. In addition to weight overlap between age classes, we found evidence of gorging in both Coast Range and Puget Trough flying squirrels. On necropsy, three heavy squirrels (152 to 165 g) had large, food-engorged stomachs weighing 24 to 71 g. We also have observed squirrels consuming over 15 g of food at one feeding on release from traps. This gorging behavior may result in dramatic weight changes throughout the year. Using multiple weights to determine age also can be misleading for "trap happy" squirrels. Squirrels that are repeatedly captured in traps also may have irregular foraging opportunities and thus exhibit weight fluctuations over the trapping period (Witt 1991).

Pelage and Molt

Pelage characteristics are commonly used to age squirrels. In 1955, Uhlig used pelage length and color, condition of the eyes and ears, eruption of the teeth, hind foot measurements, and length-weight correlations to age live nestling and subadult gray squirrels in weeks. Sharp (1958) tested and refined an aging criteria for gray squirrels based on tail-pelage characteristics which, unlike other aging methods such as bone development, could be used in the field. Sharp found subadults and juveniles could be distinguished by tail pelage even in fall when it is typically difficult to distinguish these ages in gray squirrels. In addition, Barrier and Barkalow (1967) were able to assign 80 to 95 percent of gray squirrels to one of three age categories (nestling, juvenile, and adult) based on pelage color.

Color and appearance of pelage have been used to determine age classes for flying squirrels (Davis 1963). Like many mammals, fur of nestling flying squirrels is replaced by juvenile pelage that is distinct in color and texture from subadult and adult pelage (Davis 1963, Ingles 1965). Davis was able to distinguish juvenile pelage until 5 to 6 months of age and found a Munsell soil color chart 10YR
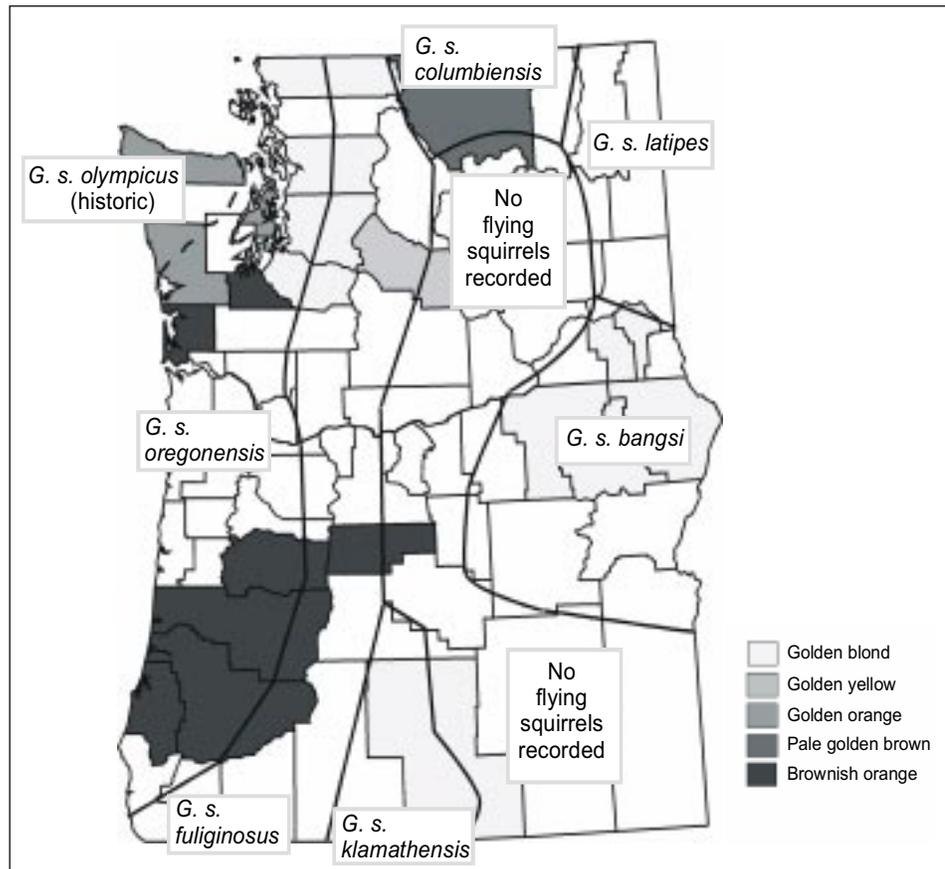
Figure 3—Regional pelage color variation of northern flying squirrels (*Glaucomys sabrinus*) in Washington and Oregon as determined from museum specimens (subspecies distribution from Booth 1947 and Hall 1981).

(Inter-Society Color Council 1955) was useful in identifying colors found in flying squirrel pelage. There are currently five recognized subspecies of northern flying squirrels in Washington (Hall 1981; fig. 3), each demonstrating a wide range of pelage coloration from "pale wood brown" to "rufous brown and pecan" (Booth 1947).

The molting patterns for southern flying squirrels have been described well (Jackson 1961, Wells-Gosling 1985). Most records indicate these squirrels have only one primary molt annually, beginning in late summer or fall. This molt begins at the nose and proceeds up and over the head and continues down the back where the molt pattern then becomes irregular. Lactating females do not begin this primary molt until after weaning, and juveniles begin molting by 12 weeks old, after they are weaned in late summer. Pelage of all squirrels begins to show considerable wear on the rump, head, and nape by spring and summer. Adults experience a partial molt, of the head and neck only, in April and May. This partial molt begins at the nose and proceeds up the face and along the cheeks. This molt is complete at 4 to 8 weeks when it reaches the back of the neck.

The molting pattern of northern flying squirrels has been described less fully than that of the southern flying squirrel. Captive squirrels appear to have only one molt per year, which begins on the face in late May or June (Wells-Gosling 1985). Davis (1963) found a distinct molt line on the shoulders of adults collected in summer but not on juveniles until September.

Hair and pelage color is affected by the kind, amount, and distribution of pigment granules, each of which produce different effects (DeBlase and Martin 1981). Cuticle texture, thickness of the hair, and amount of air space in the medulla alter how light is reflected by the hair, and therefore change the appearance of pigments. Guard hairs of flying squirrels derive color from two pigment types. Eumelanin produces blacks and browns, and pheomelanin produces reds and yellows.

The hair of most mammals is shed and replaced periodically by molting. During annual molts, all hairs are replaced in a relatively short period. The molt pattern differs with species and sometimes with the age of an individual animal (DeBlase and Martin 1981). When many mammals prepare to molt, black pigment accumulates in the skin. When new hairs start, they are deep in the skin and highly pigmented. As hairs develop, they move to the outer edge of the skin and become more erect, and pigment leaves the root, migrating out the medulla of the hair and toward its tip (Ingles 1965). Skin under fully molted pelage is clear, whereas skin under molting pelage is dark or bluish due to undeveloped hairs. Appearance of pigmentation is helpful in detecting molt.

Methods—We used Munsell soil color chart 10YR[3] to identify colors found in flying squirrel pelage on the body and tail. Color codes for tail tip, base of tail, and dorsal and ventral pelage were recorded for 77 Coast Range and 19 Puget Trough specimens. Pelage and hairs were examined under magnification for pigmentation patterns, hair thickness, and condition. Pelage length was measured (millimeters) from base to tips on rump guard hairs, and tail width was measured at the greatest width. To improve our understanding of the progression of molt and how molt related to age, we examined 60 prepared skins from the Coast Range. Skin and hair were examined under 10X magnification from the rostrum to the tail, dorsally and ventrally. Molt patterns, hair loss, guard hair abnormalities, and the length of emerging hairs also were noted.

Results—Dorsal pelage of class I squirrels generally appeared gray with a pale wash of yellowbrown; ventral pelage was generally grey with a wash of pale to bright yellow (fig. 4a). Dorsal underfur was uniform gray and highly crimped (wavy). As squirrels aged to class II and III, dorsal and ventral pelage changed to a more golden-orange/brown color (fig. 4b, c). Class II animals had mildly crimped underfur, whereas no crimping was seen in older squirrels.

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[3] Munsell Color Company, Inc., 2441 N. Calvert St., Baltimore, MD 21218.

Figure 4—Development of northern flying squirrel pelage color, length, and thickness by age class (A; top = age class I, middle = age class II, bottom = age class III), ventral pelage of an age class III adult (B), and dorsal pelage of an age class III adult (C).

Age class I dorsal guard hairs were a mix of solid black and agouti (black tipped followed by successive bands of pheomelanin—light bands, and eumelanin—dark bands) as found by Davis (1963). Class II animals had some hair similar to class I animals. Additionally, they also had agouti-tipped guard hairs followed by a golden band, giving a dark golden appearance to the pelage. Class III adults appeared more golden because the guard hair shaft at the golden band was often thicker and the golden band longer than that of class II squirrels.

In the Coast Range, average pelage length increased significantly ($F = 22.07$, $df = 2$, $p < 0.01$) with each age class and was distinctly shorter in class I individuals (table 3). Tail width was significantly narrower ($F = 17.42$, $df = 2$, $p < 0.01$) in class I and II squirrels than in class III squirrels; there was no difference between class I and II squirrels. As flying squirrels aged, tails became wider and squared at the end. There were no apparent differences in pelage length between Coast Range and Puget Trough squirrels.

In fall, we usually were able to distinguish class I squirrels by pelage color and length; juvenile pelage was most apparent in class I squirrels < 6 months old. In spring, class II squirrels were generally distinct from class III animals by their grayish golden pelage and narrower tail. In addition, the underside of class II tails often was edged with grey, whereas older animals lacked this edging. By fall, class II squirrels were nearly class III size and had begun to molt into class III pelage, becoming more golden and developing thicker pelage and a thicker tail. In the field, these two classes were indistinguishable by pelage color and length.

We examined 90 flying squirrel specimens from 22 counties (Oregon and Washington) in two museum collections (fig. 3). It was readily apparent that regional pelage variation could easily lead to misidentification of age. Adult squirrels of different subspecies displayed pelage variation from pale blond to brown. Even squirrels within the same subspecies, *G. s. oregonensis*, appeared to have varying pelage color from golden blond (King County, WA) to brownish orange (Coos County, OR). Class III flying squirrels from our study sites in Thurston County, Washington, had a grayer brown-orange pelage that closely resembled class II squirrels from our Coast Range study sites.

Thirty-four of thirty-six spring-collected (April-May) squirrels lacked signs of molt but did exhibit wear and patchiness on the head and rump. Two animals collected in June showed molt on the rostrum and forehead. This molt was indicated by dark pigmentation in the skin and the eruption of new hairs 1.5 to 2.5 mm long. Eighteen of twenty-four fall-collected (October-November) squirrels were in various stages of molt. All age classes showed similar patterns. The earliest collected animal (12 October) was the only individual to still be molting laterally. All others showed various patterns covering the neck, shoulders, back, rump, and tail. Tail molt was not evident until late November. Molt probably ends in November with the tail molting last.

Field recognition of molt patterns may be difficult. In early summer, facial molts appear to be quite distinct. Many animals, however, displayed lines similar to molt lines, which were merely irregularities in the fur. Even heavy fall molts proved

visually difficult to discern without close examination. Wells-Gosling (1985) also found molt difficult to discern because of pelage thickness.

Pelage color can be a useful aid in distinguishing age classes. Only after a wide range of known-age individuals has been examined within a region, however, should pelage characteristics be used to determine age class. We suggest carefully examining several specimens from each age class from each population to develop a feel for how coloration will appear in the field. Museum collections are a useful reference, keeping in mind that chemical alteration and "foxing" or reddening of the pelage can occur while in storage (Hodges 1989). In addition to the Munsell Soil Color Chart 10YR, alternate color charts, such as the 10R, may be needed. Color chart plates should be masked to protect them from damage and fading. Descriptions and comparisons should be made in natural light when possible as artificial light may be inadequate to accurately determine colors (Hodges 1989). Low-light field conditions and wet squirrels also can make it difficult to distinguish subtle shades in pelage color.

Molt does not seem to play a critical role in determining age. However, awareness of the timing of molt, particularly the fall molt from juvenile to adult pelage, is important. Because dorsal pelage molts in October and November, young animals may begin to display older pelage characteristics, thus making it more difficult to determine age. Fortunately, the tail is the last to molt and may still be used to determine age classes due to differing widths; class I squirrels molting into the golden pelage of class II squirrels most likely will retain the thin, gray, wispy tail into November. Additionally, in the Puget Trough, we observed that class I squirrels retained a thin, creamy white line along the ventral side of the patagium edge well into winter. This may be a key characteristic for separating class 1 squirrels from adults, once class 1 squirrels begin their first molt into adult pelage. Molt patterns may differ with altitude, climate, or habitat; each population should be individually assessed.

Reproductive Status   Sexual maturation occurs with age, and condition of reproductive organs can be used to differentiate between juveniles and adults, at least during part of the year (Morris 1972). Development of primary and secondary sexual organs is, therefore, an indicator of age class (Larson and Taber 1980). Degree of scrotum development and amount of scrotal hair and condition of mammary glands are characteristics used for aging fox squirrels—juvenile male squirrels have abdominal testes and minimally pigmented scrotums; juvenile females have minute, barely discernible nipples (Larson and Taber 1980).

Results—Reproductive characteristics of flying squirrels are described in detail in the next section. We found reproductive status to be of limited use for aging squirrels. In early fall, we could distinguish between class I and older males by external reproductive development. Testes and scrotum of class I males showed no development or were small and just developing. Testes and scrotum of class II and III males enlarged during the breeding season in almost all cases, then regressed to a moderate size but were usually distinguishable from undeveloped class I males. In winter, however, reproductive status became less reliable

because class I males began sexual development and scrotum and testes looked and felt similar to those of older squirrels. Age classes II and III males could not be distinguished by reproductive criteria in either season.

Age of females could only be distinguished by external evidence of previous reproduction. External reproductive development did not begin before first estrus in spring, 8 to 11 months after birth. Sign of previous sexual development, therefore, indicated age class III in spring, and age class II or III in fall. Lack of reproductive development, however, does not necessarily indicate age because some females do not reproduce the first year after birth, and some may remain infertile and show no development.

Recommendations for Assessing Age

We recommend using a birth-year-based age class system for northern flying squirrels. Birth-year systems follow a cohort of squirrels through time and can be directly correlated with epiphyseal notch closure. Unlike a system based primarily on reproductive competency, the birth-year-based system allows reproductive potential, reproductive success, and survival to be evaluated separately for each cohort. Distinct differences in reproductive maturation among regions make the use of the category subadult confusing because in one region, many yearlings did not breed and thus remained subadults, yet in another, yearlings readily bred and thus were reproductively adult (discussed under "Reproductive Biology"). We also discovered that comparisons among regions with different reproductive strategies can be confusing if there is not common terminology. Figure 5 provides an illustration of the overlap we observed in our studies.

Using a birth-year age-class system to describe flying squirrel age has several other advantages: (1) classes are based on a group of individuals coming into the population during a seasonal, finite period (2- to 4-month period during summer); (2) each class represents the survivorship for a given year; (3) age class is independent from trapping season; and (4) there is less variation among individuals within an age class than a reproductive class. A birth-year-based age class system avoids ambiguity, provides useful, relative ages, and can be used successfully to determine population characteristics for northern flying squirrels.

External characteristics can be used to determine age in flying squirrels provided that multiple and appropriate characteristics are examined. In the Puget Trough, we identified class I and III individuals by using a combination of facial features, weight, pelage, and reproduction. Class II individuals can be classified reliably in spring with experience. By fall, however, class II squirrels are difficult to distinguish from class III because facial features and weights are similar between class II and III, class II individuals are or have molted into the class III pelage and, in some regions, most animals have reproduced.

We believe that two extrinsic factors can improve the accuracy of age determination:

Figure 5—Age class systems used in the Coast Range (1985-90) and Puget Trough (1991-95) for northern flying squirrels. Note the "gray areas" of age determination in the traditional aging system.

- Detailed notes describing external characteristics each time an animal is captured helps biologists and data analysts make retrospective decisions on age. Notes also help technicians focus on appropriate characteristics needed to adequately distinguish age classes.
- Multiyear studies or continuous trapping over a several-year period allows class I individuals to be followed through time. This provided live examples of "known-age" squirrels for training new technicians.

Part of the high success we experienced in aging Puget Trough squirrels may be attributed to technician experience—field crew turnover rates were low; thus technicians, on average, were highly experienced. A summary of external characteristics for each age class is given in table 3.

Technique Development— Reproductive Condition and Litter Size

Knowledge of reproduction and natality is a fundamental requirement for under-standing population dynamics. Estimates of reproductive potential and attainment in squirrel populations can be obtained by examining external and internal repro-ductive organs from both sexes and by determining litter size. Color, swelling, texture, and size and development of reproductive organs, tracked over time, make it possible to determine breeding seasons and determine what proportion of the population is reproductively active at a given time (Kirkpatrick 1980). Uteri (for embryos and placental scars) and nests (for nestlings) can be examined to determine the number of young produced by reproductive females.

Observations and histological evaluations of internal organs provide the most accurate determination of reproductive status in mammals. Testis size, weight, and volume; androgen levels; spermatozoa counts; and testicular biopsies are commonly used for males, whereas ovarian activity, follicular development, and embryo development are used for females (Harder and Kirkpatrick 1994).

Various external features have been used to obtain estimates of the reproductive status in live animals. To accurately assess squirrel populations, external reproductive indicators must be recognizable and accurate. McCravy and Rose (1992) used necropsy to evaluate breeding condition in small rodents. They found nipple size was a better predictor of breeding status than condition of the pubic symphysis or vagina. In males, testis position was the best indicator of reproductive activity.

Although several authors have assessed reproductive status of flying squirrels in the field, few have described methods for doing so (Raymond and Layne 1988, Weigl and others 1992, Wells-Gosling 1985). Reproductive characteristics of southern flying squirrels have been well described by Sollberger (1943). Asdell (1964) discussed the development of the vulva for southern flying squirrels, and Wells-Gosling (1985) described the swelling of the testes. For northern flying squirrels, Muul (1969b) reported that females become sexually active in late May, when genitalia are swollen. Davis (1963) gave internal histological descriptions for stages of the breeding cycle but did not describe external or gross internal features.

Reproductive Status

Our trapping efforts in spring and fall coincided with the onset of breeding activity and influx of young of the year, respectively. Field determination of reproduction was usually based on appearance of external reproductive organs; in some circumstances, body weight and age also were used. We created reproductive categories to describe development during both breeding and nonbreeding periods (appendices 3 and 4). Males in breeding condition were called scrotal. Reproductively active females were categorized as estrus, pregnant, lactating, or postlactating. Nonbreeding squirrels were categorized by reproductive maturity—inactive males were either never active or regressed; females were nulliparous or regressed.

External and internal reproductive organs were closely examined on 226 squirrels (123 males and 103 females; appendix 5). Males were described externally by testicular and scrotal development. For females, the vulva was described by color, turgor, and whether open (opening was prominent) or closed; color, turgor, and shape of nipples were noted; and nipple length was measured. When mammary disks were distinct, diameter was measured. After external examinations, entire reproductive tracts of females and testes of males were removed and photographed. For males, length, width, and depth of both testes were measured, and shape and position (within scrotal sacs or abdomen) were described. Testis volume (length by width by depth) was calculated for one testis on each Coast Range male; testis area (length by width) was calculated for Puget Trough and Olympic Peninsula males. For females, ovaries and uterine horns were measured, described, and inspected for corpora lutea, embryos, and placental scars. Fetus number and length were recorded.

Field descriptions of reproductive condition from 107 captures of 62 Coast Range males, 72 captures of 49 Coast Range females, 54 captures of 17 Puget Trough males, 31 captures of 19 Puget Trough females, and 9 Olympic Peninsula squirrels (two males and seven females) were compared to necropsy results to

evaluate technician accuracy. In addition, we evaluated external reproduction characteristics described in the field for 2,136 male and 1,798 female captures from all three physiographic provinces.

Necropsy Results

Males—Necropsy results from 102 Coast Range males, 19 Puget Trough, and 2 Olympic Peninsula males were grouped by reproductive characteristics and placed into never-active, scrotal, and regressed categories (table 5). Coast Range squirrels accounted for 79 percent of all necropsy specimens. Males with undeveloped testicles (testes not fully developed and descended into scrota) and very small, rounded, turgid testes were classed as never active (n = 9 Coast Range, 13 Puget Trough, and 2 Olympic Peninsula). Mean testis volume was 79 mm^3 (SE 7.4 mm^3, n = 7) for age class I Coast Range males (fig. 6). Testes were positioned abdominally in three class I Coast Range males. Three Coast Range males had testicles partly descended into scrotal sacs, and one had testes positioned completely within the scrotum. In two class I Coast Range males, small testes could be felt externally. Mean testis length and width of Puget Trough and Olympic Peninsula never-active males were not significantly different from Coast Range males.

Scrotal males had well-developed testicles with enlarged, turgid testes usually within the scrotal sacs. We examined 76 Coast Range and 2 Puget Trough scrotal males. Testes volume for 70 of 76 Coast Range males caught during the breeding season exceeded 1000 mm^3 and averaged 3000 mm^3 (SE 98.2 mm^3). Age was determined by epiphyseal notch for six of eight Coast Range males that had testis volumes less than 585 mm^3; all were age class II squirrels. Testis volume averaged seven times larger for class III scrotal males than males in nonbreeding condition (fig. 6). One age class II squirrel with a testis volume of 2166 mm^3 had testes positioned entirely within the abdominal cavity, whereas four other squirrels in age classes II and III had one or both testes located partly in the abdomen or inguinal canal, with testis volume ranging from 282 mm^3 to 4355 mm^3. This suggests that there was no absolute relation among testis position, testis size, and age class. We did not explore any relation between testes position and fertility.

Males were considered regressed if testes size indicated previous development, but testes were not presently enlarged (n = 17 Coast Range and 3 Puget Trough males). Regressed testes appeared wrinkled compared to the smooth, round texture of testes found in never-active or scrotal males. During the nonbreeding season, developed scrota were easily discernible but reduced in size. Testes width and depth measured $\leq$ 50 percent of average scrotal testes size, thereby resulting in a flattened and flaccid condition. Testes length was usually not greatly reduced in regressed testes. In seven cases where testis length was almost 50 percent of average scrotal testes length, however, testes were more rounded and semiturgid but were larger than undeveloped testes. Testes were sometimes difficult to palpate from the exterior of the animal. Four Coast Range regressed males had testes located partially or entirely within the abdomen.

Table 5—Descriptions and measurements of reproductive organs and genitalia of male northern flying squirrels from the Pacific Northwest, 1985-94

| | | Scrotal | | |
Characteristic	Never active	Age class II	Age class III	Regressed
		External		
Scrotal sac	Not discernible or very small	Large, evident	Very large, evident	Small to large
Testes	Very small, rounded; firm, impalpable or palpable	Large, rounded, firm, palpable	Large, rounded, firm, palpable	Small, rounded or flat, flaccid; impalpable or palpable
		Internal		
Coast Range:				
Testes length[a][b]	6.25 ± 0.18, n = 16	16.47 ± 0.35, n = 50	20.08 ± 0.18, n = 63	10.25 ± 0.46, n = 32
Testes width[a][b]	4.07 ± 0.08, n = 16	11.34 ± 0.39, n = 50	14.22 ± 0.12, n = 63	5.60 ± 0.17, n = 32
Testes depth[a][b]	3.09 ± 0.06, n = 16	9.10 ± 0.37, n = 50	11.80 ± 0.10, n = 63	3.63 ± 0.17, n = 30
Puget Trough:[c]				
Testes length[a][b]	6.75 ± 0.73, n = 8		18.68 ± 0.12, n = 2	10.57 ± 0.20, n = 4
Testes width[a][b]	3.88 ± 0.20, n = 8		11.28 ± 0.47, n = 2	6.51 ± 0.51, n = 4
Olympic Peninsula:				
Testes length[a][b]	5.80 ± 0.16, n = 4			
Testes width[a][b]	3.56 ± 0.09, n = 4			
Testes depth[a][b]	2.84 ± 0.05, n = 3[d]			

[a] Mean (mm) ± standard error.
[b] Includes both left and right testicles from each individual.
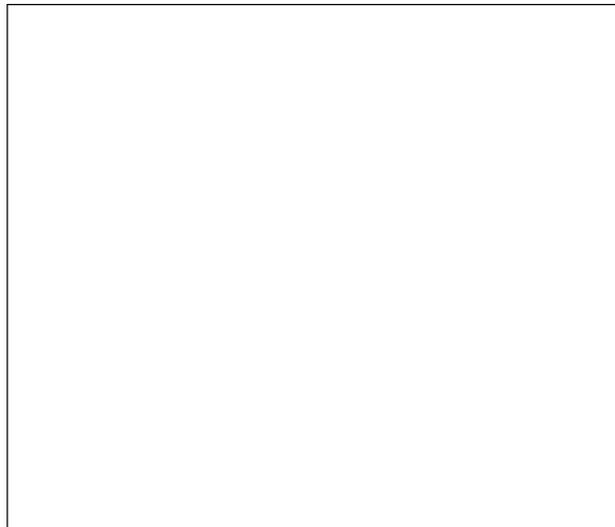[c] Testes depth not measured.

Figure 6—Testes volume (length by width by depth) of male northern flying squirrels, Coast Range, Oregon, 1985-90.

Females—Necropsies were performed on 77 Coast Range, 19 Puget Trough, and 7 Olympic Peninsula females. Reproductive condition was determined by size and appearance of uterus and ovaries, along with presence of corpora lutea, embryos, or placental scars (tables 6 and 7). Nulliparous females had short, thin, and uniform uterine horns, and uterine walls often looked translucent;

Table 6—Descriptions of reproductive organs for female northern flying squirrels Coast Range, Oregon, 1985-88

Characteristic	Nulliparous	Estrus	Pregnant	Postlactating	Regressed
Vulva	Small, white, closed	Swollen, pink, open	Unswollen, light to dark pink, open or closed	Small, pale to pink, open or closed	Small, pale, closed
Nipples	Tiny dots or small bumps (≤1 mm)	Bumps or ≤ 5 mm, flaccid to semi-turgid	Bumps or ≤ 5 mm, flaccid to turgid	3-6 mm, conical, turgid to semiturgid	2-3 mm, flaccid
Uterus	Thin, uniform, clear to pale pink	Enlarged, turgid, pink to red	Thick, extended, red	Coiled, turgid, placental scars	Flaccid, opaque, placental scars

Table 7—Internal measurements of female northern flying squirrel reproductive organs in the Pacific Northwest, 1985-95

Characteristic	Nulliparous	Estrus Class II	Estrus Class III	Pregnant	Postlactating	Regressed
Coast Range:						
Uterus length[a][b]	15.45 ± 0.41 n = 68	27.21 ± 1.85 n = 12	36.70 ± 1.31 n = 12	41.54 ± 2.86 n = 20	25.98 ± 0.99 n = 8	25.80 ± 0.86 n = 22
Uterus width[a][b]	1.35 ± 0.05 n = 68	3.37 ± 0.31 n = 12	3.93 ± 0.28 n = 12	3.12 ± 0.16 n = 20	2.14 ± 0.20 n = 8	2.24 ± 0.08 n = 22
Ovary length[a][c]	4.28 ± 0.07 n = 70	4.33 ± 0.11 n = 11[d]	5.72 ± 0.26 n = 12	5.32 ± 0.18 n = 20	5.25 ± 0.30 n = 8	4.45 ± 0.15 n= 22
Ovary width[a][c]	1.94 ± 0.04 n = 70	2.03 ± 0.12 n = 11[d]	2.80 ± 0.08 n = 12	2.53 ± 0.11 n = 20	2.81 ± 0.15 n = 8	2.25 ± 0.08 n = 22
Puget Trough:						
Uterus length[a][b]	18.60 ± 1.83 n = 8	22.91 ± 1.38 n = 2	49.90 ± 0.75 n = 2		24.48 ± 2.55 n = 4	24.01 ± 2.11 n = 6
Uterus width[a][b]	1.32 ± 0.12 n = 8	2.16 ± 0.45 n = 2	4.88 ± 0.13 n = 2		3.19 ± 0.13 n = 4	2.29 ± 0.19 n = 6
Ovary length[a][c]	3.85 ± 0.15 n = 8	4.05 ± 0.25 n = 2	5.95 ± 0.40 n = 2		4.69 ± 0.50 n = 4	3.36 ± 0.28 n = 6
Ovary width[a][c]	1.85 ± 0.07 n = 8	1.93 ± 0.07 n = 2	4.32 ± 0.17 n = 2		2.62 ± 0.09 n = 4	1.99 ± 0.13 n = 6
Olympic Peninsula:						
Uterus length[a][b]	16.52 ± 0.94 n = 8				29.20 ± 0.60[e] n = 2	19.93 ± 0.87 n = 4
Uterus width[a][b]	1.10 ± 0.05 n = 8				5.45 ± 0.05[e] n = 2	1.90 ± 0.14 n = 4
Ovary length[a][c]	4.36 ± 0.33 n = 8				7.30 ± 0.20[e] n = 2	4.67 ± 0.38 n = 4
Ovary width[a][c]	1.93 ± 0.14 n = 8				4.95 ± 0.45[e] n = 2	1.72 ± 0.13 n = 4

[a] Mean (mm) ± standard error.
[b] Includes both left and right uterine horns from each individual.
[c] Includes both ovaries from each individual.
[d] One ovary damaged.
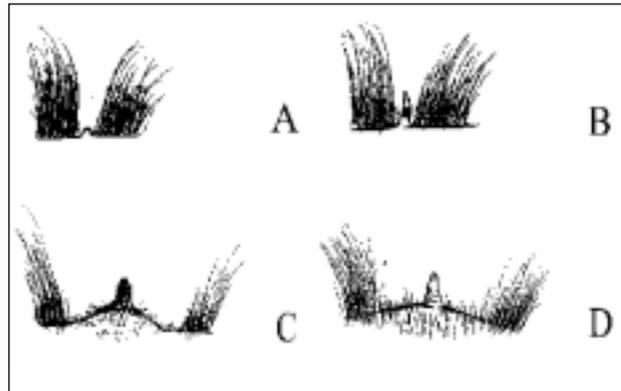[e] Olympic Peninsula females were all lactating.

Figure 7—Nipple and mammary development of female northern flying squirrels: nulliparous (A); regressed, estrous, or pregnant (B); lactating (C); and postlactating (D).

ovaries were small and smooth (Coast Range: n = 35; Puget Trough: n = 10; and Olympic Peninsula: n = 4). Nulliparous reproductive organs were sometimes coiled behind the colon and difficult to see. Externally, the vulva was closed and showed no sign of swelling or reddening, and mammary glands were imperceptible. Flying squirrels have four pair of nipples and mammae: one pectoral, two abdominal, one inguinal. Nipples were commonly described as tiny dots on the skin, whereas those that projected from the skin did not exceed 1 mm in length (fig. 7a). Twenty-three nulliparous squirrels were caught in spring; all were from the Coast Range. Twenty-one of these were aged by epiphyseal notch, and all but one were age class II.

Uterine horns of estrous females (Coast Range: n = 15; Puget Trough: n = 2) were elongated and pinkish, with thickened, turgid walls. Ovaries were larger than those in nulliparous squirrels and usually showed formation of follicles at the surface; distinct, round lumps, which varied from light to dark in color, were evident in some squirrels; indicating current ovulation. Open, swollen, and reddened vulvae were outward signs of estrus, but the amount of swelling and color differed. Nipple development at this stage ranged from no development to 5 mm in length; developed nipples were flaccid to semiturgid (fig. 7b).

In pregnant females (Coast Range: n = 10; Puget Trough: n = 1), uterine horns were reddened due to increased vascularization and were thick and extended. Either one or both horns contained embryos. Corpora lutea were generally evident on the adjoining ovary. Vulvae were found open or closed on pregnant females; there was little to no swelling, but color was usually light to dark pink. Development of nipples remained variable at this stage, the smallest measuring 1 mm in length (fig. 7b).

Only one lactating female, captured in the Olympic Peninsula, was necropsied. The uterine horns were thick and extended, and opaque pink. Corpora lutea were present in both ovaries. Mammae appeared as white, sparsely haired disks extending from the body (fig. 7c). Large fat deposits were present under the mammary disks. Nipples were pink and turgid; 5 mm long.

Seven postlactating (Coast Range: n = 5; Puget Trough: n = 2) and 18 regressed (Coast Range: n = 12; Puget Trough: n = 4; Olympic Peninsula: n = 2) females were examined. At the end of the breeding cycle, uterine horns decreased in size and became coiled and flaccid but usually retained a thickened, opaque appearance. Placental scars were recognizable in both spring and fall. Post-lactating females were distinguished externally by conspicuous mammae (10 to 24 mm in diameter) and regrowth of hair around the nipples; nipple length ranged from 3 to 6 mm. Regressed females had 2 to 3 mm, flaccid nipples and mammary glands were unnoticeable (fig. 7d). For both categories, most vulvae regressed to a small, closed, and pink to pale state.

Field Comparisons to Necropsy Results

Males—In the Coast Range, technicians correctly identified reproductive status 90 percent of the time, and distinguished between breeding and nonbreeding condition 94 percent of the time. All specimens collected in spring (n = 39) were reproductively active or developing. Two class II males were described as never active with testis volumes of 181 mm^3 and 282 mm^3, respectively (mean testis volume of age class II scrotal males = 1878 ± 182 mm^3 SE, n = 25). Because these testis were larger than for never-active age class I males, these squirrels were likely just beginning reproductive activity.

In fall, three regressed males were described as scrotal on four field occasions. Two of these squirrels had the second and third largest testis volume (323 mm^3 and 409 mm^3) of all regressed males (mean testis volume of regressed males in fall = 206 ± 29 mm^3 SE, n = 15) (testis volume for the third squirrel was not available because testis depth was not measured). Technicians had some difficulty distinguishing between inactive categories. Five of fifteen regressed males were misidentified as never active. Age class was determined by epiphyseal notch for four cases; all were age class II males. All never-active males (n = 8) were accurately assessed in the field.

In the Puget Trough, two males collected in spring were reproductively active, and were correctly identified by technicians in all captures (n = 10). In fall, technicians accurately described each of three regressed males at every capture (n = 7). Never-active males (n = 12) were correctly described 54 percent of the time (37 occasions). In 17 captures, technicians described never-active males as regressed. One never-active male was misidentified eight times, twice in the last week of November, and the rest in early December. Another never-active male with two captures in December was called regressed both times.

Females—In the Coast Range, 36 of 49 females were in nonbreeding condition, a high proportion. Forty-two of fifty captures (84 percent) of inactive females were described correctly; 36 were nulliparous. Nulliparous females were called regressed four times (three during May), and one regressed female was recorded as nulliparous. Technicians misidentified three inactive females as active during spring. Two were recorded as in estrus, and one regressed female was described as postlactating.

Thirteen necropsied females were in breeding condition; 10 of 34 specimens collected in spring and 3 of 15 specimens from fall. Technicians identified the correct reproductive code in only 5 of 22 captures. Twelve of the seventeen incorrect field descriptions involved captures of six pregnant females. All six of these females were described correctly as reproductively active but in a wrong category (estrus or lactating); pregnancy was identified only once. Each pregnant female also was called regressed once. Crown-to-rump length of embryos removed from these females ranged from 4 to 13 mm, yet none showed mammary development or abnormally heavy weights. Estrus was accurately reported in the field twice in six observations; four estrous females were recorded in the field as inactive, but necropsy notes described the vulva of one squirrel as open with no swelling, and the vulva of another as closed with only slight swelling. The three reproductively active females collected in fall were postlactating; two of these three were correctly identified by technicians.

In the Puget Trough, technicians reported the correct reproductive status for 14 inactive females 96 percent of the time (n = 25). Ten nulliparous females were accurately identified in all captures (n = 20). Age class was determined by epiphyseal notch for eight of the nulliparous females; all were age class I. Each of the four regressed females was correctly described once, and one was described as postlactating during a fall capture. Three females caught in fall and two in spring were in breeding condition. Technicians recognized reproductive activity in all cases. Two postlactating squirrels were identified in three fall captures. Another fall collected female was categorized in estrus during necropsy and was described as pregnant in the field. In spring, one estrous and one pregnant female were collected. Technicians described both as in estrus.

External Characteristics in the Field

Males—When observed ventrally, the testicles (testes and scrota) of young, never-active males were undeveloped; the skin around the groin generally appeared taut, and testes were usually not detectable. Variation in scrotal development, however, occurred among class I males, perhaps due to minor differences in age.

Some class I males had small, but detectable, scrotal sacs. Truly scrotal males had large, heavily furred scrotal sacs that protruded from the body, and testes were fully developed and enlarged, filling the scrotum. The testes of regressed males were much reduced in size and were not always palpable. Regressed testicles differed in size and shape. The scrotal sacs of some regressed males remained large and rounded, similar to scrotal males, but were empty when felt. Other regressed scrota were shrunk and flattened so that sacs were not readily seen but were distinguishable by touch.

Reproductive status of males can be accurately identified by scrotum and testes size and feel in most cases. The easiest to distinguish are age class I before late fall and class III males. Early born age class I males may be increasingly misidentified as regressed from late November-December, especially by less experienced technicians, because of beginning scrotal sac development. The moderate size of age class II males also can be a source for error. In the breeding

season, some age class II males with relatively small (perhaps still developing), active testes may appear inactive in comparison to the much larger size of age class III males. Similarly, scrota of age class II males with moderate development during their first breeding season may appear more like never active than regressed scrota during the nonbreeding season. Testes position presents an additional, yet uncommon problem for externally determining reproduction. Enlarged, active testes are not likely to be detected when located partly or entirely within the abdomen, and these males would thus be described as either never active or regressed depending on scrotum size. Some inactive males with regressed testes not positioned within the scrotal sacs showed reduced scrotum development, and their status as never active or regressed may be unclear and inconsistently identified by observers.

Females—The vulvae of nulliparous females were small (2 to 3 mm), white, and completely closed. Nipples usually appeared as small, white or pink bumps raised just above the skin, or as tiny red dots on the surface of the skin (fig. 7). The vulvae of females in estrus were noticeably swollen, and the color usually darkened from pink to red (a few swollen vulvae appeared whitish). When vulvae were swollen large, the opening inverted so that folds could be seen along inside walls. The nipples of some squirrels, previously bred or not, lengthened or became erect at this stage, but more often nipples remained inactive until pregnancy. Vulval swelling subsided at the end of estrus, but dark coloration usually was retained. At the onset of pregnancy, vulvae had an unswollen, closed appearance, yet opened easily when touched, and color began to fade. Nipple development was apparent during this stage, but timing of development seemed to differ widely from early to late pregnancy. Outward sign of mammary development occurred close to parturition. Mammae were most obvious during lactation and appeared as white, sparsely haired disks. Nipples were pink or red (often with a bright red tip), turgid, and ≥ 3 mm in length. Milk could be expressed from nipples. During lactation and postlactation, vulvae returned to an inactive state. Postlactation was differentiated by diminished mammary development and regrowth of hair around nipples. Nipples of postlactating females were long (3 to 6 mm), conical, semiturgid, and sometimes dark tipped or ringed due to scarring. Fully regressed females had imperceptible mammae but usually retained long nipples. Regressed nipples were pale and flaccid, but length and shape differed from short and slender to long and flat. Completely regressed vulvae appeared small, closed, and pale or light pink but were larger than vulvae of nulliparous females.

During the female reproductive cycle, external changes can be subtle, but accuracy in determining reproductive status is possible through careful examination. Early stages of breeding activity are detectable from the change in vulva size and color. The degree of swelling and coloring differs, however, during the progression from the onset of estrus through early pregnancy and differs among individuals. Individual condition (cold, wet vs. warm, dry) might influence vulval appearance. Comparisons of vulvae among different females with different breeding histories and in different stages of estrus and pregnancy may cause misidentification of some estrous females because sign of active vulvae with less

obvious swelling and color may be overlooked. Pregnancy is probably the most difficult stage to determine in the field. Swelling of the vulva recedes during early pregnancy and color begins to fade, yet changes in nipples, mammary glands, and abdomen do not usually occur until near parturition. In most cases, however, there is a noticeable difference between unswollen vulvae and inactive vulvae, and recognizing this difference is critical in identifying pregnancy. Vulvar tissue after swelling is deflated and flaccid, and the opening is conspicuous or becomes so by touch, as compared with the taut, firm, and closed inactive vulva. Also, the underlying, darker coloring of many unswollen vulvae provides an additional clue to sexual activity. For six Coast Range females collected during the second week of spring trapping and determined pregnant by necropsy, estrus was described four times, and pregnancy once, during first-week captures. All six females were identified as regressed on their last capture date. Two technicians noted reduced swelling but were likely unaware of the appearance of vulvae following estrus.

Although only one lactating specimen was necropsied, lactating females were observed in the field many times. Lactation is externally obvious by protrusion of some or all of the four pairs of white, and sparsely haired or hairless mammary disks, positioned along the ventral side of the abdomen. Milk usually can be expressed from nipples.

Postlactation is used to distinguish those females that are no longer nursing but show evidence of having reproduced during the year. Pairs of mammae, and long, semiturgid nipples, accentuated by the shorter hair surrounding them as hair regrows, are usually noticeable signs of postlactation. Cessation of milk production and reduction of mammary disks, however, are not clearly distinguishable at weaning, and external signs of lactating and postlactating females may be interpreted differently by technicians. Later in the breeding season, as individuals continue to regress, careful examination can still yield signs of recent reproductive activity.

Nipples are generally good indicators of breeding history for inactive females. Accuracy is highest during late summer and fall, when young of the year usually show no sign of nipple development (in many cases, nipples are difficult to find) and nipples of mature squirrels that reproduced during the year are still regressing. Nulliparous squirrels were correctly described most of the time during fall (Coast Range = 13 of 14; Puget Trough = 19 of 19), whereas accuracy dropped in spring (Coast Range = 23 of 27). Some confusion in spring may be attributed to the onset of hormonal activity causing nipples to form into small cones projecting from the skin surface before vulvar swelling indicative of estrus. Size, shape, and turgidity of regressed nipples differ widely among individuals and are affected by the amount of time passed since a litter was produced. Long (>2 mm) or flattened nipples are adequate determinants of regressed females. Reproductive history, however, cannot be determined externally for inactive females with relatively short (<2 mm in length) and slender (<1 mm width) nipples. Nipples of some females known to be regressed have resembled those of females that have never reproduced. A few age class I females have shown early development in fall with tiny conical nipples protruding from the skin, and class II or older

females that have not successfully reproduced, but have been in estrus, also develop such nipples. It is useful to include nipple length criteria in descriptions of inactive categories ($\leq$1 mm nulliparous, >1 mm regressed) to achieve consistency among technicians. Reproductive status can be refined during data review (appendix 2).

Litter Size

In studies of northern flying squirrels, direct observation of young has been the standard method to determine litter size (Davis 1963, Muul 1969a, Rust 1946, Wells-Gosling 1985). Embryo and uterine scar counts also have been used to estimate litter size. At parturition, a portion of the uterine wall is torn away by the placenta. The resulting scar on the uterine wall appears as a darkened raised band or disc in the uterine lumen (DeBlase and Martin 1981, Kirkpatrick 1980). Placental scars, however, are only an approximation of the number of young produced. Conaway (1955) found that the main source of error arises from resorption of fetuses that leaves scars indistinguishable from those left by fully developed fetuses. Counts of fetuses, or uterine swellings when fetuses are not yet developed from embryos, are considered the best index to number of young produced (Kirkpatrick 1980). Davis (1963) used embryo counts to determine litter size but encountered partial litter resorption, thereby indicating that embryo and placental scar counts could overestimate litter size.

During Coast Range studies, embryos and uterine scars were counted to determine litter size. Uterine scars appeared as red bands or stretched areas on the uterine horn. Embryos, although often under 3-mm crown-to-rump length, were easily discernable as lumps in the uterus. These lumps were cut open, and embryos were extracted and measured under magnification.

Pregnant Coast Range females (n = 8) contained a mean of 2.5 ± 0.19 embryos. Counts of uterine scars ($\bar{x}$ = 3.1 ± 0.04) were higher than embryo counts. No pregnant females were found among Olympic Peninsula and Puget Trough mortalities.

In the Puget Trough, 5 years of direct observations were made during checks of nest boxes and artificial cavities (Carey and others 1996; table 8). Mean litter size over this period was 2.8 young per adult female (range 1-4), but year-to-year variability was high in these second-growth forests.

Litter size is difficult to determine in wild populations of flying squirrels. Counts of embryos and placental scars can be done only on dead animals, but embryo resorption may bias estimates. Direct litter observations, such as those during nest box examinations, reveal the minimum number of healthy young that survive to parturition but not necessarily the number born. Number of young weaned may be the ecologically most significant indicator of reproductive success.

Table 8—Northern flying squirrel litter dates, sizes, and mean weights, during nest box checks in the Puget Trough, Washington, 1993-97

Date of capture	Age of mother	Weight of mother	No. of young	No. of males	No. of females	Mean weight of young	Estimated date of parturition[a]
		Grams				*Grams*	
16 August 1993	3	176	3	1	2	44	19 July 93
17 August 1993	3	166	4	1	3	55	14 July 93
19 August 1993	2	146	1	0	1	49	24 July 93
19 August 1993	2	—	1	0	1	82	26 June 93
23 August 1993	3	180	3	2	1	53	25 July 93
17 August 1994	—	—	2	2	0	68	10 July 94
24 August 1994	3	160	1	1	0	74	12 July 94
24 August 1994	—	—	2	1	1	97	18 June 94
24 August 1994	—	—	1	1	0	90	25 June 94
24 July 1995	3	180	4	3	1	42	1 July 95
31 July 1995	3	192	3	0	3	30	13 July 95
31 July 1995	3	158	4	2	2	50	5 July 95
8 August 1995	3	196	4	3	1	37	18 July 95
21 August 1996	2	160	2	1	1	54	23 July 96
22 August 1996	2	154	2	1	1	49	27 July 96
22 August 1996	—	—	2	—	1	60	20 July 96
22 August 1996	—	—	2	1	1	68	15 July 96
26 August 1996	2	146	1	0	1	76	13 July 96
26 August 1996	2	156	1	1	0	54	27 July 96
27 August 1996	3	157	2	1	1	76	14 July 96
27 August 1996	—	—	2	2	0	61	25 July 96
28 August 1996	3	174	3	1	2	64	23 July 96
13 August 1997	2	134	1	1	0	67	6 July 97
13 August 1997	2	118	2	1	1	39	22 July 97
13 August 1997	3	180	3	1	2	53	15 July 97
18 August 1997	3	159	1	1	0	38	28 July 97
18 August 1997	3	184	1	1	0	54	19 July 97
20 August 1997	3	179	4	2	2	43	27 July 97
21 August 1997	—	—	2	0	2	63	16 July 97
21 August 1997	2	158	3	2	—	32	2 August 97
25 August 1997	3	168	3	0	3	67	18 July 97

— = data not obtained or not available.
[a] Determined by estimating age in days by mass (Davis 1963) and back dating from date of capture.

Recommendations for Assessing Reproduction

We recommend that technicians (1) examine all external sexual features and consider the combination of signs to best determine a reproductive category, (2) describe the condition of genitalia with detailed notes, and (3) report on reproduction at every capture to determine the reproductive status of flying squirrels during live-trapping studies.

Before each trapping session, technicians should review flying squirrel reproduction, especially stages of reproductive cycles and corresponding changes in sexual organs. Sampling protocols should include descriptions of external indicators of reproductive categories, including stages within each category. The protocol establishes a standardized language and a consistent set of descriptives, and facilitates verbal and written communication among technicians and between technicians and data analysts (appendices 3 and 4). Group discussions of protocols and project objectives can reinforce learning. A summary of the protocol that includes categories, codes, and key indicators should be carried as a field reference and checklist for field examinations. For field training, new technicians should be accompanied by an experienced technician during trapping until they have seen examples of each reproductive category expected during a trapping session. As technicians gain experience, the increase in number of squirrels examined improves understanding of the reproductive cycles, recognition of reproductive stage by external signs, and confidence and accuracy in reporting reproductive status.

Reproductive Biology

Most studies of reproductive biology in *Glaucomys* have been in populations of southern flying squirrels in the Eastern United States. Southern flying squirrels have two distinct breeding periods, typically peaking in March and July (Hibbard 1935, Linzey and Linzey 1979, Muul 1969b, Sollberger 1943, Stapp and Mautz 1984). Testes of males begin to descend in January and may regress in late summer or early fall (Muul 1969b, Sollberger 1943, Wells-Gosling 1985). Females typically enter estrus slightly later, in mid-February, and are active for a shorter period of time than males (Muul 1969b, Wells-Gosling 1985). Vulvas regress 5 to 8 days after mating. Vulvas remain perforate, however, until 4 to 5 weeks after parturition (Sollberger 1943). After a 40-day gestation period, most southern flying squirrel litters are born in early April. Additional litters can be produced in fall (Muul 1969b, Uhlig 1956, Wells-Gosling 1985). Average litter size is three young (range 1-6), and fall litters are commonly larger than spring litters (Hibbard 1935, Linzey and Linzey 1979, Stapp and Mautz 1984, Wells-Gosling 1985).

There have been no definitive studies of reproductive biology of flying squirrels in the Pacific Northwest. Northern flying squirrels are reported to have a single breeding season and mate from late March through May (Wells-Gosling and Heaney 1984). Flying squirrels breed as early as March in Saskatchewan (Davis 1963) and produce offspring as late as November in California (Raphael 1984). In Saskatchewan, males become scrotal in late January and testes are regressed by June (Davis 1963). Females enter estrus as early as March and have a 16-day estrous cycle (Davis 1963). After gestation of 37 to 42 days (Muul 1969a), a single litter of three young (range 1-4) is produced (Booth 1947, Davis 1963, Rust 1946) between May 1 and June 30, with northern litters being born slightly earlier than those in southern regions (Davis 1963, Forsman and others 1994, Jackson 1961). Few litters, most anecdotal observations, have been observed in the wild. Rust (1946) found one to three young per litter (sample size unknown) in northern Idaho, with two being the most common in grass nests and three in cavity nests. Wells-Gosling (1985) captured one female in Michigan that

gave birth to a litter of six, but found the average to be three. Captive females have been found to produce litters of three to four, whereas their wild counterparts were found to have 2.5 (range 2-3) live embryos (Davis 1963, Muul 1969a).

The Reproductive Cycle in the Pacific Northwest

Males—In the Puget Trough, age class II and III males matured and became active (scrotal) by the end of January. The proportion of scrotal males peaked in May; >95 percent of all males became scrotal each year. We observed scrotal males as late as September, although testes in some males had regressed as early as late May. In the Coast Range, timing of scrotal development was similar, with most males scrotal in late May, but some squirrels retained scrotal testes until early November.

Females—Puget Trough females matured as yearlings, and most were sexually active their first spring. Both age class II and III females exhibited estrus during late April (when trapping began)—late May with a peak in early May (fig. 8). Pregnant squirrels first appeared in early May, and numbers increased until early June. Pregnancy was observed as late as July 27. Lactation began in late May and ended by October when most young were weaned. Regression of reproductive organs began as early as August, and most females were regressed by November.

Coast Range females came into estrus beginning in late April. Peak of estrus was late May to early June (fig. 9). Estrous females were captured as late as June 27. Pregnancy peaked in early June. Lactating females were captured from late May through early November with no clear general cessation of lactation. Regression of breeding females began in late August and continued through December (fig. 10). Nulliparous and nonbreeding females comprised the largest proportion of females captured in most months.

Conception and parturition—Date of parturition was estimated for litters found in nest boxes in the Puget Trough (table 8). We combined samples from 1993 to 1997 and determined mean mass for young in each litter and used mass to determine relative litter age in days based on Saskatchewan squirrels (Davis 1963). Although Booth (1946) studied the development of one litter of flying squirrels closer to our geographic region, these squirrels tended to be smaller than Puget Trough squirrels; at 365 days of age, the captive squirrels Booth examined were just beginning to approach mass and sizes of 4- to 5-month-old Puget Trough squirrels.

Age of litters ranged from 18 to 67 days. Estimates of parturition were from June 18 to August 2. Assuming a 40-day gestation (Sollberger 1943), conception was between May 10 and June 23. Peak estrus was therefore mid-May to early June. A peak of parturition in July corresponded to a consistent den shift by many female squirrels to low structures in June and July (Carey and others 1997). Female flying squirrels are known to seek out maternal dens 1 to 2 weeks before parturition (Wells-Gosling 1985). Parturition estimates from nest box data were 1 to 2 weeks later than indicated by trapping data. Puget Trough squirrels had slightly less mass than those studied by Davis (1963) in Saskatchewan.
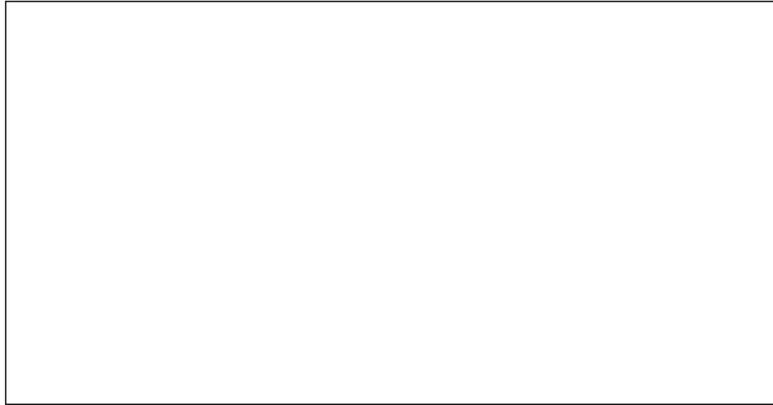
Figure 8—Percentage of female flying squirrels captured in active states of reproduction by week (Julian calendar), Puget Trough, Washington, 1991-95. Weeks with no bars indicate no trapping or sample sizes of active females <5.

Figure 9—Percentage of female flying squirrels captured in active states of reproduction by week (Julian calendar), Coast Range, Oregon, 1985-90. Weeks with no bars indicate no trapping or sample sizes of active females <5.
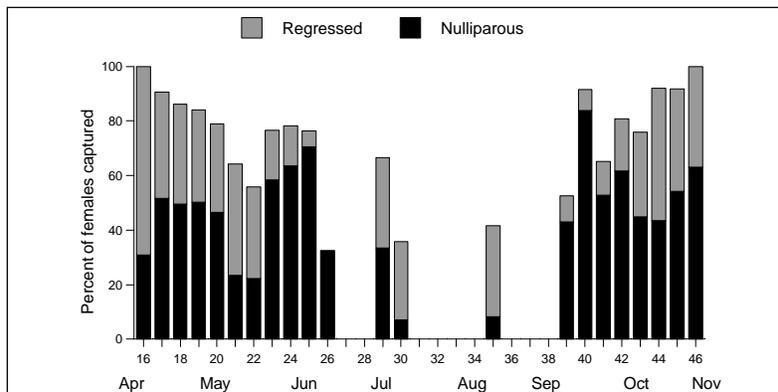

Figure 10—Percentage of female flying squirrels captured in inactive states of reproduction by week (Julian calendar), Coast Range, Oregon, 1985-90. Weeks with no bars indicate no trapping or sample sizes of inactive females <5.

Consequently, Puget Trough squirrels may appear younger than their true age. This would explain the difference in parturition dates between trapping (and necropsy) data and nest-box data. Additionally, litter size likely influences mass of young; larger litters would have more competition for milk and thus mass development would be slower than for small litters of the same age.

There were significantly more young (t = -3.11, df = 22, p < 0.01) with age class III females ($\overline{X}$ = 2.87 ± 0.29) than with class II females ($\overline{X}$ = 1.56 ± 0.24). Additionally, class III females were significantly heavier (t = -4.83, df = 21, p < 0.01) than class II females ($\overline{X}$ = 174 ± 3 for class III; $\overline{X}$ = 147 ± 5 for class II).

Breeding Season

Coast Range and Puget Trough squirrels seem to have similar reproductive cycles, but the breeding season for Coast Range squirrels is slightly later and more extended than for Puget Trough squirrels (figs. 11 and 12). Coast Range males tended to remain scrotal 3 months longer than Puget Trough males, and the females showed signs of estrus well into June and July. In the Puget Trough, pregnancy peaked in June with lactation peaking in late July, whereas peak of pregnancy in the Coast Range occurred in July and lactation in late August. In the Coast Range, lactation continued well into late November. In both studies, young appeared in the population (postweaning) beginning in August. Both the Puget Trough and Coast Range breeding seasons began considerably later than that found by Davis (1963) who found females in estrus in late March and a peak of pregnancy in late April to early May in Saskatchewan.

Although sample sizes in the Olympic Peninsula and North Cascades studies were small and conducted primarily in fall, patterns appeared similar to the Puget Trough. Male squirrels began regressing as early as July in the North Cascades and September in the Olympics, and all were fully regressed by October. Some lactating and postlactating females were found as late as October, but most adult females were regressed by November. The first young of the year were trapped in early October.

Ratios of Reproductive Activity

In the Puget Trough field study, most (90 percent) age class II and III females reproduced by summer (fig. 13). In contrast, a small proportion (39 percent) of age class II and III females in the Coast Range field studies showed signs of active reproduction (estrus, pregnancy, lactation, or postlactation) in the field. These data suggest onset of reproductive activity in age class II females is density dependant, delayed in high-density populations. Necropsy data also suggest that a large proportion of Coast Range females did not breed in any given year. Of the epiphyseal notch-aged Coast Range females (collected in all seasons), 86 percent of the age class II and 63 percent of the age class III females were nulliparous or reproductively inactive. In addition, 73 percent of age class III females captured during the breeding season (April-July) were reproductively inactive, and 89 percent of the age class II females were nulliparous. In fall, nearly twice as many necropsied females showed signs of current reproductive activity (lactation or postlactation) than did field-observed females during spring, thereby suggesting that some breeding occurred after our spring trapping sessions.
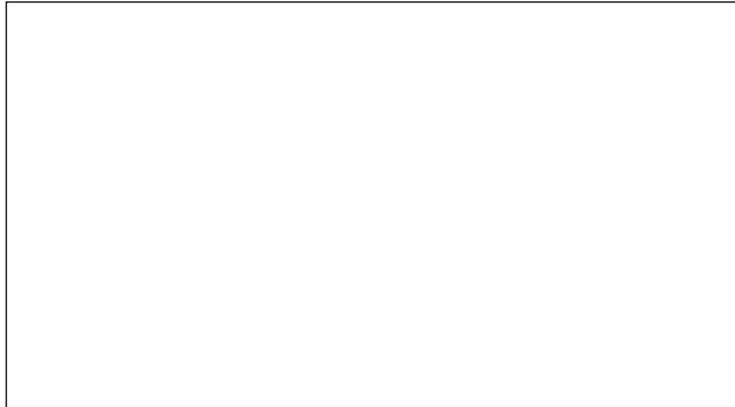
Figure 11—Projected reproductive patterns of female flying squirrels by week (Julian calendar), Coast Range, Oregon, 1985-90. Lines based on proportion of females in each reproductive class captured during live-trapping studies.
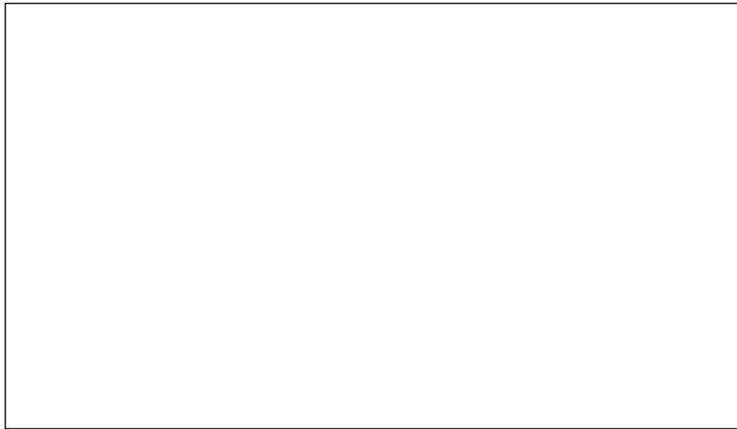

Figure 12—Projected reproductive patterns of female flying squirrels by week (Julian calendar), Puget Trough, Washington, 1991-95. Lines based on number of females in each reproductive state per trap night.
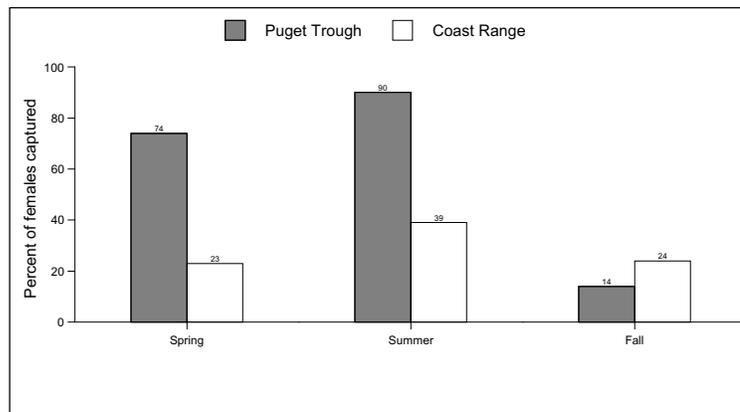

Figure 13—Percentage of female flying squirrels found reproductively active by season, Coast Range, Oregon (1985-90), and Puget Trough, Washington (1991-95).

There was no apparent difference in the percentage of inactive females between young and old stands in the Coast Range, although sample sizes for young stands were small. Overall, 68 percent of the adult females captured were inactive. During summer (June-August), when most females should be showing signs of reproductive activity, only 39 percent of female Coast Range squirrels were reproductively active.

Several factors may account for this low percentage of reproductively active females in the Coast Range field studies. Females recorded as regressed after early May each year actually may have been in the undetectable early stages of pregnancy or may have come into estrus as the season progressed but were not subsequently recaptured. However, because 76 percent of adult females in the field in fall were recorded as inactive, with no signs of recent lactation (and many were recorded as still nulliparous), a high percentage of females did not reproduce in any given year. In contrast, regressed females in the Puget Trough typically showed signs of recent lactation.

Population densities in the Coast Range young stands were, on average, 1.5 to three times higher than in the Puget Trough; densities in old-growth stands were four to seven times those in the Puget Trough (Carey 1995; Carey and others 1992, 1996). Breeding may be density dependent. Rates of reproduction of Puget Trough female squirrels were similar to those studied by Davis (1963) in Saskatchewan. Female squirrels in Saskatchewan bred at 1 year of age. All older adult females caught during spring and summer showed signs of reproductive activity. In the Puget Trough, over 70 percent of the field-assessed age class II females bred at 1 year of age, and 97 percent of age class III females showed signs of reproductive activity.

In the Olympic and North Cascades field studies, conducted primarily in late summer and fall, densities (Carey 1995) and ratios of reproductively active females fell between the Coast Range and Puget Trough. In late summer (August), 57 percent of adult females were active (lactating or postlactating), and in fall, the proportion dropped to 21 percent. Proportions were not directly comparable to Coast Range and Puget Trough because the summer trapping was conducted so late. Most adult (age class II and III) females, however, probably did breed because few nulliparous adults were trapped.

Population Characteristics

Several population characteristics may be determined from age, sex, and reproductive data. Age and sex ratios combined with information on maturation and reproductive attainment reveal many aspects of flying squirrel life history. In Saskatchewan, from a sample collected in July, 56 percent were juveniles, 28 percent young adults, and 15 percent older adults (Davis 1963). These data suggested a 50-percent mortality rate and almost a complete population turnover by the third year. Davis (1963) also found a ratio of 27 females to 26 males for juvenile squirrels and, for adults, 69 females to 81 males. This ratio was not significantly different from a 1:1 ratio, and the ratio of males to females differed little during different months sampled.

Few studies have examined northern flying squirrel populations in Pacific Northwest forests. Forsman and others (1994) explored seasonal relative proportions of juvenile and adult flying squirrels in spotted owl diets on the Olympic Peninsula, Washington. By inspecting owl pellets and assigning age categories based on size of skeletal parts, tooth development, and degree of fusion of the epiphyseal cartilage, age ratios, and timing of the initial recruitment of juveniles were estimated. Conclusions could not be drawn about the entire population because juvenile flying squirrels probably were more susceptible to predation than adults.

Sex Ratio

Sex ratios of populations of northern flying squirrels studied in all regions followed the general trend for mammal populations; all populations showed an approximate 1:1 sex ratio in fall. In both the Coast Range and Puget Trough, however, males were captured more often than females in spring and, therefore, inflated the male proportion in that season. Movements of flying squirrels during the breeding season may account for higher male captures; male flying squirrels move greater distances than females, thus covering more territory.[4] In addition, as females begin to give birth and lactate, they may be less active and less likely to be captured. Sex ratio of juveniles captured in nest boxes was 1:1 (34 males and 34 females). Sex ratio did not differ among age classes and appeared to be maintained as cohorts aged.

Age Class Ratio and Survivorship

In Coast Range and Puget Trough populations, age ratio was similar from season to season for the youngest cohort (fig. 14). In early fall, when most Puget Trough class I individuals entered the population, they accounted for about 36 percent of the population. In spring, class II squirrels accounted for about 37 percent of the population, thereby suggesting overwinter mortality was similar to older animals. Coast Range and Olympic Peninsula squirrels followed a similar pattern with class I accounting for 29 to 34 percent of the population in fall.

Age classes were equally represented for Coast Range squirrels aged by epiphyseal notch. In fall, 12 individuals from each age class were captured, in spring, 26 class II individuals and 20 class III individuals were captured, and in summer, 35 and 33 individuals, respectively, were captured. It was unclear whether necropsied individuals were an unbiased sample of the population when examining age ratio. Snap-trapped individuals were probably equally affected, but young animals may die more often in live traps than do adults. Low body weight, foraging habits, and other factors may cause young squirrels to perish in live traps more often than adults, thus skewing the age ratio of dead squirrels toward younger individuals.

We used Coast Range and Puget Trough animals initially aged as class I to evaluate survivorship between age classes. If individuals were not captured within two seasons (1 year) after last capture, we assumed they were dead (not a strictly

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[4] Carey, A.B. 1998. Unpublished data. On file with: Pacific Northwest Research Station, Forestry Sciences Laboratory, 3625 93d Ave., SW, Olympia, WA 98512.

Figure 14—Percentage of flying squirrels captured from each age class, Coast Range, Oregon (1985-90), and Puget Trough, Washington (1991-95). Age classes were assigned to Coast Range animals retrospectively based on trapping notes and history.

true assumption). Because trapping effort differed by stand, individuals in the sample were not included once they did not have the opportunity to be trapped for at least two seasons after last capture.

From age class I, 190 Coast Range and 163 Puget Trough squirrels were followed through time (table 9). Because we knew the birth year of individuals, we could follow them past age class III (unlike using epiphyseal notch or external characteristics). About 50 percent of individuals survived from class I to II in Coast Range old-growth and mixed-age stands. Only 7 percent of individuals captured in young Coast Range and 30 percent in Puget Trough stands survived to age class II. One-third of class II squirrels survived to class III in all three stand types in the Coast Range, but only 22 percent survived in the Puget Trough. Although no individuals from the sample survived beyond class III in mixed-age or young stands, almost 60 percent of class III squirrels survived to class IV in old-growth stands in the Oregon Coast Range.

In the Puget Trough, the proportion of individuals that survived to subsequent age classes diminished over time. Overall, Puget Trough squirrels were less likely to survive to the next age class than in Coast Range old-growth or mixed-age stands. During our study, we recorded squirrels living longer than data in table 9 suggests; three individuals (one Coast Range, two Puget Trough), initially captured as adults, were known to be at least 7 years old.

Implications
Environment and
Maturation

The greatest difference in flying squirrel reproductive biology between the Coast Range and Puget Trough was the proportion of females that were reproductively active. In the Coast Range, class II squirrels tended not to reproduce, and few class III individuals reproduced in any one year. In contrast, in the Puget Trough, nearly all class II and III females bred. Diet and climatic conditions are environmental factors known to influence reproductive development in mammals and thus

Table 9—Proportion of northern flying squirrels in each age class that survived to subsequent age classes, 1985-95

	Flying squirrel age class			
Region	Class I to II	Class II to III	Class III to IV	Class IV to V
Oregon Coast Range:				
Old growth	0.54 (107)	0.33 (58)	0.58 (19)	0.18 (11)
Mixed age	.43 (42)	.33 (18)	0 (6)	NA
Young	.07 (41)	.33 (3)	0 (1)	NA
Puget Trough:				
Young	.30 (163)	.22 (45)	.10 (10)	0 (0)

NA = not applicable.
Note: Sample sizes are shown in parentheses.

the age at which they become fertile (Bronson 1989). Environment could influence onset of reproduction and proportion of adults breeding through seasonal differences in harshness of climate and food availability. Coast Range winters are colder and wetter than Puget Trough winters (Franklin and Dyrness 1973, USDC National Oceanic and Atmospheric Association 1982, USDA Soil Conservation Service 1990). Harsh winters in the mountainous Coast Range could limit production of the primary food of squirrels—truffles (Carey 1995). Temperature and precipitation govern fungal productivity (Fogel 1981); temperatures <0 to 6 °C cause production to cease (Hunt and Trappe 1987). In spring, with increases in temperature and precipitation, fungi produce a burst of truffles (Hunt and Trappe 1987).

Restriction of food affects the estrous cycle, puberty, and onset of seasonal breeding (Bronson 1989). Intraspecific competition for limited food also would be more likely in the dense Coast Range populations. Small-bodied age class II females in the Coast Range may not receive enough food during winter and spring to reach a minimum body weight needed for estrus; thus, onset of reproduction could be delayed to the next year. Even age class III females also may need a burst of food availability for estrus. Variation in fungal sporocarp abundance (temporal and absolute) is marked (Fogel 1981, Hunt and Trappe 1985, Luoma 1991). Thus, variation in the nutritional status of females in spring could result in variation in the onset of estrus, breeding, and parturition. Once primary demands are met, excess energy can be used to support reproduction. When nutrients are scarce, partitioning of energy must be decided between reproductive and nonreproductive needs (Bronson 1989).

Fungal production drops in summer with drought, which also can be marked in the Coast Range (Franklin and Dyrness 1973, USDC National Oceanic and Atmospheric Association 1981). Summer drought and late (well into fall) lactation could place females in energetic deficits going into winter, further delaying or even prohibiting reproduction the next year. If young are born late, they would still be nursing during the fall burst of truffles. Young would then face the postweaning period, with its need for high energy for growth and maturation, in winter when food is scarce. Thus, late-born young would likely not breed the following year.

Puget Trough winters are mild and wet (Franklin and Dyrness 1973, USDC National Oceanic and Atmospheric Association 1982, USDA Soil Conservation Service 1990), and population densities were low. Both age class II and III squirrels gain weight rapidly in fall and early winter, and Puget Trough squirrels may enter spring with greater nutritional balance than in the Coast Range. Early spring blooms of truffles could then enable both age classes to gain adequate weight and come into estrus, with a greater synchronicity than in the Coast Range.

Greater seasonal differences in temperature, precipitation, and food availability may simply be met by delaying or prolonging maturation and reproduction in the Coast Range. Lower predictability of food abundance due to greater climatic extremes may be best approached by "hedging bets" and extending periods of reproductive activity. This would provide continued reproductive success by ensuring that the timing of maturation for some young each year would occur during periods of adequate forage production.

Density

Flying squirrel densities in the Coast Range (Carey 1995, Carey and others 1992) were much higher than in the Puget Trough (Carey and others 1996) and reduced proportions of flying squirrels breeding could reflect density dependence—the greater the density, the fewer squirrels breeding. Like other rodents, the reproductive potential of flying squirrels can be relatively high. In high-density populations such as the Coast Range, mechanisms seem to limit excessive production of offspring by large numbers of adults. Mechanisms of density dependences differ; for example, food restriction, effects on social behavior, or pheromone-mediated reproduction. In contrast, low-density populations like the Puget Trough do not need to limit the number of reproductively active adults; most individuals breed when they reach their first breeding season.

Predation

In the Coast Range, breeding season was long and various stages of reproduction (estrus, pregnancy, and lactation) overlapped (fig. 11). In contrast, flying squirrels in the Puget Trough demonstrated synchronicity in breeding condition, with distinct peaks of estrus and parturition (fig. 12). Timing of recruitment of class I individuals into the population may be an adaptation to reduce susceptibility of young to predation. Coast Range young were recruited gradually, whereas Puget Trough young were recruited all at once.

In the Coast Range, spotted owls were important predators of flying squirrels and could lower flying squirrel populations (Carey and others 1992). Owls manifested strategies that seem to reflect avoidance of depleted prey populations. They also avoided depleting prey populations by rotating among foraging patches (Carey and Peeler 1995). The extended breeding season in the Coast Range may be an adaptation to reduce high predation of weanlings by owls. Spotted owls probably track prey resources within their home range (Carey and Peeler 1996); a sudden influx of weanlings into a local population could attract or maintain intensive, continuous foraging by owls. A drawn-out breeding season and recruitment of class I flying squirrels could maintain intermittent foraging by spotted owls; fewer

young would be available for any given period of foraging. Gradual recruitment also would reduce competition for food among young squirrels and between young, naive squirrels and experienced adult squirrels until fungal blooms in fall.

Spotted owls were not present in Puget Trough stands. Weasels (*Mustela* spp.), which are less mobile than owls, appeared to be major predators of flying squirrels in these second-growth stands (Wilson and Carey 1996). Many of the maternal dens used by females in the Puget Trough were low (<2 m above-ground), and safe maternal dens may have been lacking (Carey and others 1997). Highly synchronous reproduction could "swamp" weasels with young during the critical period of nursing, when females and young occupy nests close to the ground, thus allowing some young to survive long enough to learn predator avoidance. After weaning, squirrels move to arboreal dens and are less susceptible to predation by terrestrial predators. Thus, it could be to the advantage of Coast Range populations to space weaning for predator avoidance, but for Puget Trough populations to concentrate reproduction.

Body Size and Energy Requirements

On average, Puget Trough squirrels were larger than Coast Range squirrels. In addition to density-dependent factors, differences in weight among and between populations could reflect differences in breeding season behavior and thermo-regulation. In general, home range size was larger in the Puget Trough than in the Coast Range. Stored energy (reflected in mass) was used differently by males and females during the breeding season.

Male squirrels in the Puget Trough covered large distances (>5 km) in search of females during the breeding season and thus had tremendous energy needs (see footnote 4). Weights were heavier for age class III males than for age class II males in the Coast Range during spring where large movements by males were not observed. Thus, similar weights of age class II and III males in the Puget Trough in late spring may suggest that older males come into early spring with larger weights, use more energy, and perhaps travel farther distances than class II males in search of females. In both provinces, age class III females were heavier than age class II females in spring, and mass parallels the ability of older individuals to reproduce (Coast Range) or have more offspring (Puget Trough). By fall, weights were heavier but similar between sexes and between class II and III squirrels, thereby suggesting reduced activity levels allowed accumulation of stored energy reserves (fat) for winter.

Large body size in the Puget Trough also may reflect an increased need for thermoregulation, even though the climate is relatively mild. In the Puget Trough, up to 48 percent of the dens used during the year were external nests comprised of sticks, leaves, and moss; few external nests were observed in the Coast Range (Carey and others 1997, Gillesberg and Carey 1991). External dens generally provide less thermal protection than cavities, and thus body size may be larger in the Puget Trough to compensate for increased thermoregulation needs. Additionally, with lower densities than the Coast Range, Puget Trough squirrels may have less group denning opportunities, or den in smaller groups, and therefore have fewer opportunities to reduce energy expenditures through sharing body heat.

| **Selection Factors—** | Differences in population structure and survivorship between the Coast Range |
| *r* and *K* | and Puget Trough suggest differences in survival strategy. Coast Range squirrels |

Selection Factors— *r* and *K*

Differences in population structure and survivorship between the Coast Range and Puget Trough suggest differences in survival strategy. Coast Range squirrels exhibit the *K*-selection characteristics of dense populations, low reproduction, high adult survivorship, and high juvenile survival (Wilson and Bossert 1971). Puget Trough squirrels exhibit *r*-selection traits of low-density populations, high reproduction, low survivorship of older age classes, and high juvenile mortality. The *K*-"strategists" often are found in more stable habitats; the Coast Range may provide more relatively established and secure habitat (food diversity and dens) even though climatic conditions are harsher than that of the Puget Trough. Puget Trough second-growth stands represent young, disturbed forests with low habitat diversity, and the *r*-selection strategies seen in the Puget Trough may represent a more "unstable" environment for flying squirrels.

It is always difficult to determine cause and effect in biological systems. Most situations are multifactorial, with various causes for each observed effect. As we proceed with our experiments on the influence of forest structure on flying squirrel biology (Carey and others 1996), we will gain further insight into the causes and effects. Nevertheless, being able to accurately assess age and reproduction and applying it to life history characteristics is a prerequisite for understanding the ecology of flying squirrels.

Metric Conversions

1 hectare (ha) = 2.471 acres
1 kilometer (km) = 0.6214 mile
1 meter (m) = 3.28084 feet
1 centimeter (cm) = 0.3937 inch
1 millimeter (mm) = 0.03937 inch
1 gram (g) = 0.035 ounce

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Appendix 1: Sampling Methods

The following is a series of publications on sampling methods and biology for use in designing and implementing research and monitoring efforts in Pacific Northwest forests. This list of publications does not duplicate those listed in "Literature Cited."

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Appendix 2: Arboreal Rodent Trapping Data Processing

Guidelines follow for selecting a single age and reproductive code for individual flying squirrels. For data summary and analysis, each captured individual should have a single code describing age and reproductive status for the trapping session. Animals with more than one capture, however, are sometimes described with more than one age or reproductive code. This document explains how a single code is determined for these individuals and provides guidelines for following a consistent procedure.

Guidelines for Selecting Age and Reproductive Code

Age-class system—For flying squirrels, there are three age-class codes: class I squirrels were born in the same year as the capture date (young-of-the-year), class II squirrels were born the year before the capture date, and class III squirrels were born in years earlier than one year before the capture date.

Reproductive status—There are two "inactive" codes used for both males and females: N and R. Animals that show no sign of ever having been reproductively active are N for never active (males) or nulliparous (females), whereas regressed individuals (R) show signs of past (but not present) reproductive activity. Males have only one code for current reproductive activity: scrotal (S); females have four: estrus (V), pregnant (P), lactating (L), and postlactating (G). The codes for reproductive status are viewed hierarchically: never active and nulliparous are considered the lowest level of reproduction, whereas scrotal and lactating-postlactating are the highest levels. Regressed is viewed as a higher reproductive level than nulliparous, even though we cannot be certain that regressed individuals were active in the current year. All active codes rank above inactive codes, and active codes for females are higher as reproductive condition progresses.

If an individual is caught several times and is assigned two or more age or reproductive codes, a combination of factors is used to select one code. The list below is in order of greatest to least importance in steps used to determine a single code. When the age of a squirrel has been described differently during the trapping session, guidelines 1-7 described below are used to determine the most accurate assessment of age. For reproductive status, all guidelines apply, and the objective is to assign the highest level of reproduction there is evidence to support.

- Capture history—When available, all information about an individual (such as captures in previous trapping sessions) is reviewed along with current trapping data for thorough age and reproductive assessment.
- Complete descriptions—"Complete" includes a description in the notes of all the characteristics that determine the age or reproductive code (appendices 3 and 4; tables 3, 5, and 6).
- Number of trappers using the same code—More individual trappers using one code adds credence to that code, but there must be notes that correspond with code choice for this to be a determining factor.
- Trapper experience—The more animals and seasons a trapper has observed increases reliability. Also, accuracy generally improves for all trappers as the trapping session progresses.

- Age and reproductive status—In fall, females with previous reproductive activity cannot be age class I, and age class I males and females are reproductive code N.
- Weight—Weight is of limited use in determining age or reproductive status. In fall, a weight <100 g suggests age class I, whereas a weight >140 g is likely an older squirrel (for the Puget Trough). A steady increase in the weight of a heavy female combined with evidence of postestrus suggests pregnancy. A sudden drop in weight (approximating 17 percent) within 3 to 4 days or less may indicate parturition. Flying squirrels usually give birth from late May through June in the Puget Trough.
- Population breeding stage—Participation in a trapping session and reviewing all the captures over a session provides an overall picture of the breeding stage of each population. During spring trapping, most male flying squirrels are scrotal, whereas females exhibit various reproductive stages. During fall trapping, most flying squirrels are sexually inactive. It is not uncommon, however, to capture a few females that are postlactating, and it is feasible for animals to be in active stages of reproduction. Individuals described as reproductively active in fall should be carefully reviewed for conclusive evidence regardless of the number of captures or consistency of codes.
- If a decision on the final reproduction code cannot be determined with the above guidelines, the reproductive field is blanked and the change is documented in the notes (as for all code modifications).

Appendix 3: Female Reproductive Cycle

The following are external characteristics of the female flying squirrel reproductive cycle:

Inactive

Genitalia are reduced and pale, no sign of breeding activity. Vulva not swollen, light pink to no color, closed. Mammary disks undeveloped (N) or unapparent (R). Nipple size describes past breeding history:

Nulliparous (N)—Never reproduced.

- Nipples are usually tiny pink dots or small nubs that do not project distinctly above the skin surface; or
- Nipples may show some development: small, slender, conical shape ≤1 mm in length, standing out from skin, pale to pink.

Regressed (R)—Previously reproduced.

- Nipples developed. Conical or flattened, flaccid, >1 mm long, white or light pink.

Active

Begins with changes in vulva appearance, then a progression in the development of nipples, abdomen, and mammary glands.

Estrus (V)—

- Vulva enlarging-swollen and color darkening pink to red. Vagina opening becomes more apparent through estrus until noticeably inverted and open. Nipples undeveloped, developing, or fully developed yet flaccid.
- Mammary is showing no obvious development.

It should be noted when you suspect an animal to be in post-late estrus but it could not be determined pregnant. Write R = V/P in your comments to indicate this condition.

Pregnant (P)—

- Vulva unswollen, usually retains dark coloration, labia flaccid yet easily opened
- Nipples just developing OR becoming more upright and turgid on previously bred animals. Color is darkening pink.
- Abdomen enlarging-disproportionately large during later stages of pregnancy.
- Mammary shows no development or may start to protrude.

Lactating (L)—

- Vulva reverting to small, pale state.
- Nipples developed, turgid, pink to red.
- Abdomen not distended.
- Mammary disk developed, milk production, hair loss.

Postlactating (G)—

- Nipples developed but losing rigidity and color.
- Mammary diminished, hair growing back.

Appendix 4: Male Reproductive Cycle

The following are external characteristics of the male flying squirrel reproductive cycle:

Inactive

Genitalia are reduced, underdeveloped, or absent (externally).

Never active (N)—Never reproduced.

- Scrotum absent or developing (but small). Seen primarily in males born in the current year.
- Testes tiny and undeveloped, often within abdominal cavity, descended into scrotum on some males.
- Penis positioned nearer to anus on immature animals

Regressed (R)—External signs of previous reproductive activity but not currently in breeding condition.

- Scrotum evident to very evident, usually of a size large enough to contain fully developed testes.
- Testes are small (having shrunk down to a nonbreeding condition), however, and may or may not be detectable.

Active

Genitalia are either enlarging, shrinking, or fully developed, depending on the season.

Scrotal (S)—Developed into breeding condition

- Scrotum is large, full, and obvious.
- Testes are large, palpable, and give the scrotum its full shape.

Flying squirrel males become sexually active well before females go into estrus (around May). In the Puget Trough, we have observed scrotal males as early as January. After female estrus and pregnancy, however, male testes rapidly diminish in size. The scrotal sac still remains relatively large and can be used as a factor in distinguishing adults from young of the year when trapping in fall. It is important to record notes on relative testes size so that we get an indication of when sexual regression is occurring in our populations. Also remember that some individuals will retract testes against the abdominal wall due to cold temperatures or on being touched, thereby making detection difficult.

Appendix 5: Necropsy Data Form

DISSECTOR_____

CATNUM_____ STD NAME_____ STD#_____LOCATION_____

DATE_____/____/_____ TAG1_____SPP_____ AGE_____ SEX_____ REPRO_____

TOTAL LENGTH_____TAIL_____BODY LENGTH_____ FOOT_____ EAR_____ WT._____

<div align="center">FEMALE</div>

VULVA	NIPPLES	SCARS		EMBRYOS						UTERINE HORNS	
OPEN/ CLOSED	AVERAGE LENGTH	NUMBER		NUMBER	1 C-R	2 C-R	3 C-R	4 C-R		LENGTH	WIDTH
		L									
		R									

ADDITIONAL REPRO NOTES		CORPORA LUTEA		OVARIES	
		#	AVE. DIA.	LENGTH	WIDTH
_____	L				
_____	R				
_____					

<div align="center">MALE</div>

WELL-DEVELOPED SCROTAL SAC: Y OR N   TESTES: FLACCID OR TURGID

	POSITION	LENGTH	WIDTH		COLLECTIONS				
					PELLETS	STOMACH	REPRO	SKIN	OTHER
L									
R									

<div align="center">***NOTES***</div>

_____

_____

_____

_____

PHOTOS TAKEN: Num_____ Roll#_____ Film_____ Subject _____

Appendix 6: Trapping Data Code Sheet

FIELD NAMES

DATE= D-MON-Y; use 1st 3 letters of month
SEA=   1-Spring   (15 Mar)
            2-Summer   (15 Jun)
            3-Fall   (15 Sep)
            4-Winter   (15 Dec)
WK= week (1,2)
N= night (1,2,3,4)
OBS= first,middle,last initials
STA= Station (A1,H8, etc.)
T= trap: G-ground,T-tree, L-large, S-small
        C-cavity, N-nestbox

SPP= species-(4 letter code[1])
C= capture code: 1-New Capture
                      2-Recapture
                      4-Recapture & Retag

TAG1/TAG2- 5 character eartag label
A= Age: 1-young of year
2-born in previous year (for GLSA only)
3-adult (for GLSA, 3= born before previous year)
S= sex: M-male, F-female
R= reproductive stage[2]
GRWT= wt. of cone and animal
TRWT= wt. of cone
WT= weight of animal (GRWT-TRWT)
PELN= pellet vial[3] code number
D= put '*' if dead, whether or not collected
CATNUM= Catalog number for collected dead
animals. Write in notes.
RC= put '*' if animal carries radio collar

---

[1]SPECIES CODES

SPRU-	Sprung trap	NECI-	Bushy tailed woodrat	APRU-	Mt. beaver
GLSA-	Flying squirrel	NEFU-	Dusky footed woodrat	DIVI-	Opossum
TATO-	Townsend's chipmunk	SPPU-	Spotted skunk	MUER-	Ermine
TADO-	Douglas' squirrel	SCGR-	W. gray squirrel	MUFR-	Long-tailed weasel
SYFL-	Eastern cottontail	LEAM-	Snowshoe hare		

Some common abbreviations in the 'notes' field for SPRU traps include:
NAR - no apparent reason   **NUT** - nestbox under treadle

---

[2]REPRODUCTIVE CODES

<u>Males</u>	<u>Females</u>
N- never been active	N- nulliparous
R- regressed	R- regressed
S- scrotal	V- estrus
	P- pregnant
	L- lactating
	G- post lactating

---

[3]PELLET VIAL LABEL

Stand Name	Stand #
Species	Tag #s
Station:Trap	Sex
Date (dy/mo/yr)	Observer

Appendix 7: Arboreal Rodent Live-trapping Data Sheet

STAND NAME/# _____ DATE _____ SEA _____ WK _____ N _____ PAGE : _____ OF _____ OBS : _____

STA	T	SPP	C	TAG 1	TAG 2	A	S	R	GRWT	TRWT	WT	PELN	D	RC	NOTES

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Document continues on next page.

Northern flying squirrels are the primary prey of northern spotted owls and are important dispersers of fungal spores in Pacific Northwest forests. Despite the importance of these squirrels in forest ecosystems, information is lacking on life history and methods for determining age and reproductive condition. In the laboratory, we measured epiphyseal notch, femur length, rostrum length, least interorbital breadth, rump pelage length and color, and tail width of dead squirrels. We analyzed weight, pelage color, and reproduction for field-collected data from live squirrels. Reproduction of northern flying squirrels can be reliably determined in live-trapping studies. Regional variations suggest accurate assessment of age and reproduction is a prerequisite for understanding flying squirrel ecology.

Keywords: Northern flying squirrel, maturation, reproductive biology, Oregon, Washington, live-trapping, necropsy.

Pacific Northwest Research Station
333 S.W. First Avenue
P.O. Box 3890
Portland, Oregon 97208-3890

U.S. Department of Agriculture
Pacific Northwest Research Station
333 S.W. First Avenue
P.O. Box 3890
Portland, OR 97208-3890

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