

Williamson's Sapsucker

Sphyrapicus thyroideus

FRENCH: *Pic de Williamson*

SPANISH: *Chupasavia de Williamson, Carpintero garganta roja*

Inhabiting open coniferous and mixed coniferous-deciduous forests of western North America, Williamson's Sapsucker has been considered a sensitive indicator species because of its specific habitat requirements. Like other sapsuckers, it drills conspicuous rings of holes ("sap wells") into tree trunks, specializing on coniferous sap and phloem. Breeders switch to a diet of ants during the nestling period.

Unlike most other woodpeckers, Williamson's Sapsucker exhibits spectacular sexual differences in plumage. Males are black with bright red, yellow, and white. Females are mostly cryptic brown with little contrast except for their yellow bellies. These plumage differences confused early naturalists, who thought the two sexes were separate species.

The Birds of North America

Life Histories for the 21st Century

John Cassin first described the species in 1852 and classified a female specimen as a male Black-breasted Woodpecker (*Melanerpes thyroideus*, or *Picus thyroideus*; Bent 1939, Am. Ornithol. Union 1983). This "species" underwent several subsequent name changes, including Brown-headed and Round-headed Woodpecker, or *Sphyrapicus thyroideus*. John Newberry discovered the male in 1857 and named it Williamson's Woodpecker (*Picus williamsonii*), which was renamed *Sphyrapicus williamsonii*. Finally, Henry Henshaw verified that the two

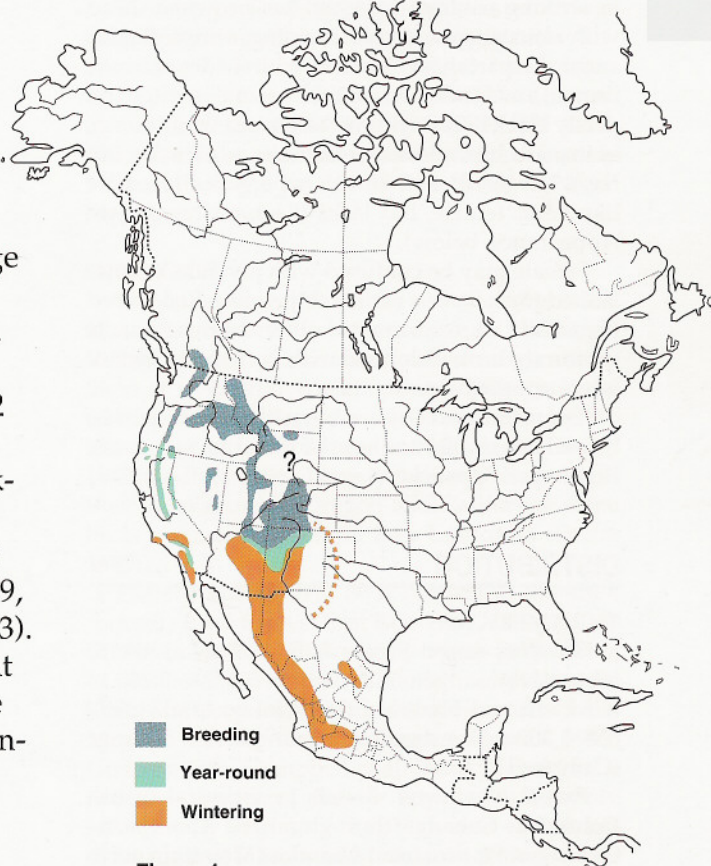
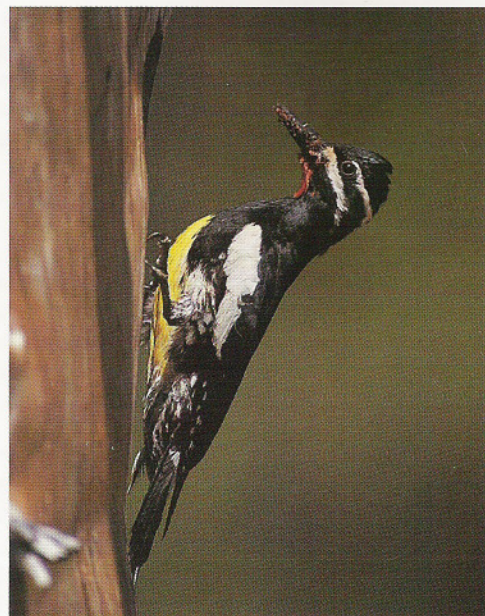


Figure 1. Distribution of the Williamson's Sapsucker. This species winters irregularly east to the dotted line.

sexes were a single species when in 1873 he was the first to observe a mated pair, at a nest in Colorado (Bent 1939). The species was named after Lieutenant Robert Stockton Williamson (1824–1882), who conducted early railroad surveying expeditions in the West Coast states (Mearns and Mearns 1992).

Williamson's Sapsucker populations declined throughout their range from 1982 to 1991, with particularly strong declines in the Pacific Northwest. Data are few, however, because of the sparse number of Breeding Bird Survey (BBS) routes in the western U.S.; more complete surveys are needed.

DISTINGUISHING CHARACTERISTICS

Medium-sized woodpecker, about 23 cm; reported values ranging from 21–23 cm (Winkler et al. 1995) to 22.5–24.8 cm (Godfrey 1986); mass 44.4–55.3 g (Dunning 1993). Male is unmistakable, with white wing-coverts, rump, supercilium, and moustachial stripe contrasting strongly with iridescent black upperparts, head, and breast; red patch on chin and upper throat in adult; belly yellow. Adult female, in striking contrast to male, has brownish head with obscure moustachial striping; wings, flanks, and upperparts heavily barred with shades of white, brown, and black; and no white wing-coverts; has partly black breast, yellow belly, and white rump, as in male. Juvenile male resembles adult male, but has white throat and whitish nape. Juvenile female like adult female, but lacks black on breast (see Appearance, below).

Female may be confused with juvenile Yellow-bellied (*Sphyrapicus varius*) or juvenile Red-naped (*S. nuchalis*) sapsuckers, but differs from both in its uniformly brownish head with no red and lack of white wing-coverts.

Churr Call and Drumming pattern (see Sounds, below) are similar to those of the often sympatric Red-naped Sapsucker.

DISTRIBUTION

THE AMERICAS

Breeding range. Figure 1. Breeds at middle to high elevation, generally between 1,500–3,200 m (Crockett and Hadow 1975, Winkler et al. 1995); 850–1,300 m in extreme northern portion of range (Campbell et al. 1990).

PACIFIC NORTHWEST. Breeds in s.-central British Columbia, Canada "throughout the Thompson–Okanagan Plateau from Anarchist Mountain north to the vicinity of Terrace Mountain and Scottie Creek (Cache Creek) and west to the Manning Park and Lytton areas" (Campbell et al. 1990). Eastern

slope of the Cascade Mtns. in Oregon and Washington, north to Okanogan and Ferry Cos., Washington (Jewett et al. 1953, Gilligan et al. 1994, Washington Breeding Bird Atlas unpubl.). Blue Mtns. in se. Washington (Jewett et al. 1953, Washington Breeding Bird Atlas unpubl.) and ne. Oregon (Gilligan et al. 1994). Wallowa Mtns. in e.-central and Warner Mtns. in s.-central Oregon; possible rare breeder in Siskiyou Mtns. (Gilligan et al. 1994; see also Small 1994).

NORTHERN U.S. ROCKY MTS. Bear Lake Co. in se. Idaho, northwest through Blaine Co., and throughout central portion of state, including Adams, Valley, Lemhi, and Clark Cos., becoming uncommon north of Idaho Co. (Burleigh 1972, Stephens and Sturts 1991). West of Continental Divide in nw. Montana, extending east of divide in sw. and s.-central Montana to Absaroka Range (Skaar et al. 1985). Northwest (Absaroka and Teton Ranges), n.-central (Bighorn Mtns.), and se. Wyoming (Oakleaf et al. 1992).

SOUTHERN U.S. ROCKY MTS. Central mountains of Utah, from southern counties north to Bear Lake and Uinta Mtns. in the northeast (Hayward et al. 1976, Walters and Sorenson 1983). Breeds throughout Colorado west of the plains, but most common in s. portions and the Front Range (Andrews and Righter 1992). Mogollon Highlands of w.-central New Mexico, north to northern highlands of w. and n.-central part of state, including Mt. Taylor, and the Chuska, San Juan, Jemez, Sangre De Cristo, Zuni, San Mateo, Tularosa, and Black ranges (Hubbard 1978). In Arizona, breeds from Mogollon Rim north to Kaibab Plateau, including White Mtns., Bill Williams Mtn., and San Francisco Mtns. (Phillips et al. 1964, Monson and Phillips 1981).

CALIFORNIA AND GREAT BASIN. Several disjunct breeding populations occur in mountains of s. California west of Mojave Desert, including San Gabriel, San Bernardino, and San Jacinto Mtns., and Mt. Pinos (Garrett and Dunn 1981). Major breeding range within Sierra Nevada–Cascade ranges from Greenhorn Mtns. north to Oregon (Small 1994). Isolated breeding populations occur in extreme north in Siskiyou, Trinity, and Warner Mtns. (Small 1994). East Warner Mtns., Sweetwater Range, and Carson Range in extreme w. Nevada, and Ruby and Pequop Mtns., Spruce Mtn., and Snake Range in east; apparently absent from central ranges of Nevada (Johnson 1975, Ryser 1985).

MEXICO. A disjunct breeding population exists in the Sierra San Pedro Martir in Baja California Norte (Kratter 1991).

Winter range. Figure 1. Winters from southern part of breeding range (at lower elevations) south to Mexico (1,000–3,500 m in w. Mexico; Am. Ornithol. Union 1983, Howell and Webb 1995).

OREGON. Rare in Klamath and Lake Cos. in Klamath Basin of s. Oregon; very rare elsewhere in the state (Root 1988, Gilligan et al. 1994).

CALIFORNIA AND GREAT BASIN. Breeding populations generally resident but some regular movement to midelevations and irregularly or casually to lowlands surrounding breeding areas Sep–Apr. Rare winter visitor to mountains of Santa Barbara Co. and San Diego Co. in the southwest. A few birds from Great Basin and Rocky Mtns. (*nataliae*; see Systematics: subspecies, below) apparently winter in mountains of e. Mojave Desert and other deserts of the Southwest (Garrett and Dunn 1981, Rosenberg et al. 1991, Small 1994). Breeding populations resident in w. Nevada but migratory in e. Nevada and Utah (Ryser 1985).

ARIZONA, NEW MEXICO, AND TEXAS. Generally winters south and west of Mogollon Rim, rarely on Mogollon Plateau in ne. Arizona (Phillips et al. 1964, Monson and Phillips 1981); casual in lowlands of lower Colorado River valley (Monson and Phillips 1981, Rosenberg et al. 1991). In New Mexico, Jemez and s. Sangre De Cristo Mtns. southward west of the Pecos Valley (Ligon 1961, Hubbard 1978). Rare and irregular winter visitor to Trans–Pecos and northern panhandle of Texas; casual on Edwards Plateau (Oberholser 1974).

MEXICO. Winters in mountains of n. Baja California Norte, and from e. Sonora and w. Chihuahua, south through Durango and Zacatecas to Jalisco and n. Michoacán; uncommon east to sw. Nuevo León and se. Coahuila (Am. Ornithol. Union 1983, Howell and Webb 1995).

Late fall and winter records east of normal range exist for coastal e. Texas and sw. Louisiana (Remsen 1991).

OUTSIDE THE AMERICAS

Not recorded.

HISTORICAL CHANGES

On basis of avifaunal literature from late 1800s to the present, DeSante and George (1994) note that Williamson's Sapsucker has expanded its range westward, resulting in increased abundance in parts of British Columbia. Campbell et al. (1990) document similar range expansion in s.-central British Columbia since 1947. Interestingly, this species formerly bred in southern part of e. Kootenay in se. British Columbia, disappearing in 1930s (Campbell et al. 1990). It has been suggested that these range shifts are a function of the distribution of western larch (*Larix occidentalis*), but no clear trend has been illustrated (Cannings et al. 1987, Campbell et al. 1990).

The isolated breeding population of n. Baja California is thought to have been recently

established and represents a 325-km southward range extension of western subspecies or a 600-km westward extension of eastern subspecies (Kratter 1991). These potential range expansions may also reflect increased fieldwork in isolated areas of the species' range.

FOSSIL HISTORY

Limited. One left humerus, identified as that of Williamson's Sapsucker, found at archaeological excavation of a bison (*Bison bison*) kill site in Casper, Natrona Co., WY. Radiocarbon dating and presence of certain other fossils place the bone in the late Pleistocene (Wilson and Rea 1976).

SYSTEMATICS

Formerly called Black-breasted Woodpecker, Brown-headed Woodpecker, Round-headed Woodpecker, and Williamson's Woodpecker (see Introduction, above).

GEOGRAPHIC VARIATION

Two subspecies differ only in bill size; no obvious geographic variation in plumage coloration. *S. t. thyroideus* (western part of range) has longer, broader, and deeper bill than *S. t. nataliae* (eastern part of range; Swarth 1917, Short 1982). Bill width differs between the 2 subspecies by approximately 1 mm, bill length by 1.5–2.5 mm (Ridgway 1914, McTaggart Cowan 1938).

SUBSPECIES

Two subspecies. Nominate race, *S. t. thyroideus* (Cassin), breeds from eastern edge of Okanagan Valley, s. British Columbia, south through mountains of w.-central Washington and Oregon, and California and extreme w. Nevada to San Jacinto Mtns. of s. California (Munro and McTaggart Cowan 1947, Godfrey 1986). Largely resident, wintering at lower elevations in Oregon and California; some birds migrate south to n. Baja California (Peters 1948).

Eastern subspecies, *S. t. nataliae* (Malherbe), formally bred from s. East Kootenay Valley, in se. British Columbia, but presently breeds from Idaho, w. Montana, and Wyoming, south through Nevada, Utah, and Colorado to central Arizona and w. New Mexico (Munro and McTaggart Cowan 1947, Godfrey 1986, Campbell et al. 1990). Named for a Mexican specimen, *nataliae* appears to be more latitudinally migratory than *thyroideus* and occurs as far south as Jalisco and Michoacán during winter (Swarth 1917, Am. Ornithol. Union 1983, Kratter 1991). The 2 subspecies appear to be largely isolated from one another, except perhaps for e. Oregon,

where intergradation may occur during breeding season (McTaggart Cowan 1938, Godfrey 1986, Winkler et al. 1995). Some birds, however, migrate west to California during winter (Raitt 1959).

RELATED SPECIES

Genus *Sphyrapicus* consists of 4 species: Williamson's (*S. thyroideus*), Yellow-bellied (*S. varius*), Red-naped (*S. nuchalis*), and Red-breasted (*S. ruber*) sapsuckers (Am. Ornithol. Union 1983, 1985). Electrophoretic analyses from 88 specimens at 39 loci by Johnson and Zink (1983) suggest that *Sphyrapicus* includes 2 lineages: *S. varius* super-species (*varius*, *nuchalis*, and *ruber*) and *S. thyroideus*—the latter representing the older of the 2 lineages and the most distinct species of the genus. Genetic distance values between *S. thyroideus* and species of the *S. varius* complex (0.186–0.142) indicate that the lineages split 3.0–3.7 million years ago, during the late Pliocene. This genetic distance indicates that *thyroideus* is "as different from its congeners as are species of different genera in the Parulidae" (Johnson and Zink 1983).

S. thyroideus had the lowest heterozygosity ($H = 0.016$) of the genus (*S. ruber ruber*, *S. ruber daggetti*, and 3 populations of *S. nuchalis* had mean value $H = 0.043$; for *S. varius*, $H = 0.022$), and among birds in general (Johnson and Zink 1983). Similarly, *thyroideus* had the lowest percentage of polymorphic loci: 7.7% (*ruber* and *nuchalis* have mean 16.4%, *varius* 12.8%).

Two hybrids with *S. nuchalis* were collected on wintering grounds: 1 male and 1 female (Short and Morony 1970). Each bird resembled Williamson's Sapsucker to greater degree than it resembled Red-naped Sapsucker. As described by Short and Morony (1970), male hybrid differed from adult male Williamson's mainly in its smaller size, an orange reddish crown and throat/upper breast, a full supercilium and broad malar stripe, and asymmetrically barred central rectrices. Female hybrid resembled female Williamson's, but possessed head pattern, including pale red crown-patch and partial wing bar, similar to Red-naped Sapsucker. Measurements of each hybrid generally fell into zones of overlap between the 2 species, although male hybrid favored Red-naped in wing and tail length, but Williamson's in tarsus length.

Male Williamson's Sapsuckers closely resemble *Melanerpes* woodpeckers—e.g., Acorn Woodpecker (*M. formicivorus*), Yellow-tufted Woodpecker (*M. cruentatus*), White-fronted Woodpecker (*M. cactorum*)—in plumage coloration. Females resemble both sexes of Gila Woodpecker (*M. uropygialis*). The presence of a distinctly juvenile plumage is also similar to some melanerpine woodpeckers—e.g., Red-headed Woodpecker (*M. erythrocephalus*)—

suggesting that *Melanerpes* may be the oldest existing lineage of *Sphyrapicus* (Phillips et al. 1964, Short and Morony 1970, Johnson and Zink 1983). Short and Morony (1970) hypothesized that an ancestral sapsucker population diverged to create *S. thyroideus* in w. North America and the *S. varius* complex in eastern regions, which then dispersed westward to give rise to modern distributions. Howell (1952) suggested that *Picoides* and *Dendrocopos* woodpeckers are the closest relatives of *Sphyrapicus*.

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

Some populations resident; others migratory. Latitudinally, *nataliae* migrates farther than *thyroideus*, reaching as far south as Jalisco and Michoacán, Mexico, but more often only as far as Sinaloa and Durango, Mexico (Davis 1962, Howell and Webb 1995). Migration patterns probably differ between sexes, with females migrating farther south than males (Howell 1953, Davis 1962, Crockett 1975). Birds also move altitudinally throughout range, commencing with postbreeding dispersal down-slope (Rockwell and Wetmore 1914, Phillips et al. 1964, Hadow 1977).

TIMING AND ROUTES OF MIGRATION

Spring. Departure dates from southern wintering grounds (Mexico) largely unknown. Williamson's Sapsucker is early spring migrant, among the first species to arrive in Idaho (Smith 1982). Migration occurs Mar–early May (Phillips et al. 1964, Short 1982). In n. Arizona, early records span from mid- to late Feb; most birds have left s. Arizona by first week of May (Phillips et al. 1964). Colorado arrival dates vary from 4 Apr in southwest to 18 Apr in northeast (Packard 1945, Hadow 1977), with several Feb and Mar records (Andrews and Righter 1992). Median arrival date over 5 yr in New Mexico is 1 May (Travis 1992). Individuals generally arrive in northwestern states during last 2 wk of Apr, but this has not been well documented and some birds arrive as early as late Mar (Bent 1939, Cannings et al. 1987). Arrives mid-Mar and Apr in Oregon (Gilligan et al. 1994), by mid-Apr in British Columbia (Campbell et al. 1990). Males arrive on breeding grounds up to 2 wk before females (Crockett and Hansley 1977, Hadow 1977, Short 1982). At Rocky Mountain National Park, CO, Williamson's Sapsucker arrived and bred an average of 2 wk before Red-naped Sapsucker (Crockett and Hadow 1975).

Fall. Departs from breeding grounds in British Columbia during first 2 wk of Sep (Cannings et al. 1987); most are gone by mid-Sep, although

occasionally found as late as mid-Oct (Campbell et al. 1990). Fall migration continues through Oct, and even into Nov in n. Arizona (Phillips et al. 1964). Median departure date over 8 yr in New Mexico was 29 Sep (Travis 1992). In s. Colorado, birds move down-slope in late Aug and early Sep; most birds have moved south by mid-Oct (Hadow 1977). Depart Oregon from late Aug to mid-Oct (Gilligan et al. 1994).

Casual east of the normal range, with records (mostly spring) for s. Alberta, s. Saskatchewan, S. Dakota, Minnesota, Illinois, Kansas, and Oklahoma (Am. Ornithol. Union 1983, Bohlen 1989, Remsen 1991).

MIGRATORY BEHAVIOR

Appears to flock during migration (Swarth 1904). Also observed foraging with small groups of Red-breasted Sapsuckers during fall in San Bernardino Mtns., CA (Rossem and Pierce 1915). Frequently observed in lower elevations below coniferous forest habitat outside of breeding season (Campbell et al. 1990, Remsen 1991).

CONTROL AND PHYSIOLOGY

No information.

HABITAT

BREEDING RANGE

Throughout range, breeds at middle to high elevations in montane spruce-fir (*Picea-Abies*), Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and ponderosa pine (*Pinus ponderosa*) forests. Also in mixed deciduous-coniferous forest with quaking aspen (*Populus tremuloides*), an important nesting substrate (Smith 1982, Sousa 1983, Conway and Martin 1993). In s. Colorado, observed in Douglas fir vegetation more frequently than expected, on basis of Douglas fir abundance (Winternitz 1976). Williamson's and Red-naped sapsuckers exhibit local segregation in Colorado through habitat selection; Williamson's favors nest sites adjacent to open ponderosa forest, and Red-naped chooses sites closer to deciduous or mixed coniferous forest (Crockett and Hadow 1975; see also Smith 1982).

In British Columbia, distribution correlates with presence of western larch, suggesting that availability of suitable nest sites may limit distribution (Cannings et al. 1987, Campbell et al. 1990). Availability of suitable nest sites—e.g., snags (i.e., dead trees)—is critical component of breeding habitat (Conway and Martin 1993). Li and Martin (1991) and Conway and Martin (1993) found a preference for snags as nest sites in Arizona, while

Crockett and Hansley (1977) found most nests in live aspen in Colorado. Availability of snags at Colorado site was not reported, however. In other regions of Colorado, majority of nests were in pine trees and less frequently in aspen snags (Niedrach and Rockwell 1939). Nonetheless, at most places, aspen snags are preferred over conifer snags (Crockett and Hadow 1975, Scott et al. 1980, Conway and Martin 1993). See also Food habits: feeding, and Breeding: nest site, below.

SPRING AND FALL MIGRATION

Found in wide variety of habitats during migration. May move down-slope during migration and into oak (*Quercus*) scrub, piñon-juniper (*Pinus-Juniperus*), deciduous riparian, and even exotic conifer plantings (Kingery and Graul 1978, Small 1994).

WINTER RANGE

In sw. U.S., winter habitat consists of low- to midelevation forests of oak-juniper and pine-oak forests and, to lesser extent, deciduous riparian and oak forests (Bock and Larson 1986). Sexual habitat segregation occurs latitudinally (see Migration, above) and altitudinally in s. Arizona; females winter at lower mean elevations than males (Bock and Larson 1986). Females appear to occupy a wider array of winter habitats compared with males (Phillips et al. 1964, Bock and Larson 1986). In w. Mexico, species appears to favor high-elevation pine-oak forests (Hutto 1992).

FOOD HABITS

FEEDING

Main foods taken. Omnivorous with high seasonal specialization. Feeds exclusively on conifer sap and phloem during prenestling period, shifting to mainly ants (Hymenoptera) after hatching of young (Stallcup 1968, Crockett 1975, Sousa 1983). Also takes other insects—e.g., beetles (Coleoptera), flies (Diptera), aphids (Homoptera)—during breeding season (Stanford and Knowlton 1942, Crockett 1975).

Apparently, sap and phloem fibers constitute primary diet during nonbreeding season (Stallcup 1968, Crockett 1975). However, fruits appear to provide substantial resource during winter. Females in s. Arizona fed largely on madrone (*Arbutus* spp.) berries; 12 of 14 females observed associated with madrone trees (Bock and Larson 1986). Also consumes juniper berries, berries of exotic plants, and unknown berries (Beal 1911, Russell 1925, Bock and Larson 1986).

Microhabitat for foraging. Forages mainly in conifers and snags (dead trees), rarely in aspen, favoring living pines during breeding and non-breeding seasons (Stallcup 1968, Smith 1982). In Colorado ponderosa pine forests, foraged mostly in live pines (97–99% of observations) and almost exclusively on trunk (96–97% of observations) with no significant seasonal differences (Stallcup 1968). In ne. Oregon, foraged most frequently in ponderosa pine and Douglas fir trees, less frequently in western larch and lodgepole pine; >90% of all foraging observations were in live trees ($n = 129$; Bull et al. 1986). Trees used for foraging had average diameter at breast height (dbh) of $41 \text{ cm} \pm 8.1 \text{ SD}$ and height of 21 m in ne. Oregon ($n = 129$; Bull et al. 1986).

Foraging heights range from low-level bare trunk to tree crown; no seasonal differences in height (Stallcup 1968, TEM). Foraging height averaged $10 \text{ m} \pm 6.2 \text{ SD}$ in ne. Oregon ($n = 129$; Bull et al. 1986). Short (1982) reported birds occasionally foraging for ants on ground at base of foraging trees, and suggested that birds may follow ants out of tree. Foraging-microhabitat preferences differ sexually; males use tree limbs and ground more than females, which use trunks more in Colorado (Crockett 1975), although such differences are not true in Arizona (TEM).

In Colorado, breeding pairs often take sap from 4 or 5 different trees (Crockett 1975). Douglas fir and ponderosa pine were most common of 5 coniferous species used as sap trees in Colorado (Crockett 1975); Douglas fir used in Oregon (Bull et al. 1986). Sap trees chosen were smaller than expected on basis of availability; Douglas fir sap trees smaller than ponderosa pine sap trees (Crockett 1975). In California, lodgepole pine preferred, but hemlock (*Tsuga*), white fir (*Abies concolor*), Jeffrey pine (*Pinus jeffreyi*), and aspen are also used (Grinnell and Storer 1924). Pine and juniper used during winter in s. Arizona (Bock and Larson 1986). Birds use same sap trees year after year. In California, sap trees did not differ from undrilled trees in bark thickness, stem diameter, vigor, or dominance, but wounded or scarred trees were used more frequently for sap trees (Oliver 1970).

Food capture and consumption. Mostly sapsucking and insect-gleaning from bark surface of tree trunks. Drills concentric rings of shallow wells (holes) in sap trees, which it checks periodically for sap reserves and trapped insects. Also removes sections of bark to facilitate greater sap drainage and/or to directly eat underlying layer of phloem fibers (Stallcup 1968). In Oregon, 75% of foraging observations were at sap wells, 25% pecking on trees ($n = 129$; Bull et al. 1986). Of 2,713 ponderosa pine trees examined in ne. California, 5.9% had recent (<3 yr old) sapsucker wells (Oliver 1970).

Hops up main stem of pine trees, gathering ants off surface of bark (Stallcup 1968). Occasionally pecks and probes for insects beneath surface of bark (Bent 1939). In Arizona, observed gleaning aphids from underside of canyon maple (*Acer grandidentatum*) leaves (RCD, TEM, CJC). Also flycatches infrequently (Short 1982, TEM).

DIET

Major food items. Breeding birds feed mainly on sap and ants, the latter constituting the primary nestling diet (Beal 1911, Crockett 1975, Sousa 1983). Carpenter ants (*Crematogaster* sp.) and wood ants (*Formica* sp.) constitute majority of ants consumed (Short 1982). Other insects (e.g., beetles, flies, aphids) also taken (Stanford and Knowlton 1942, Crockett 1975). In 24 specimens examined for food content, insects (ants and beetles) predominated (Martin et al. 1951). Nonbreeding birds consume sap and phloem primarily (Martin et al. 1951, Stallcup 1968, Crockett 1975), but also fruits, including those of piñon and madrone (Beal 1911, Russell 1925, Bock and Larson 1986, Remsen 1991). See also Breeding: parental care, below.

Quantitative analysis. Stomach contents of 17 specimens, collected from Jun to Sep, consisted of 86% ants, 1% various insects (crane flies [Tipulidae], click beetles [Elateridae]), and 13% vegetable matter (cambium; Beal 1911). See also Martin et al. 1951.

FOOD SELECTION AND STORAGE

No information.

NUTRITION AND ENERGETICS

No information. Wild-caught birds can subsist 1–2 wk on combination of sugar water and mealworms (*Tenebrio*) in captivity (E. Walters pers. comm.).

METABOLISM AND TEMPERATURE REGULATION

No information. Although birds roost under conifer boughs, in captivity birds can subsist in outdoor pens with temperatures as low as 0°C (E. Walters pers. comm.).

DRINKING, PELLET-CASTING, AND DEFECATION

Observed drinking water from small puddle (Crockett 1975). No information on pellet-casting or defecation.

SOUNDS

VOCALIZATIONS

Development. Capable of weak vocalization soon after hatching, and beg almost constantly thereafter, becoming increasingly louder with time (Crockett

and Hansley 1977). Nestlings become audible from within nest cavity 1–2 wk after hatching (RCD, TEM) and begin producing "weak guttural rolls or scolds" from nest just before fledging (Crockett and Hansley 1977). Twittering Calls, as described by Crockett (1975), are high-pitched, squeal-like nestling calls, often audible from considerable distance during latter part of nestling stage, that intensify at feeding.

Vocal array. Calls only; no song. Following Crockett 1975, vocalizations classified into 6 types, but high variability.

CHURR CALL. Figure 2A. Often given in association with Drumming (Fig. 2B; see Nonvocal sounds, below), consists of 1–6 (or <15) *cheur* notes and functions in territorial announcement, pair formation, mate location, and even as aggressive alarm (Crockett 1975, Hadow 1977, Short 1982). Mainly a male territorial vocalization; females occasionally utter higher-pitched Churr Call (Hadow 1977).

CHATTER CALLS. Vary from slow *ch-ch-ch* series to rapid bursts (few and up to 37 notes); usually given softly as communication between mates, often precopulatory (Crockett 1975, Short 1982).

CA-HAW. "Consists of 2 hoarse syllables, the second being lower in pitch, longer in duration, and less emphatic than the first." Given at beginning of territorial or courtship interaction; also used as alarm call.

RATTLE CALL. Rapid guttural trill. Often used at the end of territorial or courtship encounters.

SCOLD OR ALARM CALL. The most common vocal response to intruders near nest or sap tree; a short, sharp, hoarse guttural note, which drops rapidly in pitch.

SCREAM CALL. A "shrill, high-pitched call," often given when bird is caught and held by humans.

Phenology. During breeding season, frequency of Churr Call decreases significantly after pairing, increasing again just before fledging (Hadow 1977).

Places of vocalizing. Males most often give Churr Call from trees within 30 m of nest; also observed giving this call from sap wells, from perches adjacent to nest, and from within nest cavity (Hadow 1977).

Repertoire and delivery of songs. See above.

Social context and presumed function of vocalizations. Churr Calls serve in mate attraction and territory advertisement, much the same as song in oscine passerines (Hadow 1977 and references therein). Churr Calls followed conspecific Drumming (6.9%) and conspecific Churr Calls (14.9%), preceded (4.0%) and followed (4.0%) nest exchanges, preceded copulation events (2.0%), but most often (57.4%) were result of no obvious stimulus (Hadow 1977). See above.

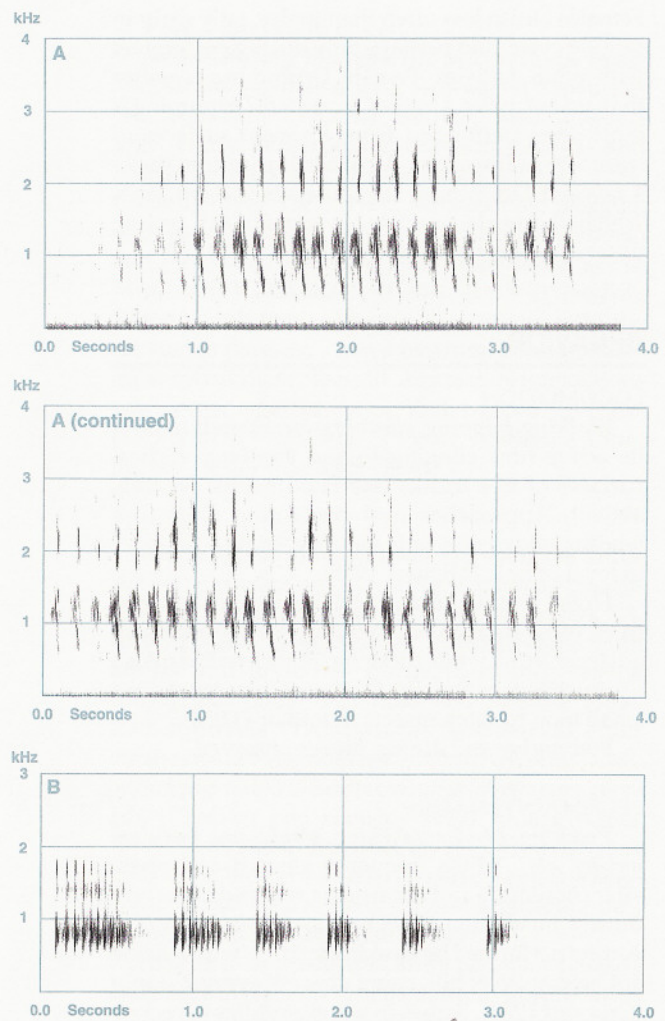


Figure 2. Sounds produced by adult male Williamson's Sapsucker. A. Churr Call. B. Drumming. Sonograms from recordings in the collection of the Library of Natural Sounds, Cornell Laboratory of Ornithology (LNS #49020, recorded in Sierra Co., CA, 15 Jun 1990). Prepared by the staff of the Borror Laboratory of Bioacoustics, Ohio State University.

NONVOCAL SOUNDS

From Hadow (1977), except where noted. Drumming (tattooing) is communication within *Sphyrapicus* consisting of steady roll (or 2) of taps followed by single loud taps (frequently 3 or 4) at irregular intervals (Howell 1952; Fig. 2B). Drumming pattern and rhythm of Williamson's Sapsucker is similar to that of Red-naped Sapsucker, but slower and more regular, with longer beats (Howell 1952, Crockett 1975). Performed mainly by male, Drumming is most common in early morning during pair formation, serving much the same function as Churr Call (Howell 1952, Hadow 1977). After pair bond forms, Drumming restricted to late afternoon.

Females Drum less often than males, only early in nesting cycle, and perhaps only during encounters with other females. Female Drumming is softer than that of males. Unlike Churr Call, Drumming is most often performed from resonant surfaces of trees >30 m from nest. Most territories contain 2–4 favored Drumming sites, usually a dead limb, which the birds select by systematically testing different areas (Hadow 1977, Short 1982).

BEHAVIOR

LOCOMOTION

Walking, hopping, climbing, etc. Spends most of its active time clinging to and climbing vertical surfaces of tree trunks (see Food habits: feeding, above). Approaches nest containing young by landing above nest hole and descending "jerkily" to level of hole (Michael 1935).

Flight. Flight undulating. Flies directly between trees, often from crown to base, after ascending an adjacent trunk while foraging (Stallcup 1968). Also fly-catches occasionally, flying out from trunks in a small loop to catch insects in midair (TEM).

Swimming and diving. Never observed.

SELF-MAINTENANCE

Preening, head-scratching, stretching, bathing, anting, etc. Adults frequently stretch and preen after copulation and upon being relieved at the nest during incubation (Crockett and Hansley 1977). Anting performed by stroking feathers with a single ant held at tip of bill, using new ant every 2–3 min (Crockett 1975). Bathes in water puddles (Crockett 1975).

Sleeping, roosting, sunbathing. Roosts in natural or previously excavated cavities during nonbreeding season; fledglings do not roost in nest cavity (Short 1982). Adults often nap between parental care activities by clinging to the side of a tree, occasionally for periods >60 min (Crockett 1975). Sunbathes frequently, regardless of temperature, by facing away from sun, spreading tail feathers, extending wings, holding head back, and raising crown feathers (Crockett 1975).

Daily time budget. No information.

AGONISTIC BEHAVIOR

Physical interactions. Male defends territory, especially during establishment, often chasing conspecific males (Crockett and Hansley 1977). Males occasionally chase sympatric Red-naped Sapsucker males, and even other woodpeckers (Hadow 1977, Short 1982). Both males and females will chase a variety of birds that come near the nest cavity (TEM).

Communicative interactions. Intruder conspecific males and resident males often Drum or exchange Churr Calls within sight of each other, culminating in retreat of the intruder or aggressiveness by resident male (Hadow 1977). Females interact vocally with neighboring females, through Drumming or Churr Calling during early nesting activities (Hadow 1977).

SPACING

Territoriality. Male establishes territory on basis of location of the chosen nest site; female plays small role in territory establishment and maintenance (Hadow 1977, Short 1982, Sousa 1983). Estimates of territory size vary from 4 ha (Thomas et al. 1979) to 6–7 ha (Short 1982). Crockett (1975) reported home ranges in Colorado from 4 to 9 ha (average 6.75, $n = 10$). Birds may return to same territory annually or may switch territories (Crockett 1975, TEM).

Males often respond to conspecifics by chasing and fighting. Fights consist of one to many aggressive displacements, often involving physical combat, in which either bird may show dominance (Crockett 1975, Hadow 1977). Often intruder males retreat without aggressive behavior, exhibiting Moth Flight Display, which consists of a short, straight flight of rapid, shallow wing-beats (Crockett 1975, Hadow 1977, Short 1982). Birds also respond to territorial intruders with Bouncing, or Fluttering, Flight Display, in which aggressor approaches intruder with deep undulations and high amplitude wing-beats (Crockett 1975, Short 1982). Wings-Up Display often follows Bouncing Flight: upon landing, holds both wings outstretched above back and breast, and puffs out throat-feathers to expose red and yellow colors of male (Crockett 1975). In Bobbing-Wagging Display, gives Chatter Call, raises crest, flattens plumage, puffs out breast, and then points bill up and raises and lowers head or swings it from side to side (Crockett 1975). Territorial behavior decreases throughout nesting cycle, eventually becoming limited to protection of nest tree (Sousa 1983).

Some interspecific territoriality with sympatric Red-naped Sapsuckers, but interactions are rare after territory establishment. Hadow (1977) observed 11 such interspecific encounters, in which Williamson's won 7 and Red-naped won 4. Territories of these 2 species often border each other (nests within 15 m), but are frequently located in relation to species-specific foraging habitat (see Habitat: breeding range, above), resulting in minimal interspecific contact.

Individual distance. Territorial as pairs during breeding season and intolerant of conspecifics entering territory. One pair/40 ha in California (Bock

and Lynch 1970); 4.1 pair/40 ha in n. Colorado (Stallcup 1968) and 1 pair/17 ha in s. Colorado (Winternitz 1976). Individuals are tolerant of conspecifics during migration (see Migration: migratory behavior, above).

SEXUAL BEHAVIOR

Mating system and sex ratio. Monogamous; 1 pair per territory. Sex ratio unknown, but some males remain unmated during a breeding season (Crockett and Hansley 1977).

Pairbond. Pairs remain together during breeding season, parting after young fledge. Female may abandon pair as result of unsuitable nest-site choice by male (Crockett and Hansley 1977). Pairs may remate in subsequent years, remaining near original territory, but data are sparse.

Males initiate copulation, often through series of precopulatory displays in response to female solicitation. In Bouncing (Fluttering) Flight, male approaches his mate from above, giving Chatter Call, and descends slowly (fluttering) to perch beside her (both birds calling). Then, after series of Bobbing-Wagging Displays (see Spacing, above), initiates copulation (Crockett 1975, Short 1982). Typical copulation event lasts about 15 s, usually near nest, but never in nest tree (Crockett and Hansley 1977). The female, crouched on branch with drooped wings, is usually mounted from left side; male approaches while chattering, fluttering wings, and jerking its tail (Michael 1935, Crockett and Hansley 1977). Once on top, male curves his tail beneath his mate's and "slowly slips off to the left as he copulates" (Crockett and Hansley 1977, Short 1982). Both sexes often preen after copulating.

Sexual recrudescence (postfledging courtship and nesting behavior) usually involves members of differing nesting pairs and has been documented in Williamson's Sapsucker (Crockett and Hansley 1977). Birds have been observed displaying, excavating, and prospecting previously excavated cavities, but nothing further.

Extra-pair copulations. Not documented.

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. Pairs territorial during breeding season; little toleration of conspecifics. Closely related heterospecifics (Picidae) occasionally experience hostility from territorial males (Hadow 1977, Short 1982). Forms small conspecific flocks during migration (Swarth 1904; see Migration: migratory behavior, above). Apparently does not associate with conspecifics during winter. Yellow-bellied Sapsuckers forage with overwintering insectivorous mixed-species flocks, but this behavior has not been reported for Williamson's Sapsucker.

Play. None known.

Nonpredatory interspecific interactions. Interspecifically territorial with Red-naped Sapsucker (see Agonistic behavior, above). Also interacts with Hairy Woodpecker (*Picoides villosus*) and Northern Flicker (*Colaptes auratus*; Short 1982, Cannings et al. 1987). Has been observed foraging with groups of Red-breasted Sapsuckers (Rossem and Pierce 1915). Russell (1947) reported a pair of Mountain Chickadees (*Parus gambeli*) feeding Williamson's Sapsucker nestlings, along with the sapsucker parents, when a partition between the 2 adjacent cavities collapsed. Aggressive interactions with other species—e.g., Violet-green Swallow (*Tachycineta thalassina*), Pygmy Nuthatch (*Sitta pygmaea*)—for nest sites (TEM).

PREDATION

Kinds of predators; manner of predation. Three *Accipiter* species of w. North America—Sharpshinned Hawk (*A. striatus*), Cooper's Hawk (*A. cooperii*), and Goshawk (*A. gentilis*)—take both adults and juveniles during breeding season throughout range (Reynolds and Meslow 1984). Red squirrels (*Tamiasciurus hudsonicus*) enter cavities to take eggs and nestlings in Arizona (TEM), as do long-tailed weasels (*Mustela frenata*) in Colorado (Crockett and Hansley 1977). House Wrens (*Troglodytes aedon*) are probably the only avian nest predators. Western terrestrial garter snakes (*Thamnophis elegans*) have been observed entering nest cavities (Crockett and Hansley 1977).

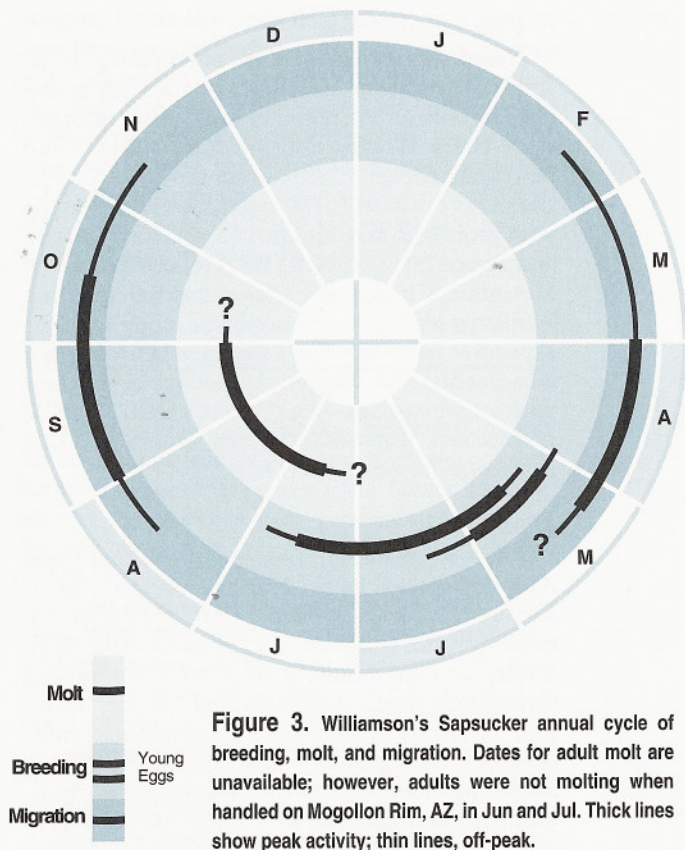
Response to predators. Birds flee when chased and freeze in place upon detection of avian predators (Crockett and Hansley 1977). Both sexes scold and attack ground and arboreal predators near nest. Adults perform Raised-Crest Display: elevate crown-feathers and give Alarm Calls (Crockett 1975). After a weasel raided a nest in Colorado, both parents and a neighboring female behaved excitedly, constantly giving various calls, for 50 min (Crockett and Hansley 1977).

BREEDING

PHENOLOGY

Pair formation. Male establishes territory when he arrives on breeding grounds and pairs form soon after females arrive, 1–2 wk later (Crockett and Hansley 1977, Short 1982).

Nest-building. Excavation begins shortly after pair formation, within 3 wk of female arrival (Hadow 1977), and lasts 3–4 wk (Short 1982). Extends from mid-Apr to third week in May in ne. Oregon (Bull et al. 1986).



First/only brood per season. See Figure 3. Only 1 brood/season. Egg dates are 23 Apr–15 Jun in British Columbia (Campbell et al. 1990). On Mogollon Rim, AZ, first eggs of first clutches laid 27 Apr–30 May (median date 14 May, mode 12 May, $n = 148$; TEM). Nesting period lasts from third week in Jun through Jul in s. Colorado (Winternitz 1976). Nestling dates from 9 nests in New Mexico: 20 May–13 Jul (Travis 1992). Nestling dates from 35 nests in British Columbia: 8 May–15 Jul (Campbell et al. 1990). In ne. Oregon, parents feed nestlings late May–mid-Jul; fledging dates for 19 nests: 19 Jun–20 Jul (Bull et al. 1986).

Second/later brood(s) per season, if any. No second broods recorded, but some birds renest if first nest fails early (TEM).

NEST SITE

Selection process. Nests in cavities (newly excavated in most cases; e.g., 79% of 28 nests on Mogollon Rim, AZ; Conway and Martin 1993, Martin 1993). Male begins establishing territory before female arrives on breeding grounds. Williamson's and Red-naped sapsuckers have similar nest-site preferences and may sustain ecological separation by selecting nest sites on basis of proximate foraging habitat (see Habitat: breeding range, above). On

basis of foraging preferences, Williamson's tends to select nest sites in areas close to conifer-dominated forest that has few aspens, while Red-naped chooses deciduous (i.e., aspen)-dominated areas (Smith 1982). Degree of fungal infection can play a role in nest tree selection, because infected trees may have softer core, making them easier to excavate (Conner et al. 1975). In Colorado, 65% of 40 nests were in trees infected with the fungus *Fomes igniarius* (Crockett and Hadow 1975). Nest trees in Wyoming were live aspen with fungal conks on bark and other signs of heart rot (Loose and Anderson 1995). In Arizona, nest trees of Williamson's Sapsucker had fewer conks than those used by Red-naped Sapsucker, Hairy Woodpecker, or Downy Woodpecker (*Picoides pubescens*; J. Schepps, S. Lohr, and TEM unpubl. data). However, dead trees (snags) had fewer conks than partly live or live trees, and Williamson's Sapsuckers chose snags 85% of the time ($n = 164$; TEM); thus, the number of conks are a poor indicator of tree hardness when snags are included. In fact, Williamson's Sapsucker chooses softer trees than Red-naped Sapsuckers or Hairy Woodpeckers, but not Downy Woodpeckers (J. Schepps, S. Lohr, and TEM unpubl. data).

Microhabitat. On Mogollon Rim, AZ, drainage bottoms preferred over ridge tops (Conway and Martin 1993; see also Sousa 1983), and nest sites tend to have more live and dead aspen and more green ground cover in a 0.1-ha patch surrounding the nest than at random patches, but no difference in numbers of live conifers (Conway and Martin 1993, TEM). The 0.1-ha patch surrounding nest sites in Oregon had higher live and dead stem density, lower basal area, higher upper canopy height, higher percentage of ground cover, fewer stumps, and larger logs than surrounding habitat (Bull et al. 1986).

Site characteristics. Usually nests in aspen, where available (Crockett and Hadow 1975, Smith 1982, Sousa 1983, Li and Martin 1991, Conway and Martin 1993). Most studies, however, have failed to quantify aspen availability, which may be largely responsible for nest-site variation, including documented subspecific variation. Crockett and Hansley (1977) observed more nests in live than in dead aspen, but snag availability was not documented. In a study in Arizona in which aspen and conifer snag availability was measured, aspen snags were actively selected compared to live aspens and conifer snags (Conway and Martin 1993). In Arizona, 98.5% of nests ($n = 202$) were in aspen and 85.4% of the aspens were dead (TEM). In ne. Oregon, half (51%) of nests were in snags ($n = 86$; Bull et al. 1986). Prefers western larch in ne. Oregon (Bull et al. 1986). Nests also found in ponderosa pine and spruce in New Mexico (Travis 1992), as well as

Douglas fir, and even a power pole in British Columbia (Campbell et al. 1990). Most nests in British Columbia are in conifers (Campbell et al. 1990).

Average nest height (above ground) in Colorado, 2.4 m ($n = 40$; Crockett and Hadow 1975); in Arizona, 13.1 m \pm 5.3 SE ($n = 31$), correlated with nest tree height but not nest tree dbh (Conway and Martin 1993); in New Mexico, 3–16 m ($n = 9$; Travis 1992); in British Columbia, 2–18 m high ($n = 25$; Campbell et al. 1990). Mean dbh of 3 nest trees in Wyoming: 28.7 cm; larger dbh than that of available aspen trees (Loose and Anderson 1995). Snags used for nesting in ne. Oregon had larger dbh (70 cm \pm 26.4 SD), greater height (24 m \pm 10.1), fewer branches, and higher frequency of broken tops (14%) than available snags ($n = 86$; Bull et al. 1986).

NEST

Construction process. Although earlier studies suggested that only the male excavates, working "several hours a day over 3–4 wk" (Short 1982), female observed excavating at least some of the time (TEM).

Structure and composition matter. Inside cavity, small bed of wood chips and shavings serves as bed for eggs (Flanagan 1911).

Dimensions. Little information. An Oregon cavity, excavated in a partly dead pine, measured "8 in [20 cm] deep and about 5 in [12.5 cm] wide at the bottom" (Bendire 1895). In Arizona, nest cavity measurements (cm) as follows: opening width 4.17 \pm 0.10 SE ($n = 30$); opening height 4.17 \pm 0.10 ($n = 30$); inner width 9.14 \pm 0.56 ($n = 23$); inner depth 26.67 \pm 1.45 ($n = 16$; TEM).

Microclimate. In Colorado, 58% of nests ($n = 57$) facing south, compared to 18% facing north, a significant difference (Crockett and Hadow 1975). Nest orientation may play role in maintaining higher nest temperatures during early part of breeding season, but this has not been well studied. Conway and Martin (1993) found no significant pattern of nest orientation and more extensive samples in Arizona ($n = 201$) continue to show no orientation preference (TEM).

Maintenance or reuse of nests, alternate nests. Birds may reuse cavities of previous years (Michael 1935, Crockett 1975, Crockett and Hansley 1977), but quantitative evidence suggests that old cavities are a relatively small percentage of nests (21%, $n = 28$ [Conway and Martin 1993]; 15.6%, $n = 149$ [TEM]). However, birds commonly reuse same nest tree between years, excavating new holes (TEM).

Nonbreeding nests. Unmated males will excavate cavities and maintain territories throughout breeding season, although there is much variation; e.g., 1

bachelor excavated 4 cavities in 3 different conifers, while other bachelors abandoned their territories early in breeding cycle (Crockett and Hansley 1977).

EGGS

Shape. Ovate to elongate ovate; some approach ovate pyriform (Bendire 1888, Sclater 1912, Bent 1939).

Size. Measure 23.6 mm (range 20.1–25.91) \times 17.3 mm (15.4–18.3, $n = 81$ eggs; Bent 1939). For *S. t. nataliae*: 23.52 mm (21.28–26.03) \times 17.33 mm (15.86–19.33, $n = 20$ clutches, 110 eggs; Western Foundation of Vertebrate Zoology [WVZ]). For *S. t. thyroideus*: 23.94 mm (20.66–26.54) \times 17.85 mm (15.79–18.98, $n = 21$ clutches, 118 eggs; WVZ).

Mass. Average 3.8 g (7% of female body weight [54 g]; Yom-Tov and Ar 1993).

Color. Pure china white; slightly glossy (Bent 1939).

Surface texture. No information.

Eggshell thickness. Average empty eggshell mass for *S. t. nataliae*: 0.258 g (range 0.205–0.340, $n = 20$ clutches, 110 eggs; WVZ); for *S. t. thyroideus*: 0.275 g (0.223–0.321, $n = 21$ clutches, 118 eggs; WVZ).

Clutch size. Usually 4–6, occasionally 3–7 (Bent 1939, Martin and Li 1992, Martin 1995). In Colorado, average 4.38 eggs/nest ($n = 8$; Crockett and Hansley 1977). On Mogollon Rim, AZ, 4.91 \pm 0.15 SE ($n = 23$; TEM). Clutch size correlation with latitude ($r = 0.12$) is not significant ($n = 49$; Koenig 1986).

Egg-laying. One egg laid/d; thus, laying lasts 3–5 d (on basis of 4- to 6-egg clutch; Crockett and Hansley 1977). Vocalization and Drumming (see Sounds: nonvocal sounds, above) decreases, except for early morning, and adults become inconspicuous during this period (Crockett and Hansley 1977, Hadow 1977). Crockett and Hansley (1977) observed that females stayed close to nest during egg-laying, often preening or napping beside or within nest cavity.

INCUBATION

Onset of broodiness and incubation in relation to laying. Incubation begins before clutch is complete (Crockett and Hansley 1977). Subject to high annual variation; average incubation initiation dates over 3 consecutive years (1972–1974) in Colorado were 26 May ($n = 3$), 1 Jun ($n = 11$), and 28 May ($n = 12$; Crockett and Hansley 1977). On Mogollon Rim, AZ, incubation initiation dates varied from 1 May to 3 Jun; no significant differences among years (TEM). Incubation observed mid-May–mid-Jun in ne. Oregon (Bull et al. 1986).

Incubation patch. Single medial abdominal patch, on both male and female.

Incubation period. Begins before clutch is complete, lasting 12–14 d in Colorado (Crockett and

Hansley 1977). Measured as the period beginning with the day the last egg is laid to the day the first egg hatches. Averages 13 d (range 12–14); on Mogollon Rim, AZ, 12 d more common than 14 (TEM).

Parental behavior. Both parents incubate, keeping eggs covered almost constantly (Crockett and Hansley 1977). Males stay on eggs overnight, but no significant difference in diurnal male and female incubation times; males were attentive 52.5% and females 47.7% of daylight hours, and bouts lasted 32–33 min (Crockett and Hansley 1977).

Hardiness of eggs against temperature stress. No information.

HATCHING

Preliminary events and vocalizations. Not recorded.

Shell-breaking and emergence. All eggs hatch within 1–2 d (Crockett and Hansley 1977).

Parental assistance and disposal of eggshells. Not recorded.

YOUNG BIRDS

Condition at hatching. Altricial, eyes closed, naked, and "bright flesh-pink in color" (Crockett and Hansley 1977).

Growth and development. Eyes open at 7–14 d of age, and first feathers, still sheathed, appear at about 7 d; birds are fully feathered after 14 d (Crockett and Hansley 1977). Sexually dimorphic plumage patterns appear immediately (Bendire 1888, Crockett and Hansley 1977). Unlike most other Picidae, juvenile *Sphyrapicus* do not exhibit abbreviated inner primaries (Chapin 1921). Because incubation begins early in laying period, nestling ages differ by 1–2 d, resulting in size differences because of age and differential food consumption (Crockett and Hansley 1977). No data on growth rates or mass at differing ages.

PARENTAL CARE

Brooding. Both parents brood young. Nest attentiveness is very high (99.8%) during first week after hatching, but declines as nestlings acquire down feathering (49.7% attentiveness by day 14; Crockett and Hansley 1977). Adult exchanges of brooding activity follow a similar pattern: they are most frequent early in nestling period (Crockett and Hansley 1977). Brooding becomes limited to nighttime hours by week 3 (Crockett and Hansley 1977).

Feeding. Each parent feeds nestlings, rotating brooding and foraging activity for first 2 wk. Feeding rates, while initially low (15- to 24-min foraging bouts), typically increase dramatically during week 3 (1 feeding/3 min). Feeding rates

decline to 1 feeding/35 min just before (3–4 d) fledging (Crockett and Hansley 1977, Short 1982).

Unlike most other ant foragers, this species does not regurgitate food to its young (Short 1982). Carries food, mostly ants, in throat, mouth, and bill (Crockett 1975, Short 1982, RCD, TEM, CJC). See Food habits: feeding, above, for details.

Nest sanitation. Both adults, but mainly male, remove fecal material from nest, about every other visit (Michael 1935, Short 1982). Fecal material includes soaked wood chips and, in older nestlings, gelatinous fecal sacs. Adults continually excavate wood shavings inside nest cavity to improve sanitation by covering and soaking up fecal material (Crockett and Hansley 1977).

Carrying of young. Not known.

COOPERATIVE BREEDING

Not known to occur. Although not tolerated by parents, unmated males will feed nestlings of an adjacent pair (Crockett and Hansley 1977). Bachelor males will also replace males who abandon brood before fledging, feeding both nestlings and fledglings (Crockett and Hansley 1977).

BROOD PARASITISM

Not known to occur.

FLEDGLING STAGE

Departure from nest. Occurs 31–32 d after hatching (Martin and Li 1992) and usually requires 1–2 d, but often up to 3–4 d, for entire brood to leave nest (Crockett and Hansley 1977). On Mogollon Rim, AZ, young have left nest as early as 26 d and as late as 33 d after hatching (TEM). Parents coax fledging birds out of nest cavity by withholding food near the hole (Crockett and Hansley 1977). Once fledglings emerge, they do not reenter the cavity, but fly to nearby tree to be fed by parents (Crockett and Hansley 1977). Fledglings quickly learn how to forage independently (gleaning insects), but may also be fed by parents during first 2 d after fledging (Crockett and Hansley 1977).

Growth. Little information. Young at fledging resemble adults in size, but have shorter wings and tail.

Association with parents or other young. Adults quickly disperse after young leave nest, and males often abandon young 1–2 d before they fledge. Crockett and Hansley (1977) have observed male parents as far as 3.5 km and females 1.5 km from their nests (still active) late in day of fledging. Siblings usually separate quickly as well, but sometimes remain together, foraging on home range from 1 to several weeks.

Ability to get around, feed, and care for self. Young can fly after they depart nest, to some degree. Beg for food following initial flight. Bark-gleaning is an easily learned feeding technique, compared to probing and pecking, and allows for relatively early independence (Crockett and Hansley 1977).

IMMATURE STAGE

Few data. Juveniles are independent and largely insectivorous prior to migration. Experience high predation from *Accipiter* hawks (Crockett and Hansley 1977).

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding; intervals between breeding. Breeds yearly. Both sexes can breed in first year.

Clutch size. See Breeding: eggs, above.

Annual and lifetime reproductive success. Egg mortality occurs naturally, though it has not been accurately measured. Reports of hatching success vary from 60 (Grinnell 1908) to 72.2% (Crockett and Hansley 1977). On Mogollon Rim, AZ, nesting success (percentage of nests that successfully fledged at least one young, on basis of Mayfield [1961, 1975] method) varies among years from 89.4 to 100% (averages 96.1, $n = 204$ nests [TEM]; see also Li and Martin 1991, Conway and Martin 1993). Daily mortality rate from egg-laying to nest-leaving was 0.000813 ± 0.00036 SE ($n = 6,135.5$ exposure days; TEM). Successful nests in Arizona fledged average of 3.67 young ± 0.21 SE ($n = 18$ nests; TEM), while 3.17 young per nest (equal sex ratio) were fledged in Colorado ($n = 12$ nests; Crockett and Hansley 1977). Of 9 nests in Arizona for which both clutch size and number of fledged young were known, clutch size was 5.22 ± 0.28 SE and number of fledged young was 3.89 ± 0.31 SE, indicating hatching failure and/or nestling mortality of 1.33 young per nest (TEM). Egg versus chick mortality not known. Lifetime reproductive success not known.

Number of broods normally reared per season. One brood per year. Dawson's (1923) casual mention of the species "nesting twice in a season" was probably either erroneous or referred to a re-nest attempt, perhaps as the result of a failed nest. Renesting after a successful brood has not been recorded, and is seemingly impossible, given life history characteristics of breeding (e.g., length of excavation process, nestling period, etc.) relative to season length.

Proportion of total females that rear at least one brood to nest-leaving or independence. Not directly studied with color-marked birds.

LIFE SPAN AND SURVIVORSHIP

No information.

DISEASE AND BODY PARASITES

No information.

CAUSES OF MORTALITY

Exposure. Nest trees are occasionally blown down by strong wind on Mogollon Rim, AZ (Li and Martin 1991, RCD, TEM, CJC).

Predation. Predation on adults is difficult to document. Piles of feathers in Arizona indicate occasional predation on adults. Nest predation probably accounts for 100% of complete nest failures on Mogollon Rim, AZ, but partial brood loss (see Measures of breeding activity, above) is probably due to other factors as well.

Competition with other species. No information.

RANGE

Initial dispersal from natal site. Of >100 young banded in Arizona, none were resighted over 4 yr (TEM).

Fidelity to breeding site and winter home range. Birds often return to same territory, even same nest tree, year after year (Dawson 1923). Return rates of banded birds to breeding sites between years is not yet documented. No information for winter.

Dispersal from breeding site or colony. No banded birds recovered, except those resighted on Mogollon Rim, AZ, study area. Of 67 birds (sexes and ages combined) banded in 1993, 16 (24%) were resighted in 1994 or 1995; of 65 birds banded in 1994, 14 were resighted in 1995 (TEM).

POPULATION STATUS

Numbers. Few data; needs study. This species usually fairly common in habitats where it occurs. Price et al. (1995) report <5 individuals detected per Breeding Bird Survey (BBS) route per year.

Trends. Analysis of BBS data indicates a decreasing population trend (DeSante and George 1994). Populations showed highly significant declines throughout U.S. range from 1982 to 1991, with particularly strong declines in Pacific Northwest (U.S. Fish and Wildlife Service BBS unpubl. data). Price et al. (1995) report 60% decline from 1984 to 1993. However, data are few because of the sparse number of BBS routes in western U.S., and more complete surveys are needed.

Wildlife agencies in Oregon and Utah refer to this sapsucker as a "sensitive species," having either a "declining population and limited range or habitat," or an "undetermined status" (Atwood 1994).

POPULATION REGULATION

Not adequately studied. Potential factors include nest-site availability (Li and Martin 1991, Conway and Martin 1993) and influence of forest management techniques that affect snag availability and fire suppression. Requires particularly soft substrates for excavating and generally softer substrates than other woodpeckers (J. Schepps, S. Lohr, and TEM unpubl. data). Soft substrates may be less common and lost more quickly following storms or as result of logging practices and may be expected to be most common in old forests where snags may be left standing longer. For example, Mannan and Meslow (1984) found the sapsucker in old growth (+200 yr), but not in rotation-age (85 yr) forest (see also Dobkin 1994).

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Shooting and trapping. No information.

Pesticides and other contaminants/toxics. No information, but as an ant-eating species, possibly vulnerable to forest spraying.

Collisions with stationary/moving structure or objects. Adult female died after flying into mirrored window of building in Alberta (Pinel 1993).

Degradation of habitat. Apparently able to withstand considerable disturbance. For example, when aspens and snags were spared during a logging operation, breeding density of Williamson's Sapsucker was not significantly affected spatially (logged versus unlogged) or temporally over 2 yr (Franzreb and Ohmart 1978). Observed foraging on logs in clear-cuts (Loose and Anderson 1995). Jewett et al. (1953) report habitation of postfire early successional forest. Similarly, Bock and Lynch (1970) document nesting in snags in previously unoccupied areas 5–8 yr after fire, although birds foraged in adjacent interior forest (see also Bock et al. 1978, Sousa 1983). In Pacific Northwest, snag dbh of 30.5 cm is minimum size capable of supporting a nest cavity (Thomas et al. 1979); however, size requirement varies across tree species and, therefore, geographic region (Sousa 1983 and references therein).

Although Williamson's Sapsucker seems to tolerate habitat disturbances like fire and even some logging practices (see Habitat: breeding range, above; but see Raphael et al. 1987), Aney (1984) found sapsuckers exhibit significant forest area (size) effects. In Pacific Northwest, 371 snags (of at least 30.5 cm dbh) per 100 ha are necessary to support "maximum populations" (Thomas et al. 1979).

Disturbance at nest and roost sites; human/research impacts. Tolerant of close human proximity and activities at nest. On Mogollon Rim, AZ, nest trees are climbed and nestlings are temporarily removed and banded without causing adult abandonment (TEM). Crockett and Hansley (1977) sawed into 4 nests, without negative effects.

MANAGEMENT

Forest management plans should emphasize conservation of groups of large snags, rather than random assortment of variably sized snags (Conway and Martin 1993). Patches of snags and areas of high snag density should be preserved, especially those in drainage bottoms or other low-lying areas (Conway and Martin 1993). Fire in mixed coniferous forest that creates snags may increase breeding densities (Bock and Lynch 1970). Availability of sap trees (often large conifers) also should be important.

APPEARANCE

MOLTS AND PLUMAGES

Hatchlings. Naked at hatching.

Juvenal plumage. Information on timing and sequence of Prejuvenal molt (which takes place within the nest cavity) lacking. Completely feathered and in Juvenal plumage at fledging.

Juvenile male resembles adult male, but lacks glossy appearance, has white throat instead of red, and has more white on nape that sometimes connects with white above eye; also, bases of black back-feathers have white wedge marks, and bird is more barred on upperparts, wings, and tail; black on breast is less pronounced, and yellow belly is pale (Short 1982). Juvenile female resembles adult female, but is still more dull and brown, shows more barring throughout, and lacks black on breast (Short 1982).

Basic I plumage. Prebasic I (Postjuvenal) molt occurs early (Jul–Aug); most birds acquire Basic I plumage by late Aug or early Sep (Short 1982). Molt includes all body-feathers and most flight-feathers. Molt of primaries begins in nest with replacement of 2 innermost minute Juvenal primaries; all primaries are replaced within 3–4 mo after fledging (Pyle and Howell 1995; see below). All primaries and rectrices are replaced; Juvenal primary-coverts and most Juvenal secondaries are retained, but some birds replace 4–5 secondaries (Pyle and Howell 1995). Basic I plumage very similar to Definitive Basic (adult) plumage.

Basic II plumage. Prebasic II molt is essentially complete except all birds replace 1–4 primary-coverts and most birds retain 1–5 secondaries (Pyle

and Howell 1995). Basic II plumage same as Definitive Basic (adult) plumage.

Basic III plumage. Prebasic III molt is essentially complete except a few birds may still retain 1–4 secondaries (Pyle and Howell 1995). Basic III plumage same as Definitive Basic (adult) plumage.

Definitive Basic plumage. Definitive Prebasic molt complete; occurs mid-Jul–late Sep. Flight-feathers molt before migration; body molt continues into migration. Colors follow Smithe 1975 and are based on specimens at the Academy of Natural Sciences, and on skins of recently collected (<15 yr) specimens at Louisiana State University Museum of Zoology (LSUMZ).

MALE. Nasal tufts, lores, and moustachial stripe are white, forming long, narrow stripe under eye from bill to side of neck; supercilium white, begins just above eye and continues to neck where curves inward toward middle of nape. Chin and upper throat Scarlet (14); remainder of head, neck, mantle, breast, and tail Jet Black (89), back and breast glossed blue-green. Feathers of lower back black with white markings; center of rump and uppertail-coverts white; sides of rump and uppertail-coverts black; some feathers between center and sides have both black and white. Wing-coverts black, except median-coverts all or mostly white, and outermost 5–6 greater-coverts white with inner web entirely or mostly black; white portion of wing-coverts forms conspicuous patch; remiges Sepia (219; appear blackish), with several small white spots on outer webs of 3–5 of the outermost primaries (except outermost primary always unmarked), or all primaries may be unmarked; tertials may or may not have small white subterminal marks. Lower breast to lower belly yellow in center; sides of upper belly black; feathers on sides of lower belly and on thighs black, barred with white; undertail-coverts black, broadly margined with white. Undersides of remiges deep gray, broadly spotted on inner webs with white; underwing-coverts white, broadly barred with black.

FEMALE. Plumage pattern substantially different from that of male. Head Dark Drab (119B) to tawny or buffy; sides of crown above eye, rear crown, and upper nape, as well as malar area, streaked with black. Some females show some orange reddish or black feathers on chin and throat. Feathers of mantle, breast, and wings Jet Black (89), all feathers barred off-white (but barred Sepia (on breast). Remiges Sepia with small white spots on outer webs. Rectrices black, with widely spaced off-white to Sepia barring on outer portion of each web. Breast variable, may be entirely barred (but darker at center) or solid black at center and barred only on sides of breast. Feathers of sides, thighs, and undertail-coverts off-

white, barred black; center of breast and belly pale yellow. Underwings as in male.

BARE PARTS

Bill and gape. In hatchlings, gape ("swellings at the corners of the mouth") colored flesh pink and retained up to 7 d after fledging (Crockett and Hansley 1977). Adult bill black in summer, purplish slaty brown in winter (Ridgway 1914).

Iris. Deep reddish brown in adults (Ridgway 1914); also described as chestnut brown (Short 1982) and dark brown (LSUMZ).

Legs and feet. Grayish olive (Ridgway 1914) or dull greenish gray in adults (LSUMZ); or dark gray (Short 1982).

MEASUREMENTS

See Table 1. Note that length of female tail exceeds that of male (Ridgway 1914, cited by Short 1970). Otherwise, no difference between the sexes.

PRIORITIES FOR FUTURE RESEARCH

Williamson's Sapsucker is poorly studied throughout most of its range, and almost all breeding-biology information comes from two study areas: Rocky Mountain National Park, CO, and Mogollon Rim, AZ. Similar information for other parts of its range, particularly the Sierra Nevada–Cascade ranges of the western subspecies, is lacking. Winter ecology is poorly known. Introductory work on winter ecology raises interesting questions (e.g., sexual habitat segregation) and should be extended into Mexico, where the species is unstudied. Migration ecology and habitat use has, perhaps, received the least attention. Population trend data are few and are badly needed.

This species, although genetically distinct, occurs sympatrically, in part, with Red-naped and Red-breasted sapsuckers. Ecological patterns and superficial similarities with congeners and other picids have led to speculation and investigation of history, including some molecular work. Greater study of this unique species regarding ecological and evolutionary similarities and differences among related species is needed.

ACKNOWLEDGMENTS

We thank the Blue Ridge Ranger Station of the Coconino National Forest, AZ, and the Chevelon Ranger Station of the Apache Sitgreaves National Forest, AZ, for their support of this work. We thank

Table 1. Linear measurements (mm) and mass (g) of adult Williamson's Sapsucker. Data shown as mean (range).

	Various locations ¹	Alberta ²
Exposed culmen length		
Male	25.6 (23.0–28.0)	
Female	24.2 (21.5–28.5)	21.0
Wing-chord length		
Male	136.8 (131.5–139)	
Female	136.2 (132.5–143)	134.7
Tail length		
Male	83.2 (70.5–88.5)	
Female	84.1 (78.0–89.0)	
Tarsus length		
Male	21.5 (20.5–22.5)	
Female	21.0 (20.0–22.5)	
Breeding mass ³		
Male	47.6 (44.4–55.3)	
Female	47.6 (44.4–55.3)	

¹Data from Ridgway 1914 (males, $n = 20$; females, $n = 17$).
²Data from Pinel 1993.
³Data from Mogollon Rim, AZ (TEM).

L. Kiff and Sam Sumida and the Western Foundation of Vertebrate Zoology for egg size information. The Library of Natural Sounds, Cornell Laboratory of Ornithology, provided the sonograms, for which we are grateful. We also thank Steve Cardiff and the Louisiana State University Museum of Zoology. The research has been funded by the National Science Foundation (BSR-9006320, DEB-9407587, and DEB-9527318); the BBIRD (Breeding Biology Research and Monitoring Database) program of the Global Change Research Program of the National Biological Service; U.S. Fish and Wildlife Service; and the Arizona Game and Fish Agency. Cover photo © Brian E. Small.

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The Birds of North America is supported by charitable and governmental organizations including: The Office of Migratory Bird Management (USFWS), National Fish and Wildlife Foundation, The McLean Contributionship, The Geraldine R. Dodge Foundation, The Richardson Foundation, and the American Birding Association. Benefactors of this program include Wallace C. Dayton and Joseph and Helen Taylor.

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RECOMMENDED CITATION

Dobbs, R. C., T. E. Martin, and C. J. Conway. 1997. Williamson's Sapsucker (*Sphyrapicus thyroideus*). In *The Birds of North America*, No. 285 (A. Poole and F. Gill, eds.). The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C.

