ERIC L. WALTERS, EDWARD H. MILLER, AND PETER E. LOWTHER

Sphyrapicus ruber

FRENCH: *Pic à poitrine rouge*
SPANISH: *Chupasavia pechirroja*

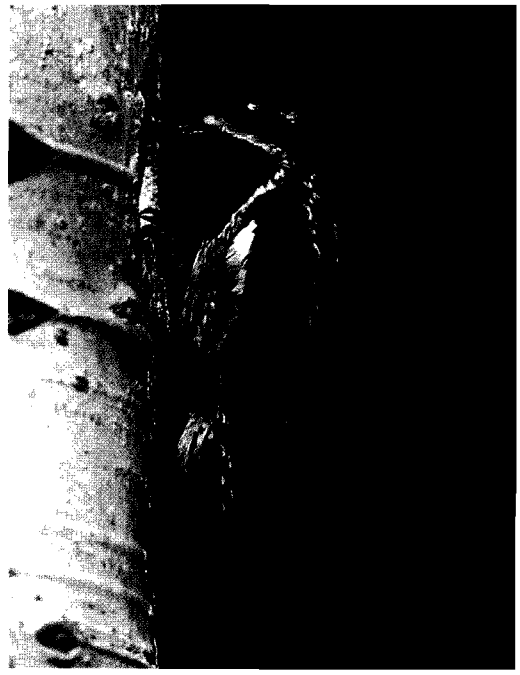
Red-breasted Sapsucker

Sphyrapicus nuchalis

FRENCH: *Pic à nuque rouge*
SPANISH: *Chupasavia nuquirroja*

Red-naped Sapsucker

Red-breasted Sapsucker © Brian E. Small



Red-naped Sapsucker © Brian E. Small

Red-breasted and Red-naped sapsuckers, together with the Yellow-bellied Sapsucker (*Sphyrapicus varius*), form a superspecies. These 3 species have, for the most part, separate distributions but were long treated as forms of a single species—the "Yellow-bellied Sapsucker"—until 1983, when systematic studies showed distinctions sufficient to warrant taxonomic treatment as separate species. Most of the early literature and research on this complex refer to Yellow-bellied Sapsuckers of eastern North America (found generally east of the Rocky Mountains). Limited, but more recent, work has focused on populations of the Red-naped Sapsucker of the Rocky Mountain trench region from central British Columbia to Arizona and populations of the Red-breasted Sapsucker with coastal distribution from northern British Columbia to California. The biology of these 3 species appears to be quite similar.

The Birds of North America
Life Histories for the 21st Century

The name "sapsucker" has been applied to the woodpecker genus *Sphyrapicus* because these birds create sap wells in the bark of woody plants and feed on sap that appears there. Sap wells are shallow holes drilled through outer bark to the underlying phloem or xylem tissues. When Red-naped Sapsuckers first arrive at their breeding areas, they often drill sap wells in the xylem of conifers and

quaking aspen (*Populus tremuloides*). Once temperatures increase and sap begins to flow, these birds switch to phloem wells in aspen or willow (*Salix* spp.), if available. Red-breasted Sapsuckers occupy similar areas in all seasons and usually make wells in conifers for most of the year. Both species create elaborate systems of sap wells and maintain this resource throughout the day to ensure sap production. Because of this large investment in maintenance, sapsuckers defend wells from other sapsuckers, as well as from other species. When feeding young, sapsuckers usually forage for arthropods—especially ants (Formicidae)—and some of these prey items are dipped in sap wells, perhaps for added nutritional value.

Other species make use of sapsucker wells to supplement their food intake with sap or with insects attracted to the sap. Rufous Hummingbirds (*Selasphorus rufus*), for example, appear to be closely associated, ecologically, with both Red-breasted and Red-naped sapsuckers; they place their nests near sap wells, follow sapsuckers in their daily movements, and may even time their migration to coincide with that of sapsuckers so they can feed off the sap wells. In addition, sapsuckers excavate nest cavities that often provide nesting or roost sites for other species of birds (for example, Mountain Bluebirds [*Sialia currucoides*]), and even some mammals (for example, northern flying squirrel [*Glaucomys sabrinus*]) that cannot excavate their own.

In areas where their ranges overlap, Red-breasted and Red-naped sapsuckers are known to hybridize. The first major study of the breeding biology of these species was by Thomas Howell, who conducted 163 hours of observations at 14 nests in a hybrid zone in Modoc County, California (Howell 1952). Most recent work on these species has focused on Red-breasted–Red-naped sapsucker hybrid zones in Oregon (Trombino 1998) and on the breeding biology of Red-naped Sapsuckers in Nevada (Fleury 2000) and British Columbia (Walters 1996). Reference to, and comparisons with, Yellow-bellied Sapsucker studies aid our understanding of these species (see Walters et al. 2002).

In this account, where the species is not noted, the text refers to both Red-breasted and Red-naped sapsuckers.

DISTINGUISHING CHARACTERISTICS

RED-BREASTED SAPSUCKER

Small–medium woodpecker; length about 20–22 cm; mass 39–68 g. Entire head red except for black spot in front of eyes and white line from lore to nostril; red on head extends to nape and over breast. Large white wing-patch, back black with variable amounts of white or yellow spots, belly yellow. Sexes alike. Juveniles retain brownish plumage until Prebasic I molt in early fall, after which variegated brown head and body plumage largely replaced by red and black adult coloration. Adults not usually confused with other sapsucker species except in areas of overlap, where hybrids can occur. Juvenile Red-breasted Sapsucker with head and breast more uniformly dark in comparison with juvenile Red-naped and Yellow-bellied sapsuckers.

RED-NAPED SAPSUCKER

Small–medium woodpecker; length about 19–21 cm; mass 32–66 g. Black bib on upper breast, prominent red forehead with black band at rear, nape red, black stripe along side of head bordered by 2 white stripes, crown and nape black, large white wing-patch, back blackish (with yellowish tinges), rump white, and underparts buffy or yellow-tinged. Throat red in male, chin and upper throat white and lower throat red in female but extent of red variable; throat-patch bordered by black. Some females with reduced or no red on forehead and reduced or no white on throat, but otherwise similar to male in plumage and size. Juveniles retain brownish plumage until Prebasic I molt (by first fall), after which variegated brown Juvenal head and body plumage replaced by black, white, and red coloration of adult.

Sometimes confused with Yellow-bellied Sapsucker because of individual variation in amount of red on nape in both species (usually Red-naped Sapsucker with red nape, Yellow-bellied Sapsucker with broad white stripe), because of increased amount of red on throat of female Red-naped Sapsucker (usually female Red-naped Sapsucker with white chin), or because of hybrid individuals in areas of range overlap. Male Red-naped Sapsucker with little to no black border around red chin and throat. Back of Red-naped Sapsucker with less white than Yellow-bellied Sapsucker; white creates a more marbled appearance and tends to be in longitudinal bands that extend down each side of back; underparts paler yellow.

DISTRIBUTION

THE AMERICAS

Breeding range. Figure 1. *Red-breasted Sapsucker.* Breeds from se. Alaska (Kessel 1986, Armstrong 1995), extreme nw. British Columbia, coastal (including Queen Charlotte and Vancouver Is.) and central interior British Columbia (east to Manning Provincial Park along eastern slope of Pacific and Cascade ranges, and north to Meziadin Lake and

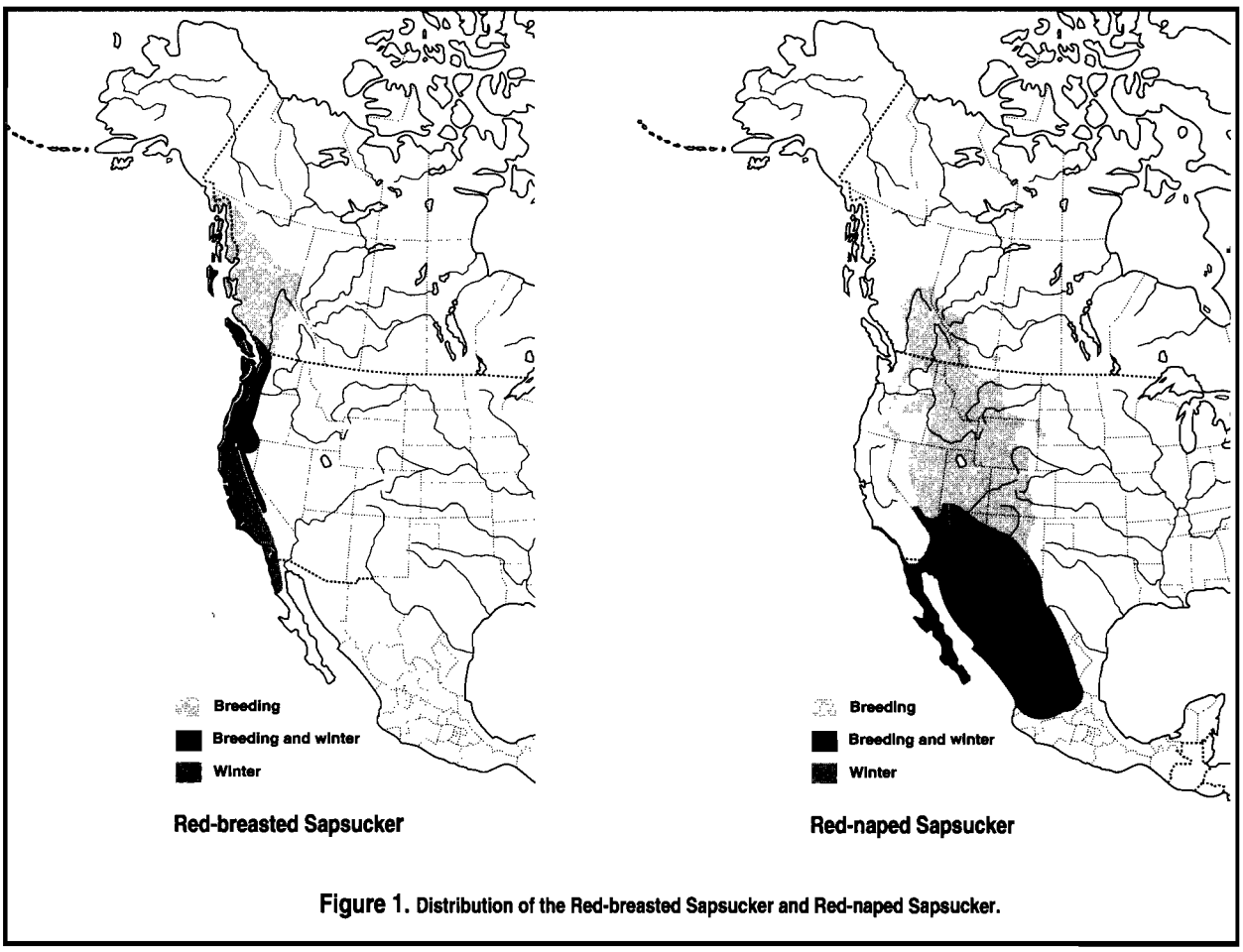


Figure 1. Distribution of the Red-breasted Sapsucker and Red-naped Sapsucker.

Tupper Creek; Campbell et al. 1990) south throughout the western halves of Washington (east to central Cascades but not yet confirmed from most of Olympic Peninsula; Smith et al. 1997) and Oregon (east to central Cascades and Lake Co. in south; Gilligan et al. 1994). South of Oregon, breeds in California from Del Norte Co. east to Modoc Co.; in the northern Coast range south to Lake and Sonoma Cos. (with small disjunct population in Olema Valley of Marin Co.; Shuford 1993); throughout the Cascades-Sierra axis south to ne. Kern Co.; disjunctly at Mt. Pinos and surrounding mountain ranges; the San Gabriel and San Bernardino Mtns.; the Mt. San Jacinto area; Pine Mtn. (very rarely); and mountains of San Diego Co., including Palomar Mtn., the Cuyamaca Mtns., and (possibly) Laguna Mtns. (Small 1994). Also breeds in Lake Tahoe region of extreme w. Nevada (Nevada Breeding Bird Atlas [BBA] unpubl.) and possibly in Mohave Co. of w. Arizona (Am. Ornithol. Union 1998), but not recorded during 1993–2000 Arizona BBA (T. Corman pers. comm.). Rare summer visitor to Blue and Wallowa Mtns. of Oregon (Gilligan et al. 1994). Rare breeder in s.-coastal Alaska as far west as Kodiak I. (Kessell 1986).

Red-naped Sapsucker. Breeds in Rocky Mtn. region north to central s. and se. British Columbia (north to Cinema and Yoho National Park [NP] and west to Tatla Lake and Manning Provincial Park; Campbell et al. 1990), sw. Alberta (in mountains north to Banff NP and Sundre; Semenchuk 1992). From Canada, breeds south through Idaho, w. and s.-central Montana (east to Blaine, Stillwater, and Bighorn Cos.; Montana Bird Distribution Committee 1996), w. and central Wyoming (Luce et al. 1999), n. Nevada (west to Santa Rosa and Desatoyo Mtns.) and e. Nevada (south to Sheep and Spring Mtns.; Nevada BBA unpubl.), Utah, and w. and central Colorado (east to Larimer and Las Animas Cos.; Barrett 1998), to nw. and se. Arizona (Coconino, Navajo, Apache, Greenlee Cos.; Arizona BBA 1993–2000 unpubl.), sw. and ne. New Mexico (south to Mogollon, Sacramento, and Guadalupe Mtns; and east to Sangre de Cristo Mtns.; Hubbard 1978), and w. Texas (2 records only, Jeff Davis and Culberson Cos.; Oberholser 1974). Also breeds from

n. Washington south through eastern slopes of Cascades (rarely to western slopes) and other mountain ranges of central and e. Washington and Oregon (Gilligan et al. 1994, Smith et al. 1997). Isolated populations also occur west of the Rocky Mtns. in the Warner Mtns. of extreme ne. California (occasionally) and extreme nw. Nevada, the White Mtns. of e. California, and w. Nevada (Small 1994, Nevada BBA unpubl.), and east of the Rocky Mtns. in the Cypress Hills of se. Alberta and sw. Saskatchewan (Semenchuk 1992, Smith 1996), and the Black Hills of S. Dakota (Peterson 1995) and adjacent portions of extreme ne. Wyoming (Luce et al. 1999, and extreme se. Montana (Montana Bird Distribution Committee 1996). Summer records also in w. Lyon and s. Douglas Cos. of w. Nevada (Nevada BBA unpubl.), and may also breed on eastern slopes of Sierra Nevada and in Sweetwater Mtns. of California (Howell 1952). See also Am. Ornithol. Union 1998.

Hybrid zones. Overlap between Yellow-bellied and Red-breasted sapsuckers in n. British Columbia (near Telegraph Creek and Tupper [near Dawson Creek] southwest to Vanderhoof and Stoner; Campbell et al. 1990).

Overlap between Yellow-bellied and Red-naped sapsuckers in sw. Alberta (from Clearwater River west of Caroline to Porcupine Hills west of Claresholm; J. Hudon pers. comm.), and some hybridization occurs in this area.

Overlap between Red-breasted and Red-naped sapsuckers in British Columbia includes 100 Mile House, Kleena Kleene, and Nulki Lake (Campbell et al. 1990); overlap with some hybridization occurs along crest of Cascade Mtns. in Washington (Smith et al. 1997); nw. Deschutes, Lake, and Klamath Cos., OR (Browning 1977, Trombino 1998); Modoc Co., CA (Howell 1952, Johnson and Johnson 1985); and Eureka Co., NV (T. Floyd pers. comm.). Overlap also at several sites in e. Sierra Nevada along California–Nevada border (but no hybrids reported): Sierra and Mono Cos., CA; and Lyon, Mineral, and Clark Cos., NV (Johnson and Johnson 1985).

The area of overlap between Red-breasted and Red-naped sapsuckers in British Columbia (<100 km south of Yellow-bellied–Red-breasted overlap area) only 2.4 km wide in 1950 (Howell 1952). Recently, however, hybrid pair observed at Hat Creek, British Columbia (>200 km south of area of overlap observed by Howell [1952], EHM, ELW). Both Yellow-bellied–Red-breasted and Red-breasted–Red-naped hybrid zones expected to eventually converge near Prince George, British Columbia (Scott et al. 1976).

Migration accounts for numerous records of hybrid individuals outside of hybrid zones: Red-naped × Red-breasted (*S. r. daggetti*) hybrids in Arizona; Sonora, Mexico; s. California; n. California; Santa Cruz I., CA (Howell 1952, Browning 1977); and New Mexico (Devillers 1970); Red-naped × Red-breasted (*S. r. ruber*) hybrid in Del Norte Co., CA (Howell 1952); Red-breasted (*S. r. ruber*) × Red-breasted (*S. r. daggetti*) hybrids in California (Devillers 1970); and Red-naped × Red-breasted (subspecies not indicated) in Santa Barbara Co., CA (Lehman 1994); and s. Nevada, where many winter (T. Floyd pers. comm.).

Winter range. Figure 1. *Red-breasted Sapsucker*. Winters from coastal and sw. British Columbia (rarely in se. Alaska and casually in interior British Columbia) south through breeding range, and throughout the remainder of California (west of deserts) to nw. Baja California (Campbell et al. 1990, Gilligan et al. 1994, Small 1994, Armstrong 1995, Howell and Webb 1995, Am. Ornithol. Union 1998, T. Floyd pers. comm.).

Red-naped Sapsucker. Winters from s. California (sparingly along coast north to Los Angeles Co. and exceptionally north to Oregon, sparingly along western slopes of Sierra Nevada, and more commonly along Colorado River; Gilligan et al. 1994, Small 1994), s. Nevada, southernmost Utah (locally to n. Utah), and central New Mexico south to s. Baja California, and on the Pacific slope and in the interior of Mexico from Sonora, central Coahuila, and s. Nuevo León south to n. Jalisco (Howell and Webb 1995, Am. Ornithol. Union 1998). Winters casually north to s. Oregon (Klamath Co.; Gilligan et al. 1994) and n. Utah (Am. Ornithol. Union 1998), on offshore islands of California (Small 1994), and south to Guatemala and Honduras, where may have formerly occurred more regularly (Howell 1952, Howell and Webb 1995, Am. Ornithol. Union 1998).

Other records. *Red-breasted Sapsucker*. Casual in s.-coastal and e.-central Alaska (west to Kodiak and Middleton Is. and Tok; MacIntosh 1990), Alberta, and extreme sw. Utah (Am. Ornithol. Union 1998). Accidental in s. Arizona (T. Corman pers. comm.) and McLennan Co., Texas (Lockwood and Shackelford 1998).

Red-naped Sapsucker. Casual or accidental in sw. British Columbia, Kansas, w. Nebraska, Oklahoma, and se. Louisiana (Am. Ornithol. Union 1998).

OUTSIDE THE AMERICAS

Not recorded.

HISTORICAL CHANGES

Red-breasted Sapsucker range extending eastward in Warner Mtns. (Modoc Co.), n. California (Johnson and Johnson 1985), but receding in cen-

tral British Columbia (Scott et al. 1976). Red-naped Sapsucker may have formerly wintered south to Honduras (Howell and Webb 1995).

FOSSIL HISTORY

One fossil of *Sphyrapicus* sp. known from Pleistocene of s. California (Howard 1962).

SYSTEMATICS

GEOGRAPHIC VARIATION; SUBSPECIES

Red-breasted Sapsucker. Two subspecies recognized. *S. r. ruber* (Gmelin 1788) primarily year-round resident of coastal forests from Alaska to Oregon; larger, male wing length 123.5–133.5 mm (n = 10; Ridgway 1914) and with more red than southern form. *S. r. daggetti* Grinnell 1901 breeds in California and Nevada; male wing length 118–127.5 mm (n = 10; Ridgway 1914). Some populations make seasonal movements. These subspecies meet with some abruptness in s. Oregon between Klamath Lake region and Pacific Coast (Howell 1952). Sexes monomorphic, except in Queen Charlotte Is., British Columbia, where male 6% larger than female in bill size (Miller et al. 1999). No subspecific differences in vocalizations or Drumming reported. See Devillers 1970, Dunn 1978, Short 1982, Kaufman 1990, Lehman 1991.

Red-naped Sapsucker. No variation described; no subspecies.

RELATED SPECIES

Yellow-bellied, Red-naped, and Red-breasted sapsuckers form closely related complex. Plumage differences among these species mainly in amount of red on head. Taxonomic history of this group varied as opinions changed on whether some or all of these forms should be considered specifically distinct. Evidence from distribution, ecology, plumage, assortative mating, and genetics support treating this complex as 3 separate species making up the superspecies *Sphyrapicus varius* (Short 1969, 1982; Am. Ornithol. Union 1983, 1985, 1998; Johnson and Zink 1983; Johnson and Johnson 1985; Cicero and Johnson 1995). In addition to hybridization occurring between these 3 species where they meet, hybrids between Red-naped and Williamson's (*S. thyroideus*) sapsuckers also known (Short and Morony 1970).

Genus *Sphyrapicus* endemic to North America and sister group to *Melanerpes* (Short 1982, Cicero and Johnson 1995). Williamson's Sapsucker is sister group to superspecies *S. varius*, but considered fairly distantly related and perhaps not included in *Sphyrapicus* (Johnson and Zink 1983). Yellow-bellied Sapsucker possesses unique anatomical arrangement of hind-limb muscle within Piciformes (all 3 parts of *M. iliotibialis lateralis* reduced; Swierczewski and Raikow 1981); condition of this muscle in other sapsucker species unknown. Superspecies *varius* split from common ancestor with Williamson's Sapsucker during Pliocene, followed by divergence of Yellow-bellied Sapsucker from Red-breasted Sapsucker plus Red-naped Sapsucker in Pleistocene and divergence between Red-breasted and Red-naped sapsuckers subsequent to that (Cicero and Johnson 1995).

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

Red-breasted Sapsucker. Variation in extent of migratory habits dependent upon subspecies. In general, short-distance migrant. *S. r. ruber* "almost resident" but moves from inland breeding areas to coastal areas and foothills during winter (Devillers 1970: 49). *S. r. daggetti* does not have extensive migration but winters at lower elevations throughout California and nw. Baja California (Howell 1952, Devillers 1970). No information available on migration patterns of hybrids (Trombino 1998).

Red-naped Sapsucker. Mostly complete, short-distance migrant. Moves south from breeding range into Mexico, Baja California, s. California, Arizona, and New Mexico, although some winter within breeding range in Arizona and New Mexico.

TIMING AND ROUTES OF MIGRATION

Red-breasted Sapsucker. *Spring.* Recorded Baja California through Mar (Howell and Webb 1995). In California, departs Santa Barbara Co. mid-Mar to Apr (Lehman 1994). In British Columbia, leaves wintering areas on coast by late spring and arrives at interior breeding sites by late Mar; peak movement through Apr and into May (Campbell et al. 1990). In Oregon hybrid zone, Red-breasted Sapsuckers return 2–3 wk before Red-naped Sapsuckers (Trombino 1998).

Fall. In British Columbia, departs interior by late Aug; increases in numbers at coastal areas by early Sep (Campbell et al. 1990). In Oregon, migrates south to inland valleys and foothill areas, often found in areas unsuitable for nesting (Gilligan et al. 1994). Arrives in Santa Barbara Co., CA, in Sep (Lehman 1994). Recorded Baja California beginning Oct (Howell and Webb 1995).

Red-naped Sapsucker. *Spring.* In Sonora, Mexico, latest date 30 Apr (Russell and Monson 1998). In Santa Barbara Co., CA, latest departure in late Mar (Lehman 1994). In sw. Colorado, early Apr (Hadow

1977). For n. Utah and s. Idaho, arrives early May (Smith 1982b). In Oregon, arrives mid-Apr to May (Gilligan et al. 1994). In nw. Montana, late Apr (McClelland 1977). In British Columbia, as early as late Mar, main movement in Apr (Campbell et al. 1990).

Fall. In British Columbia, late Aug to mid-Sep, a few as late as early Oct (Campbell et al. 1990). In Oregon, early Aug–late Oct, peak Sep (Gilligan et al. 1994). In Santa Barbara Co., CA, arrives early Oct (Lehman 1994). In Sonora, Mexico, earliest date 17 Sep (Russell and Monson 1998).

MIGRATORY BEHAVIOR

Red-breasted Sapsucker. Sometimes in groups of 3 or 4 individuals during fall; groups may include Williamson's Sapsuckers (van Rossem and Pierce 1915).

Red-naped Sapsucker. Females more common than males in southern areas of wintering range; males more common in northern areas (Howell 1953). In Texas, both sexes appear equally common during fall migration, but most wintering birds are males (Lockwood and Shackelford 1998). In Colorado, transients establish feeding territories during Mar in junipers (*Juniperus* sp.) before moving to breeding grounds at higher elevations; by early Sep, movement down to piñon pine (*Pinus edulis*)-juniper habitats (Hadow 1977).

CONTROL AND PHYSIOLOGY

No information.

HABITAT

BREEDING RANGE

Red-breasted Sapsucker. Breeds from near sea level to 2,900 m elevation in coniferous forests that include western white pine (*Pinus monticola*), lodgepole pine (*P. contorta*), western hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii*), red fir (*Abies magnifica*), and spruce (*Picea* sp.); also in deciduous and riparian habitat including bottomlands of quaking aspen and cottonwood (*Populus* sp.); and in old-growth and second-growth forests of coast mountains. Also known to use orchards, power line rights-of-way, and burns in British Columbia (Campbell et al. 1990). More likely to breed in areas with snags (dead trees) than without (Marcot 1983).

In Alaska, breeds in spruce-hemlock coastal forests (Kessel 1986). In British Columbia, coastal populations nest in Douglas-fir-western hemlock-western white pine forests (Allaye-Chan 1981, Joy 2000); interior populations found in spruce forests (Zimmerman 1998). In sw. Washington, nests in Douglas-fir-western hemlock forests (Lundquist 1988). In Oregon, mainly in Douglas-fir-western hemlock forests and also nests on edges of 100–200+ yr-old Douglas-fir stands and old-growth near clearcuts (Mannan et al. 1980, Bate 1995); in sw. Oregon, primarily in riparian habitats (Mannan 1977). In n. California, nests in red fir-lodgepole pine-aspen forests (Raphael 1980).

Red-naped Sapsucker. Breeds in deciduous and mixed woodlands including aspen groves in open ponderosa pine (*Pinus ponderosa*) forests, aspen-fir parklands, logged forests where deciduous groves remain, aspen groves in open rangeland, birch groves, montane coniferous forests (e.g., Douglas-fir, larch [*Larix* sp.], spruce, fir), and, occasionally, subalpine forest edges and residential gardens from 300 to 3,000 m elevation (Flanagan 1911, Hadow 1977, Short 1982, Campbell et al. 1990, Winkler et al. 1995). Not found breeding in oak (*Quercus* sp.) or oak-pine forests (Howell 1952) or on edge of woodlands (Dobkin et al. 1995). Often associated with willow (used for creating sap wells; Daily et al. 1993, Walters 1996).

SPRING AND FALL MIGRATION

Red-breasted Sapsucker. Specific information on habitat use by migrating individuals lacking, but given similarity of summer and winter habitats and small migratory movements, habitat probably similar to that used in other seasons.

Red-naped Sapsucker. Found in diverse habitats, including orchards and pine-oak woodland (Short 1982). Common spring and fall transient through mountains and lower elevations of Oregon (Gilligan et al. 1994).

WINTER RANGE

Red-breasted Sapsucker. Winters from near sea level to 3,000 m (Winkler et al. 1995); individuals nesting in inland forests tend to move to more coastal habitat, often wintering in protected lowlands (Nehls 1985). In British Columbia, frequents deciduous and coniferous woodlands from open black cottonwood (*Populus trichocarpa*) bottomland, red alder (*Alnus rubra*) and maple (*Acer* sp.) regrowth, and riparian woods to dense, coastal Douglas-fir and western red cedar (*Thuja plicata*)-western hemlock forests (Campbell et al. 1990). In Oregon, often found at localities that do not support nesting (Gilligan et al. 1994).

Red-naped Sapsucker. Found in diverse habitats, including orchards and pine-oak woodland (Short 1982). In Arizona, found in riparian woodlands, oak savanna, oak-juniper, pine-oak, and pure-oak woodland in mountains to 1,700 m (Bock and Larson 1986); in Mexico, found from 0 to 2,500 m (Winkler et al. 1995).

FOOD HABITS

FEEDING

Main foods taken. Sap, fruit, and arthropods (Beal 1911).

Microhabitat for foraging. *Red-breasted Sapsucker.* Foraging individuals in California spent 73% of their time on live trees, 21% on snags, 3% on logs, 1% on the ground, and 1% in the air (n = 71 observation periods [each observation period about 10 min]); in trees, individuals foraged 78% of time on trunk, 18% on live branches, 2% on dead branches, and 2% in foliage (n = 91 observation periods; Raphael and White 1984, M. G. Raphael pers. comm.). Forages in old-growth forests, as opposed to mature or young forests, when available (Lundquist 1988). Sap wells made in western hemlock, subalpine fir (*Abies lasiocarpus*), red alder, Scotch pine (*Pinus sylvestris*), Pacific silver fir (*A. amabilis*), lodgepole pine, Douglas-fir, broadleaf maple (*Acer macrophyllum*), white birch (*Betula alba*), aspen, willow, Jeffrey pine (*P. jeffreyi*), red fir, white fir (*A. concolor*), and mountain ash (*Sorbus sitchensis*; Beal 1911, Ziller and Stirling 1961, Raphael and White 1984, Lundquist 1988, Zimmerman 1998). In 6.5-ha study plot of subalpine fir forest in central British Columbia, sap wells found on 259 of 1,740 trees; mean size of sap trees 25 cm diameter at breast height (dbh; range 10–45, n = 259; Zimmerman 1998). In western hemlock forest on Moresby I., Queen Charlotte Is., British Columbia, sapsucker feeding evidence found on 8 of 79 trees and 4 of 30 trees in 2 study plots (about 0.1 ha each); many foraging scars toward base of trees, location at which cambium less likely to freeze than farther up tree during cold weather (Ziller and Stirling 1961).

Red-naped Sapsucker. Sap wells in xylem made early in spring. Xylem sap wells characterized by series of parallel circular holes usually completely surrounding stem or trunk; these wells typically associated with conifers such as Rocky Mountain juniper (*Juniperus scopulorum*), Douglas-fir, lodgepole pine, hybrid white spruce (*Picea engelmanni* × *glauca*); quaking aspen and black cottonwood also used (Loose and Anderson 1995, EHM, ELW). Switch to deciduous trees once these species leaf out. Sap wells during breeding season usually tap phloem tissue; phloem sap wells characterized by rectangular shape and surround stem or trunk (collectively known as "well system"); exploratory wells (about 2 × 5 × 1 mm deep) made in off-set rows (Ehrlich and Daily 1988). At Hat Creek, British Columbia, some well systems (516 of 1,198) worked such that upper portion of wells continually elongated (mean length 177.4 mm ± 98.4 SD [range 23–698, n = 516]); if not maintained, sap flow stops; for 1,198 phloem wells (23% in active use and most in willows), mean lowest point 1.85 m ± 0.77 SD (range 0.23–5.78) above ground, mean highest point 1.96 m ± 0.78 SD (range 0.23–6.17; Walters 1996). Most nesting pairs had series of defended wells in deciduous scrub thickets (comprising willow, swamp birch [*Betula pumila*], water birch [*B. occidentalis*], chokecherry [*Prunus virginiana*], and mountain alder [*Alnus tenuifolia*]); willow clumps only used for single season, partly because many stems die from sapsucker damage (Walters 1996). In Colorado, 72% of willow bushes showed evidence of sapsucker foraging; within individual bush, 28% of stems showed evidence of foraging, 98% of these dead (Ehrlich and Daily 1988).

Food capture and consumption. Sapsuckers are specialized for sipping sap; tongues shorter and less extensible than those of other woodpeckers, and tipped with stiff hairs to allow sap to adhere (Howell 1952, Oliver 1968). Some insects may be trapped in sap (e.g., ants and small flies [Diptera]) and so sapsuckers may also capture insects while tending sap wells (Sutherland et al. 1982).

Red-breasted Sapsucker. Forage with variety of techniques. Insects often captured using either gleaning or fly-catching techniques (Oliver 1968). In nw. California during breeding season, 81% of foraging time gleaning, 10% fly-catching, 9% drilling, and only 1% sapsucking (n = 93 observation periods [each period about 10 min]; Raphael and White 1984; M. G. Raphael pers. comm.).

Red-naped Sapsucker. Foraging techniques include sap feeding at wells (including drilling), feeding on aspen buds, gleaning insects (including bark removal), and fly-catching; feeding on aspen buds and fly-catching observed exclusively in quaking aspen; gleaning performed on quaking aspen, Douglas-fir, and black cottonwood (Walters 1996). Insects captured for delivery to young held in bill and sometimes taken to sap wells prior to feeding young; adults often crush prey items prior to feeding young (Wible 1960). During breeding season, majority of foraging time spent maintaining wells and searching for insects to feed nestlings (EHM, ELW).

DIET

Major food items. Sap (from variety of perennial plant species), insects, also bast (inner bark [cork cambium, phloem] and cambium layers), fruit, and seeds.

Quantitative analysis. *Red-breasted Sapsucker.* Of 34 specimens (29 collected Oct–Dec, none Apr–Aug), 68.9% of stomach contents animal material (42.5% ants, 4.0% beetles [Coleoptera], 7% Hymenoptera other than ants, 15% other prey) and 31.1% plant material (12.7% fruit, 6.0% seeds, 11.1% cambium; Beal 1911).

Red-naped Sapsucker. No quantitative data available for this species. Of 313 specimens (not distinguishing Red-naped Sapsuckers from Yellow-bellied Yapsuckers), 50.7% of stomach contents plant material (28.1% fruit, 16.5% cambium, and 6.1% miscellaneous plant parts) and 49.3% animal material (34.3% ants, 6.0% beetles, 5.4% spiders [Araneida] and miscellaneous insects [mayflies (Ephemeroptera); stoneflies (Plecoptera); grasshoppers, crickets and tree hoppers (Orthoptera); caterpillars and moths (Lepidoptera); and flies (Diptera)], 2.6% wasps [Hymenoptera], and <1% true bugs [Hemiptera]); cambium ingestion peaked in Apr representing 48% of diet at that time, but analyses conservative since much fluid passes almost immediately out of stomach prior to stomach-contents analysis (Beal 1911).

FOOD SELECTION AND STORAGE

Red-breasted Sapsucker. Appears attracted to trees with evidence of either previous sap wells or other injury that allows sap to exude (Oliver 1968, 1970).

Red-naped Sapsucker. Observed making sap wells in willow that showed no evidence of previous sap wells or other injury; other wells in Douglas-fir and quaking aspen that had been used in previous years (ELW). Early migrants feed on xylem wells in conifers (e.g., Douglas-fir, Rocky Mountain juniper) upon arrival to nesting area, switch to xylem wells in deciduous trees as buds start to form (e.g., black cottonwood, quaking aspen); eventually create phloem wells in deciduous scrub thickets (e.g., willow; Walters 1996, EHM, ELW).

NUTRITION AND ENERGETICS

Red-breasted Sapsucker. Sugar concentration of variable willow (*Salix commutata*) sap ranged from 13.4 to 16.2% (n = 64 well systems) and mountain alder sap ranged from 15.8 to 18.1% (n = 51 well systems); sap concentration did not vary throughout day (Sutherland et al. 1982).

Red-naped Sapsucker. Wild-caught individual in captivity refused to consume sugar water or mealworms (*Tenebrio* sp.) but survived >1 wk (ELW). Sugar concentration in willow sap wells ranged from 7.0 (diluted by rain) to 48.5% (mean 29.0%, n = 97 measurements from 7 well systems); concentration approximately 20% in morning and increased throughout day (Ehrlich and Daily 1988). Radio-tagged individual at Hat Creek, British Columbia, foraged at willow sap wells 1.4 km from nest (Walters 1996; see Behavior: spacing, below).

METABOLISM AND TEMPERATURE REGULATION

Red-naped Sapsuckers return to breeding areas usually when snow still present (Smith 1982b, EHM, ELW). Females roost on trunks of conifers below branch at night during breeding season when ambient temperature <0°C (ELW). Captive females kept at ambient temperatures as low as 0°C during night showed no signs of hypothermia, despite fasting (ELW).

DRINKING, PELLET-CASTING, AND DEFECATION

Red-naped Sapsuckers spend much time attending sap wells; presumably receive all water requirements from this source because not observed drinking water (ELW). As in Yellow-bellied Sapsucker (see Walters et al. 2002), Red-naped Sapsucker usually uses tree near cavity to which fecal sacs from nestlings transported (see Breeding: parental care, below; Howell 1952, EHM, ELW). No information on pellet-casting. Red-breasted Sapsucker presumably similar.

SOUNDS

VOCALIZATIONS

Diverse array of complex, variable, and intergrading vocal and nonvocal sounds, used in many circumstances over short to long distances. All sounds produced by both sexes. Information in this section for Red-naped Sapsucker, unless mentioned otherwise; Red-breasted Sapsucker assumed similar.

Development. Figures 2A–B (see Fig. 3A for Red-breasted Sapsucker). Not studied in detail, but changes from young nestlings' soft calls with wheezy quality to older nestlings' loud, incessantly repeated calls. Some structural differences between young and old nestlings. Calls of young nestlings soft; many have wheezy or creaky quality due to rapid repetition of brief elements. Calls cover broad frequency range due to broadband noise or harmonics; most energy at about 1–2.5 kHz. Older nestlings (mean mass 41.3 g) averaged 2.2 kHz in frequency at maximal amplitude, 8.1 kHz in frequency range, and 4.35 dB relative sound pressure level (Briskie et al. 1999). Varied sounds include clicks of about 1 ms duration, click-trains, harmonically rich elements with much noise, long sections of broadband noise, etc. When parents absent from nest, older chicks vocalize incessantly, making it easy for humans to find nests. Relatively low frequency and high amplitude of nestling calls make nests readily located by predators, but nest predation low on this species in Arizona study area (Briskie et al. 1999). Over development, calls increase in amplitude, frequency, frequency range, harmonic clarity, rhythmicity, and duration. Many rhythmically repeated calls have sharp onset, which imparts clicklike quality, followed by harmonically rich frequency-modulated portion (often with broad-

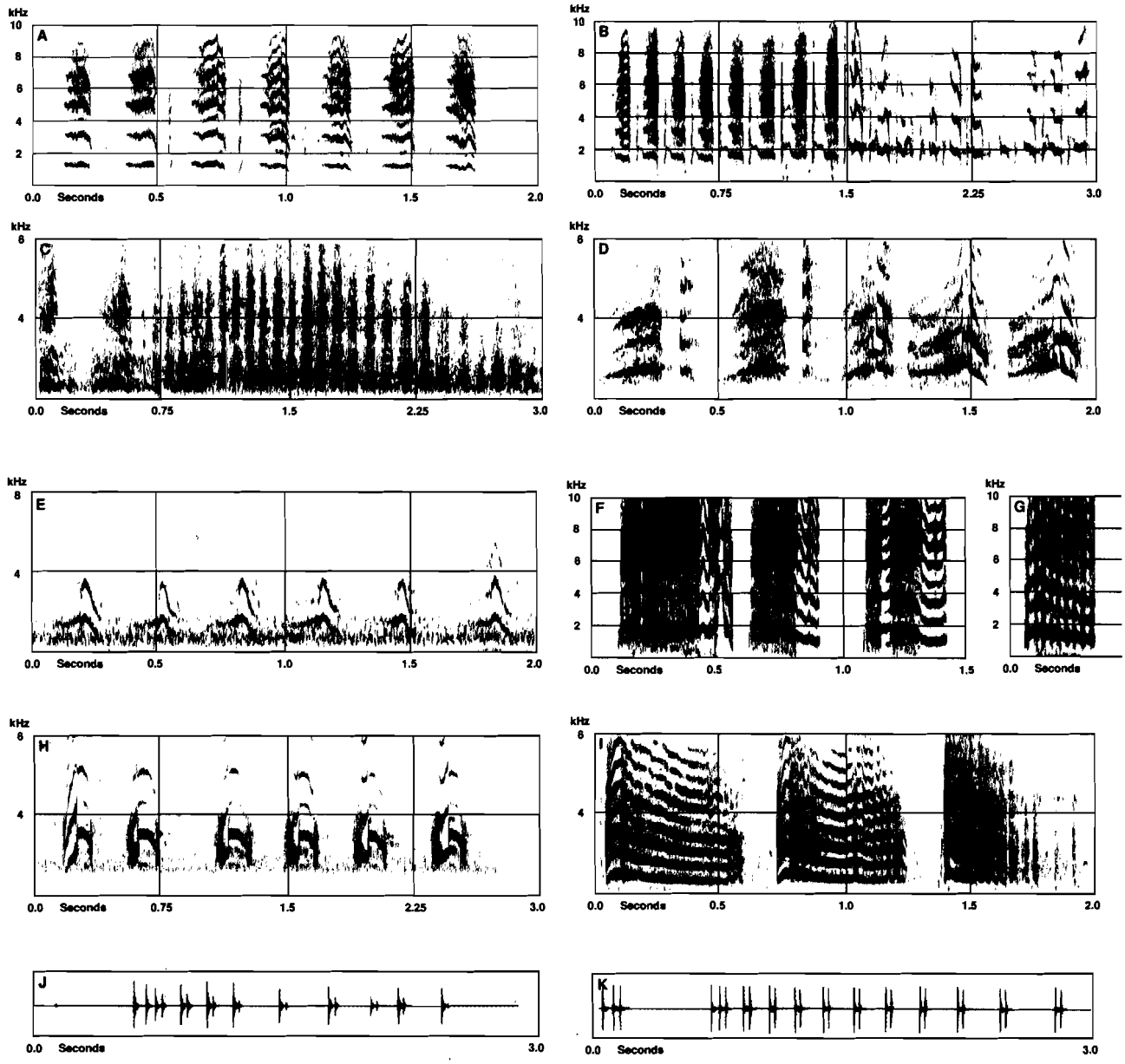


Figure 2. Vocalizations of Red-naped Sapsuckers. A. Calls of undisturbed young nestlings (Macaulay Library of Natural Sounds [LNS], Cornell University, no. 50125, recorded 8 Jul 1990 at Little Cultus Lake, OR). B. Calls of same nestlings as in A, showing transition from repetitive calling by unattended chicks to calling when adult arrives with food (LNS no. 50125). C. Interaction Calls, end of series (first call incomplete) by male at nest excavation in response to approach of mate and overlapping female's Dry Chatter as she flies toward and lands near excavation (11 May 1992). D. Interaction Calls (14 May 1992). E. Interaction Calls by male hopping toward female (14 May 1992). F. Scream Call (3 from series; natural intervals shown) by male in hand (29 Jun 1991). G. Scream Call showing strong rhythmic frequency modulation by female in hand (2 Jul 1991). H. Squeal Call by lone male (4 May 1992). I. *Waa* Calls (LNS no. 47711; 24 Jun 1990 near Walla Walla, WA). J. Drumming, waveform (near Creston, British Columbia, recorded by EHM 24 May 1991). K. Drumming, waveform (LNS no. 50301; 18 Jun 1990 near Beaverhead, MT). C, D, E, F, G, and H all recorded by EHM at Hat Creek, British Columbia, on dates indicated. Prepared by EHM using a Kay Elemetrics Computerized Speech Lab 4100, with an effective frequency resolution of 162 Hz and a 200-point FFT transform size, except H for which values are 126 Hz and 256 points.

band noise). Noise less prominent or absent from calls of older nestlings but harmonic structure retained. Some calls suggest 2 sound sources. Many variations or different kinds of calls given by nestlings as they move or interact with one another in nest cavity, or when parent arrives with food: in latter circumstance, nestling calls increase in amplitude, frequency, and variation in both frequency and temporal characteristics (see Fig. 2B). Recordings suggest that normally only 1 nestling vocalizes at a time, as in Yellow-bellied Sapsucker (Gibbon 1970).

Vocal array. *Dry Chatter.* Figure 2C. Call mildly harsh ("dry") or raspy to human ear. Comprises series of similar rapidly repeated elements. Duration of Dry Chatter few to >10 s, sometimes with brief silent period embedded (EHM). Harmonic structure (peak of fundamental about 1.3 kHz) overlain by slight to extensive broadband noise (energy to >8 kHz). Repetition rate of elements about 10/s (element duration 60–70 ms, with intervals 30–40 ms). Given when paired bird of either sex flies away from or toward the other, such as during interactions or after one bird is relieved at nest. Most common early in nesting season. Dry Chatter noted during moth-flight display (see Behavior: agonistic behavior, below) in interactions between territorial bird and intruder or between paired birds early in breeding period; given by both sexes (EHM, ELW).

Interaction-Call Complex. Figures 2C–E (see Fig. 3B for Red-breasted Sapsucker). Complex of intergrading vocalizations used by interacting birds, ranging from loud calls used in agonistic interactions to soft short-distance calls. Sometimes given in flight by territorial bird when supplanting or chasing conspecific intruder, during aggressive-social displays between sapsuckers not in same family, or toward other woodpecker species. One common high-intensity form 2-part utterance, one part being about 500 ms long, and rising slowly from about 1 to about 1.6 kHz (with broadband noise and some frequency modulation), other part brief (about 20 ms at most) and tonal, with strong harmonic structure (first 4 elements in Fig. 2D). Another common high-intensity form longer (400–700 ms), begins with noisy section followed by harmonic section that increases rapidly to peak of 2.5–3 kHz, then declines rapidly to near starting frequency (last 3 calls in Fig. 2D). Third distinctive form shown in Figure 2E. Much intergradation occurs in Interaction Calls, especially in short-range calls like those in Figure 3B. Variable soft Interaction Calls extremely common, invariably given by mates or family members (after fledging) whenever individuals meet or approach one another; especially common between mates near nest, e.g., during approach or changeover during incubation. Nestlings learn to associate this call type with presence of adults and being fed, and adults delivering food to old nestlings commonly stop near nest tree and utter this call (EHM, ELW).

Scream Call. Figures 2F–G. Birds in hand (e.g., for banding) utter high-amplitude harmonically rich calls in almost rhythmic pattern (often punctuated by struggling or pecking at hand). Utterances may be bouted (e.g., several calls separated by silences from other brief sets of calls) or given in long series. Subjectively, birds that seem to be in greater distress utter calls with noisy sections that occur in bouts. Calls shown about 150–450 ms long with fundamental frequency of about 1–2 kHz (EHM, ELW).

Squeal Call. Figure 2H. Homologue of this call in melanerpines widely referred to as *churr* (Hadow 1977) or Squalling Weep Call (*weep, wee-urp,* or *kwee-urk*; Short 1982: 174) because of its harsh quality to human ear. In sapsuckers however, call mainly tonal so sounds different to humans. Brief set of rhythmically repeated and similar elements. Elements typically start and end with broadband noise overlying harmonic structure and exhibit sharp increase in frequency to central harmonic portion (peak fundamental frequency about 3.0–3.2 kHz). For Red-naped Sapsuckers in Colorado, mean duration of elements 0.2 s (range 0.1–0.3, $n = 54$); mean interelement interval 0.2 s (range 0.1–0.5, $n = 43$); "top" of fundamental frequency, mean 2.5 kHz (range 0.8–3.0, $n = 50$); mean 9.0 elements/call (range 2–16, $n = 44$) before pair formation, 4.4 elements/call (range 1–7, $n = 45$) after pair formation (overall mean, 6.2 [range 1–16, $n = 151$]; Hadow 1977). For same species at Hat Creek, British Columbia, mean 5.8 elements/call (range 1–10; $n = 134$; EHM, ELW). Squeal Call most common early in nesting cycle with brief recrudescence when young about to fledge; mainly uttered by males; frequently elicits Squeal Call, Drumming, or flight approach toward caller by conspecific bird (e.g., approach by female to male calling on copulation branch). Given by both sexes and commonly alternated with or used interchangeably with Drumming. Squeal Calls may also be given by unpaired males attempting to attract female over short distance (EHM, ELW). Also used in other situations (mainly by males). For breeding Red-naped Sapsuckers in Colorado, 57% of Squeal Calls by males apparently spontaneous, 9% in response to Drumming, 9% occurred several minutes before copulation, 9% given before entering nest cavity to excavate, 6% in response to conspecific Squeal Calls, 6% given while perched with mate, and the others given a few minutes before or after nest exchange ($n = 47$; Hadow 1977). Functions of Squeal Calls seem to be related mainly to obtaining

a mate and sexual activity, as evidenced by these data and the trend for Squeal Calls to occur mainly in the breeding season and to resurge if male loses his mate (EHM, ELW).

WAA CALL. Figure 2I. *Waa* Call given often as low-intensity alert call when bird disturbed. Call commonly repeated; declines progressively in frequency. *Waa* Calls are harmonically rich calls of 340–600 ms duration. Frequency peaks at about 0.9–1.4 kHz near beginning of call, then declines slowly over remainder. *Waa* Call often incorporates sections of broadband noise and almost rhythmic frequency modulations of the carrier frequency. Harsh *Waa* Call, common variant, occurs in takeoff and flight, when call abbreviated and strongly modulated (last call in Fig. 2I). *Waa* Call with broad contextual use but always seems to signal "alertness to danger, to the unexpected, unusual or strange," such as sudden detection of another animal (not just predators) as in Yellow-bellied Sapsucker (Lawrence 1967: 19). Harsh *Waa* Call given most often around time when young emerge from nest, especially in taking flight or in making short flights (e.g., in presence of human observer), hence seems to be high-intensity extreme form of *Waa* Call (EHM, ELW).

Geographic variation. None described.

Phenology. Most sounds used only in breeding season. *Waa* Calls given year-round, less frequently in migration and on wintering grounds than during breeding season (Bent 1939). Drumming and Squealing by Red-naped Sapsuckers during breeding season in Colorado show highest activity in prepairing period (about 50 Drums and 6 Squeal/h in study area), followed by sharp decline during nest excavation (to about 2 Drums and 1 Squeal/h); Drumming and Squealing activity subsequently remain at low levels (about 2 Drums/h during incubation and 0–1 Drum/h thereafter; about 0.1 to 0.2 Squeal/h from incubation through postfledging; Hadow 1977). Males that do not acquire mates presumably also contribute to local Drumming and Squealing activity for considerable portion of breeding season. Harsh *Waa* Calls occur around hatching, and males that lose mates early in breeding season exhibit resurgence of Drums and Squeals. Unpaired males presumably responsible for most Drums and Squeal Calls after incubation begins (EHM, ELW).

Daily pattern. Few data on nocturnal vocalizations. Presumably nestlings and brooding males of both species vocalize to one another at night. During breeding season in Colorado, Drumming and Squealing showed strong daily patterns, with highest activity from 05:00 to 07:00; Drumming activity gradually declined until 15:00 to 17:00, then increased slightly until 19:00 to 21:00, after

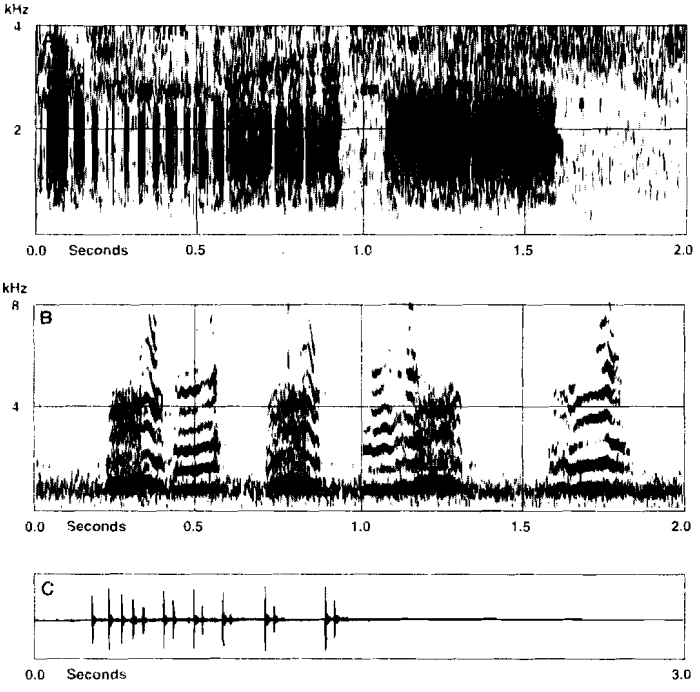


Figure 3. Vocalizations of Red-breasted Sapsuckers. A. Calls of very young undisturbed nestlings (LNS recording no. 47586; near Loyalton, CA, 15 Jun 1990). B. Interaction Calls in changeover during incubation; incoming individual gave calls with broadband noise (first, third, and fifth of 6 calls shown; near Masset, Queen Charlotte Is., British Columbia, recorded by EHM 12 May 1984). C. Drumming waveform (near Masset, British Columbia, recorded by EHM 12 May 1984). Prepared by EHM using a Kay Elemetrics Computerized Speech Lab 4100, with an effective frequency resolution of 162 Hz and a 200-point FFT transform size.

which birds roost for night; Squealing activity declined steadily from early morning until late evening (Hadow 1977).

Places of vocalizing. Most sounds produced when on trees, but Harsh *Waa* Calls and some *Waa* Calls given aerially. Interaction Calls often occur during flight (e.g., when one individual follows another); Dry Chatter Calls given only in flight. During breeding season *Waa* Calls given most often near nest but also by birds far from nest. Dry Chatter Calls given by birds leaving presence of mate or other bird following interaction. Squeal Calls often occur with Drums, so are uttered at Drumming posts; some Squeals given while perched high in tree (sometimes at top). In Colorado, location of Squeal by male Red-naped Sapsuckers categorized as in trees <30 m from nest, 42%; in trees >30 m from nest, 27%; while perched outside nest, 14%; at sap wells, 9%; at copulation perch, 7%; and from nest cavity, 2% ($n = 59$). Interaction Calls take place in diverse locations: short-range Interaction Calls given on nest tree (e.g., by hole during many

exchanges), on nearby trees, or wherever mates or family members meet (Hadow 1977).

Repertoire and delivery of songs. Notion of "song repertoire" does not apply to woodpeckers, unless several different Drumming modes occur (an unstudied possibility). For information on delivery of Drums, see Nonvocal sounds, below.

Social context and presumed functions. See above.

NONVOCAL SOUNDS

Nonvocal sounds include sounds produced by the bill striking various surfaces and by wings during display flights.

Array of sounds. DRUMMING. Figures 2J–K (see Fig. 3C for Red-breasted Sapsucker). Produced by striking a surface rapidly and forcefully with tip of bill. Most Drumming by males, but females of both species also Drum (Hadow 1977, Trombino 1998, EHM, ELW). Drums usually begin with several rapidly repeated strikes in "introductory roll" (often increasing in rate of striking within roll), followed by pause, then more strikes in irregular cadence (Hadow 1977, Trombino 1998, EHM, ELW). Among woodpeckers, Drum of sapsuckers notable for "slowness and irregularity" (Short 1982: 174). Drums highly variable in duration and temporal patterning, even successive Drums by undisturbed lone birds; nevertheless, they are individually distinctive (Trombino 1998). Drums characteristically exhibit couplets (occasionally triplets) following introductory roll (Trombino 1998, EHM, ELW; see Fig. 2K), possibly because bill held close to Drumming surface after each strike so that elastic surface of substrate strikes bill tip; brief uniform interval (<10 ms) within couplets makes it unlikely that Drumming birds strike surface twice in rapid succession. In closely related and behaviorally similar Yellow-bellied Sapsucker, Drums do not communicate about habitat quality (Eberhardt 1997); this probably also applies to both Red-naped and Red-breasted sapsuckers. Drums of males likely provide information to prospecting females and competing males about Drumming individual's identity and quality (EHM, ELW).

Drumming is long-distance signal given mainly by males, occurs mainly early in breeding season, and recurs if male loses mate. Like Squeal Call, Drumming likely serves to simultaneously attract mates and communicate presence in and occupancy of an area to competing males. Context of 54 Red-naped Sapsucker Drums categorized as follows: 48% spontaneous, 17% in response to conspecific Drumming, 17% occur during pauses in aggressive interactions with conspecific birds, 6% occur several minutes before copulation, 4% given in response to conspecific Squeal Calls, 2% occur when perched with mate, and remainder given around time of nest exchange; in separate sample of 39 Drums, 54% occurred near (< 30 m) nest tree, others farther away (Hadow 1977). Drumming occurs in many other social interactions, such as counterdrumming between males or between interacting male and female. Full understanding of functions of Drums must consider both dynamic social interactions and role of females.

Drums of male Red-naped Sapsuckers (n = 94; Hadow 1977) characterized as follows: mean Drum duration, 1.7 s (range 0.6–2.8); mean introductory roll duration, 0.2 s (range 0.03–0.4); mean number of strikes/Drum, 8.7 (range 2–14); mean number of strikes in introductory roll, 5.3 (range 1–12); mean overall rate of striking, 5.0 strikes/s (range 3.1–8.2); and mean rate within introductory roll, 23.8 strikes/s (16–50). At Hat Creek, British Columbia, intervals between successive Drums (n = 335) by males that were not interacting (e.g., counterdrumming) with other birds averaged 27.7 s (median 24 s, range 3–92; EHM, ELW).

Drums of Red-breasted Sapsuckers characterized as follows: mean Drum duration, 1.5 s; mean strikes/Drum, 17.7; rate of striking for entire Drum, 12.6/s; rate of striking for introductory roll, 21.7/s; and mean interval between strikes, 0.09 s (Stark et al. 1998). Short (1982) reported rates of striking as 4–6/s. Discrepancies among authors may be due to differences in recognizing couplets as 1 or 2 strikes (see above).

Coordinated Drum-Dueting between mates has been observed in Red-naped and Red-breasted sapsuckers and their hybrids (Trombino 1998; see also Howell 1952). Drumming varied significantly between sympatric Red-naped Sapsucker and Red-breasted Sapsucker, with twice as many doublets within Drums of Red-naped Sapsuckers as for Red-breasted Sapsucker, but allopatric Red-naped and Red-breasted sapsuckers did not differ in their Drumming (Trombino 1998).

RITUALIZED TAPPING. Given by both sexes in rhythmically repeated bouts, in both species (EHM, ELW). Ritualized tapping occurs during excavation, when the bird present at the nest hole begins to tap (generally at the lower rim of the hole) in a stilted and exaggerated manner upon the arrival of the relieving bird; also occurs within nest cavity if excavating individual is in cavity when relieved. Ritualized Tapping declines over the excavation period but remains common in diverse encounters between mated birds (e.g., during changeover while incubating) and may occur on nest tree or nearby trees during approach or departure.

DISPLACEMENT TAPPING. Given by both sexes. Tempo resembles pattern of feeding birds. Resembles Ritualized Tapping during changeover at nest

in being executed stiffly and taking place at single location. During incubation or brooding, relieving bird often taps 1 to several times at 1 or several places on nest tree before or as approaching nest hole. During incubation or brooding, attending adult occasionally taps inside nest cavity (apparently unrelated to presence of nearby mate) which may just reflect maintenance or enlargement of nest cavity. Displacement Tapping also occurs in other diverse circumstances: agonistic interactions with conspecific birds; interactions between sexes early in pair formation; after arrival at feeding station occupied by other birds; or when interrupted in an activity (e.g., when returning to nest with food) by arrival of human.

Feeding and Excavation Sounds. Tapping in the context of feeding or excavation variable in amplitude and temporal pattern, depending on activity (e.g., boring for food, drilling new sap wells, maintaining or enlarging existing sap wells) and nature of substrate. However, all such tapping includes some bouts of rhythmically repeated strikes. Exploratory tapping also occurs frequently, in testing surfaces for Drumming, drilling, and excavation; exploratory tapping tends to be soft and of irregular cadence, with occasional bouts of rhythmically repeated strikes. Humans can sometimes detect excavating sapsuckers over distances of tens of meters by sounds of excavation (EHM, ELW).

Wing Sounds. Two kinds of communicative wing sounds produced in Red-naped Sapsucker. Winnow (*sensu* Kilham 1962) is snipe-like winnow produced only when bird in flight and Ruffle (*sensu* Kilham 1962) occurs when wings produce noise as they beat rapidly and with shallow amplitude (EHM, ELW). Wing sounds presumably similar in Red-breasted Sapsucker. Wing-clapping, observed in Yellow-bellied Sapsucker (see Walters et al. 2002), not reported for Red-naped or Red-breasted sapsuckers.

BEHAVIOR

Behavior probably similar for all 3 species of sapsucker in *Sphyrapicus varius* complex. Differences in behavior between Red-breasted and Red-naped sapsucker can be considered minimal; specific descriptions of behavior given here are for Red-naped Sapsucker, unless noted otherwise; more extensive description of Yellow-bellied Sapsucker behavior provided by Walters et al. 2002.

LOCOMOTION

Walking, hopping, climbing, etc. Sapsuckers hop ("hitch") vertically up and down trees, as well as when moving laterally (e.g., when approaching a nest hole from the side); also hop on horizontal surfaces such as tree limbs or rail fences (EHM, ELW).

Flight. Intermittent flight widespread in woodpeckers, and Red-naped Sapsucker shares this mode of flap-bounding flight (Tobalske 1996): flight characterized by vertical undulations in flight path caused by alternating flapping and nonflapping phases, with wings held fully flexed during nonflapping phase. Level flight begins with period of continuous flapping (of 8–30 wing-beats across 6 species [including Red-naped Sapsucker] studied by Tobalske [1996]). Bound phases begin during mid-upstroke motion and flapping phases after bounds begin with continuation of upstroke. For flap phases of Red-naped Sapsucker, there were 2–7 flaps/phase with wing-beat frequencies of 8–12 flaps/s ($n = 30$), flapping phases lasted 233–700 ms, intervening bound phases lasted 67–683 ms, and overall flapping made up 33–88% of flying time. This manner of flight elaborated in ritualized "exaggerated bouncing flight" display (*sensu* Lawrence 1967). Speed during level flight averaged 9.3 m/s (range 6–12, $n = 13$; measured for flights of individuals near nest; Tobalske 1996). Sapsuckers are skilled flyers, as evident from conspecific high-speed chases through vegetation; they also spend much time fly-catching in spring (EHM, ELW), which may be attributed to their pointed wings (feature common to melanerpine woodpeckers that fly-catch; Tobalske 1996).

Swimming and diving. Not known to swim.

SELF-MAINTENANCE

Preening, head-scratching, stretching, bathing, anting, etc. Maintenance behavior of Red-naped and Red-breasted sapsuckers similar (EHM, ELW) to that described for Yellow-bellied Sapsucker in an aviary (Kilham 1983) and in the wild (Lawrence 1967). All sapsucker species scratch head directly; i.e., without lowering wing (Kilham 1983: Fig. 54). As in Yellow-bellied Sapsucker (see Walters et al. 2002), Red-naped Sapsucker performs unilateral "leg-wing stretch" with only wing extended its full length down and back and ipsilateral foot remains on substrate or moves only short distance to secure better grip. One or both wings stretched dorsally partly (Kilham 1983: Fig. 52) or fully. Legs stretched posteriorly singly or (rarely) both if individual rests on belly on horizontal branch. Sapsucker picks with bill deep within contour feathers of breast, shoulders, wing-coverts, and base of tail; rectrices and remiges drawn through bill. Occasionally bird rubs bill against preen gland, then rubs foot, which may function to transfer oil to head via scratching. Preening bouts typically punctuated by shaking

and fluffing plumage. Female preens more than male during nest excavation.

Sleeping, roosting, sunbathing. Most information known for Red-naped Sapsucker and presumed similar for Red-breasted Sapsucker. As in other woodpeckers, male sleeps in nest cavity during excavation (beginning during late excavation when cavity sufficiently large enough), incubation, and when nestlings <25 d old (Walters 1996, EHM, ELW); may continue until all of young have fledged (Howell 1952). Female roosts on tree trunk, usually under base of a limb (Walters 1996). After young fledge, young and adults roost solitarily on tree trunks and do not return to nest cavity (EHM, ELW). Roosting habits during migration not known. During sunbathing, fully fluffs nape-, dorsal-, and scapular-feathers, orients back toward sun, and partly spreads wings (and possibly tail), and holds this posture for at least several minutes; if individual on horizontal surface, both legs may be extended posteriorly (EHM, ELW).

Daily time budget. No known quantitative studies.

AGONISTIC BEHAVIOR

Physical interactions. Both sexes engage in agonistic behavior in vicinity of nest, near mate, and at sap wells; greatest intensity and frequency of engagements occur early in nesting cycle. Extreme aggression between adult males early in spring sometimes occurs where males grasp one another by bills and fall to ground without relinquishing their grasp (Howell 1952, EHM, ELW).

Communicative interactions. Striking ritualized postures and movements used in agonistic (and sexual) behavior involve complex vocalizations and both static and dynamic optical signals from plumage. Descriptions of displays and postures based on behavioral inventory compiled in Short 1982 and descriptions from Lawrence 1967 and Short 1982 for Yellow-bellied Sapsucker. Descriptions here apply to Red-naped Sapsucker; because sexes of Red-breasted Sapsucker have similar plumage, sexual discrimination more on behavioral than on optical cues (Short 1982), and some displays for Red-breasted Sapsucker may differ from descriptions presented here.

Bill-Directing Posture. At greatest intensity, bill points horizontally at other bird, head extends forward, with body and tail aligned with head and bill. Considered threatening.

Bill-Raised Posture. Individual raises bill upward, sometimes beyond 90° vertical; posture displays throat-patch and orients bill away from opponent; considered submissive.

Bowing Display. Involves both raising (Bill-Raised Posture) and lowering (Bill-Directing Posture) head, with emphasis on lowering movements; more often between sexes than to another individual of same sex.

Head-Swinging. Ritualized and repetitive side-to-side motion of head, involving Bill-Directing and Bill-Raised postures; used in aggressive same-sex encounters.

Wing-Flicking. Rapid flick out and in of 1 or both wings; used in agonistic encounters.

Wing-Droop Posture. Modification of Wing-Flicking; wings held away from body and wrists dropped with wing tips lifted and crossing over rump.

Crest-Raising. Crown-feathers erected; used in aggressive encounters.

Throat-Fluffing. Feathers of throat (red in male; red and white in female) spread and displayed to opponent or prospective mate; incorporated as part of Bill-Raised Posture. Both Crest-Raising and Throat-Fluffing occur also when mates meet during incubation exchanges or when feeding young and when Drumming (Lawrence 1967: Fig. 6).

Aggressive-Social Display (Lawrence 1967: Fig. 2). Aggregate of movements and postures. Individuals face each other with head and bill pointed upward and swing stiffly from side to side in an arc (Bill-Raised Posture). Wings held slightly out from body, with bend of wing slightly lowered and flicked (Wing-Flicking), throat-feathers erected (Throat-Fluffing) and crest-feathers raised and lowered (Crest-Raising), and tail spread and held against substrate; from side, dorsal outline of body deeply concave. Vertical bobbing movements of body often occur (Bowing Display; Lawrence 1967). High-intensity Interaction Calls accompany these displays (see Sounds: vocalizations, above).

Several kinds of display flights occur during breeding season (Lawrence 1967): "exaggerated bouncing flight," "swooping flight" (as when individual approaches familiar and frequently used place such as Drumming post), and "moth flight" (characterized by head lowered and shoulders hunched and wings beaten rapidly but with shallow amplitude). Moth flight associated with agonistic and sexual interactions, but also occurs in other contexts, such as when male carries feces from nest cavity to disposal site. Dry Chatter Call (see Sounds: vocalizations, above) typically occurs in moth flight early in breeding (see Locomotion: flight, above).

SPACING

Territoriality. Early in breeding cycle, individuals advertise presence and defend more or less exclusively occupied space that includes nest tree; also defend sap wells. Later in nesting cycle will chase conspecific individuals from immediate

vicinity of nest or sap wells, but does not advertise occupancy of space around them.

Red-breasted Sapsucker. Early studies in ne. California suggested that territories extended 46–137 m from the nest; territory larger in open areas and smaller in dense forest (Howell 1952). Near Hope, British Columbia, 2 adults ranged 229 m and 457 m from nests; larger distance was to feeding area of Douglas-firs (Kelleher 1963). At Currie Creek on Vancouver I., British Columbia, mean breeding territory size 5.9 ha using radio-telemetry (n = 7; Manning and Shepard 1999). Red-breasted Sapsuckers show high overlap with Williamson's Sapsuckers in forest types; both species locate nests as if interspecifically territorial (i.e., no difference in distance between species and distance within species; Raphael and White 1984).

Red-naped Sapsucker. In Colorado, mean territory size 1.67 ha (range 0.70–2.63; n = 8; Young 1975); in Blue Mtns. of Oregon and Washington, estimated territory size 4 ha (Thomas et al. 1979). At Hat Creek, British Columbia, radio-telemetry data on 5 males and 5 females (n = 10 different nests) gave mean territory size 13.2 ha (range 5.6–45.2); home-range estimates did not differ between males and females; 95% of movements <500 m from nest, extreme movement 1.4 km from nest was for maintenance of sap wells in willow (Walters 1996). Home ranges noncircular due to environmental features not used (e.g., agricultural fields, ponds). Site fidelity (i.e., regular home-range use) imposed by presence of nest and sap wells regularly used and maintained. Neighboring breeding pairs tended to avoid one another, so parts of some home ranges exclusively occupied; minimal distance between nest trees 100 m (Walters 1996). Nests near edges between old-growth and open clearcuts where scattered birch had grown rapidly since timber harvest, territory size 2 ha with nests as close as 91 m apart; in dense old-growth habitat, territories 8–10 ha (McClelland 1977).

Individual distance. Before fledging takes place, adults rarely in close proximity to one another except sometimes during excavation, agonistic interactions, courtship or sexual behavior, changeover during incubation or brooding, or coincidental meeting at nest during food delivery to nestlings (EHM, ELW).

SEXUAL BEHAVIOR

Mating system and sex ratio. Socially monogamous, but genetic evidence points to some mixed parentage in Red-naped Sapsucker (1 brood with mixed maternity; S. A. Fleury pers. comm.). Equal sex ratio based on sex of fledglings from 27 nests of Red-naped Sapsucker (EHM, ELW).

Pair bond. Apparently monogamous. Pair bond maintained throughout breeding season, including period of fledgling care; usually re-established between years if mate survives. At Hat Creek, British Columbia, pair bonds among 10 color-banded pairs maintained for 9 of 11 year-to-year opportunities when both members survived; 1 banded pair remained together for at least 3 seasons (EHM, ELW). In Nevada, 17 of 18 pairs remained together in subsequent year (Fleury 2000). Fidelity to mate may be partly attributable to general site fidelity or perhaps even fidelity to particular trees (see Breeding: nest site, below) that are commonly reused for nesting.

Courtship displays. As in Yellow-bellied Sapsucker (see Walters et al. 2002), displays used by Red-naped Sapsucker for courtship (except for copulation) and in agonistic encounters essentially indistinguishable. Agonistic components apparent even during changeovers at nest during incubation and during feeding of fledglings (see Agonistic behavior, above). Copulation begins in late excavation, peaks during egg-laying period, and may continue even after start of full incubation. Copulation described as similar for Red-naped Sapsucker, Red-breasted Sapsucker, and interspecific pairs: male solicits copulation by uttering Squeal Call from horizontal branch near nest, with soft Interaction Calls if female approaches; usually female precedes male to branch and perches crosswise, droops her wings slightly and holds them away from body, lifts tail, and may throw her head back until bill points nearly posteriorly ("sometimes appearing to rest it on her interscapular region"; Howell 1952: 247–248). As described for Yellow-bellied Sapsucker (see Lawrence 1967), male hovers down upon female's back from above or hops toward her with crown-feathers fully erect, bib ruffled, wings drooping and sometimes flapping weakly, back deeply depressed, and fanned tail scraping the branch. Male grasps female with his feet before sliding down her left side and swings posterior part of his body beneath female's uplifted tail to achieve cloacal contact, while his tail presses against her right flank; many variations in this general form and sequence, but male's movement from female's dorsum down her left side seems invariant. Copulation lasts up to 10 s, sometimes followed by Displacement Tapping (EHM, ELW; see also Lawrence 1967; see Sounds: nonvocal sounds, above).

Extra-pair copulations. Of 14 Red-naped Sapsucker nests in central Nevada analyzed using DNA fingerprinting, there was no genetic evidence of extra-pair fertilization (S. A. Fleury pers. comm.). See also Breeding: cooperative breeding, below.

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. Not very social. Loose aggregations sometimes occur in migration (see Migration: migratory behavior, above).

Play. No information (but see Walters et al. 2002).

Nonpredatory interspecific interactions. Most interspecific interactions involve defense of nest or sap wells.

Red-breasted Sapsucker. Interspecific helping behavior documented at 2 nests in hybrid zone in Oregon: hybrid female (offspring from *S. r. daggetti* × *S. nuchalis* cross), Red-naped Sapsucker female, and male Red-breasted Sapsucker all fed young at 1 nest; female Red-breasted Sapsucker, male Red-breasted Sapsucker, and male Williamson's Sapsucker all fed young at another nest (Trombino 2000).

Some migrant hummingbirds use sap from sap wells as primary source of energy. Anna's (*Calypte anna*) and Rufous hummingbirds associated with sap wells; up to 5 hummingbirds observed following individual sapsucker, presumably to find fresh sap wells (Grinnell and Storer 1924, Sutherland et al. 1982). Other species observed feeding on sap at sap wells include Ruby-crowned Kinglets (*Regulus calendula*; Taylor 1920, Danforth 1938), White-crowned Sparrow (*Zonotrichia leucophrys*; Danforth 1938), Nashville Warblers (*Vermivora ruficapilla*), Orange-crowned Warblers (*V. celata*), Wilson's Warblers (*Wilsonia pusilla*), and jumping mice (*Zapus princeps*; Sutherland et al. 1982).

Red-naped Sapsucker. Williamson's Sapsucker aggressive toward and behaviorally dominant to Red-naped Sapsucker (Young 1975). Red-naped and Red-breasted sapsuckers have nested as close as 15 m in same stands (Crockett and Hadow 1975), but usually Red-naped Sapsuckers nest closer to other species of woodpeckers (e.g., Downy Woodpecker [*Picoides pubescens*], Hairy Woodpecker [*P. villosus*], Northern Flicker [*Colaptes auratus*]) than to Williamson's Sapsuckers (Hadow 1977; see also Spacing, above). In central New Mexico, Red-naped Sapsuckers did not respond aggressively to broadcast Drums (n = 137 trials) or Squeal Calls (n = 25) of Williamson's Sapsuckers; Williamson's Sapsuckers reacted to Red-naped Sapsucker Drums (15 of 90) and Squeal Calls (13 of 13) broadcasts by Drumming, vocalizing, or approaching (Young 1975).

Sap wells attract species that feed on sap, creating potential for defense of well from birds or mammals or for predation on insects feeding on sap. In Colorado, other species at sapsucker wells for 84% of observation time (n = 54 h); sapsuckers said to be keystone species because of assemblage associated with sap wells (Ehrlich and Daily 1988). Sap wells appear to be a particularly important resource to Rufous, Broad-tailed (*Selasphorus platycercus*), and Calliope (*Stellula calliope*) hummingbirds and may even dictate timing and nature of migration in some species (Woodbury 1938, Wiegert 1959, Ehrlich and Daily 1988, EHM, ELW). Red-breasted Nuthatches (*Sitta canadensis*) place sap (from sapsucker wells) around their cavity entrances (McClelland 1977). Red squirrels (*Tamiasciurus hudsonicus*) and northern flying squirrels observed using cavities in same tree as sapsucker nests without apparent conflict (Walters and Miller 2001) but former known predator of Yellow-bellied Sapsucker (see Walters et al. 2002).

PREDATION

Kinds of predators. *Red-breasted Sapsucker.* No information but likely similar to Red-naped Sapsucker.

Red-naped Sapsucker. Remains of radio-tagged adult found in nest of Cooper's Hawk (*Accipiter cooperii*; Walters and Miller 2001); also taken by Sharp-shinned Hawk (*A. striatus*) and Northern Goshawk (*A. gentilis*; Reynolds and Meslow 1984, Squires 2000). Known predators at nests include black bear (*Ursus americanus*; Franzreb and Higgins 1975, Walters and Miller 2001), deer mouse (*Peromyscus maniculatus*; Walters and Miller 2001), weasel (*Mustela* sp.; Daily 1993, Walters and Miller 2001, S. A. Fleury pers. comm.), House Wren (*Troglodytes aedon*; Walters and Miller 2001), and gopher snake (*Pituophis melanoleucus*; S. A. Fleury pers. comm.).

Manner of predation. Most mammalian predators take adults, young, or eggs at nest. For Red-naped Sapsucker, bears take nestlings (and potentially adults; predation of roosting male Williamson's Sapsucker documented) by gnawing or clawing to gain access to entrance; deer mice take eggs; weasels take roosting males or nestlings; House Wrens destroy eggs and place their own nest over eggs or young (Walters and Miller 2001). Gopher snake takes nestlings (S. A. Fleury pers. comm.).

Response to predators. In response to threats (i.e., potential predators), sapsuckers excitedly utter "alarm" calls (*Waa* or Harsh *Waa* Calls; see Sounds: vocalizations, above). Adults swoop down and sometimes strike potential predator, including researchers climbing nest trees to band nestlings (EHM, ELW). Red-breasted Sapsucker chased chipmunk (*Tamias* sp.), possible but undocumented predator, from near nest; some individuals dodge to avoid attacks of House Wrens, and others chase them (Howell 1952).

BREEDING

PHENOLOGY

Pair formation. *RED-BREASTED SAPSUCKER.* Difficult to determine when pair formation occurs for individuals with limited migration but presumably occurs shortly after arrival, as has been shown for Yellow-bellied Sapsucker (Walters et al. 2002) and Red-naped Sapsucker (see below).

RED-NAPED SAPSUCKER. Pair formation within 3 wk of arrival (Hadow 1977). In British Columbia, arrives late Mar or early Apr (Campbell et al. 1990); paired by at least third week of Apr (EHM, ELW).

Nest-building. *RED-BREASTED SAPSUCKER.* Excavation begins in late Apr–early May in sw. British Columbia (Kelleher 1963) but presumably occurs earlier (prior to 25 Apr, date of earliest nests) elsewhere in British Columbia (Campbell et al. 1990; see below).

RED-NAPED SAPSUCKER. Excavation begins within 3 wk of arrival (Hadow 1977); by at least third week of Apr in British Columbia (EHM, ELW), in mid-May in Montana (McClelland and McClelland 2000) and central Nevada (S. A. Fleury pers. comm.). Excavation can be delayed due to cold or other inclement weather (EHM).

First/only brood per season. Figure 4. *RED-BREASTED SAPSUCKER.* Egg-laying as early as 25 Apr (calculated) in British Columbia; young in nest from 10 May to 20 Jul (n = 109; Campbell et al. 1990).

RED-NAPED SAPSUCKER. At Hat Creek, British Columbia, mean clutch-initiation date of 25 May (range 18 May–16 Jun, n = 22) in one year; 29 May (range 22 May–15 Jun, n = 18) in another; overall mean hatch date 11 Jun (range 2–28 Jun, n = 40), mean fledge date of last chick 10 Jul (range 30 Jun–29 Jul, n = 40; ELW, EHM). In central Nevada, mean date of clutch initiation for 1-yr-old females 6 Jun ± 5.77 SD (n = 13); for 2-yr-old females, 28 May ± 7.16 SD (n = 16); and for 3-yr-old females, 31 May ± 8.10 SD (n = 9; Fleury 2000, S. A. Fleury pers. comm.). First chicks hatch in early Jun in Colorado (Hadow 1977), mid-Jun in central Nevada (S. A. Fleury pers. comm.). Young fledge second week of Jul in Colorado, third week of Jul to early Aug in Wyoming (Hadow 1977), mid-Jul to early Aug in Montana (McClelland and McClelland 2000) and central Nevada (S. A. Fleury pers. comm.).

Second brood per season. *RED-BREASTED SAPSUCKER.* No records of second broods; presumably will renest if first fails early in breeding season (as in Red-naped Sapsucker, see below).

RED-NAPED SAPSUCKER. No records of second broods, but pairs sometimes renest if first nest fails (EHM, ELW).

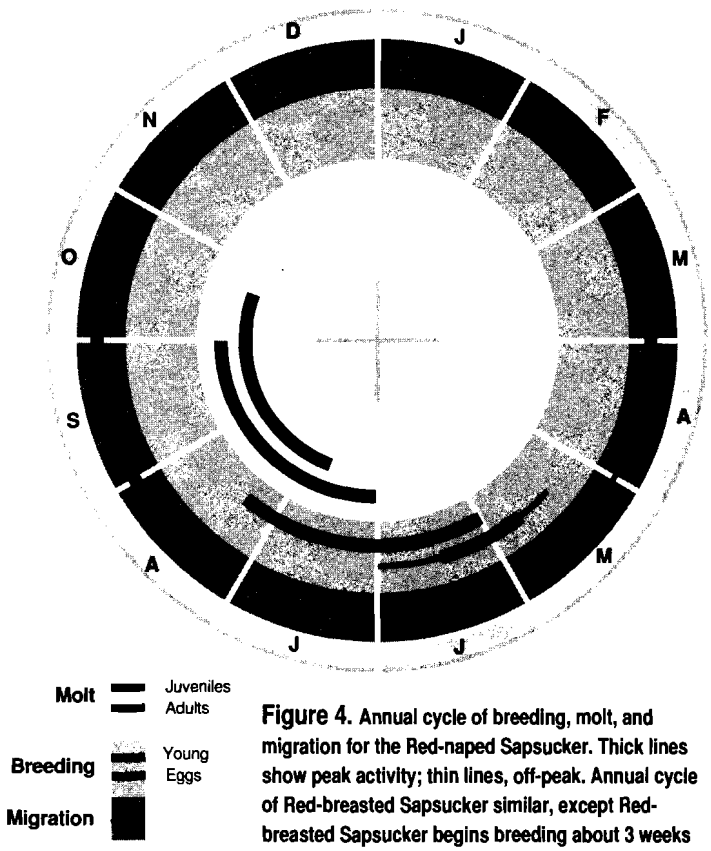


Figure 4. Annual cycle of breeding, molt, and migration for the Red-naped Sapsucker. Thick lines show peak activity; thin lines, off-peak. Annual cycle of Red-breasted Sapsucker similar, except Red-breasted Sapsucker begins breeding about 3 weeks earlier, extent of molt ending 1 month sooner and timing of fall movements not well known and some populations resident.

NEST SITE

Selection process. *RED-BREASTED SAPSUCKER.* No information.

RED-NAPED SAPSUCKER. Nest site apparently chosen based on proximity to foraging areas rather than on characteristics of nest tree stand (Crockett and Hadow 1975). Adults often return to breeding site of previous year, often same tree and sometimes same cavity (Fleury 2000, EHM, ELW). Initial cavity or tree may be abandoned during excavation and another selected (Walters 1996).

Microhabitat. *RED-BREASTED SAPSUCKER.* Nest cavities made in dead trees or dead portions of live trees. On n. Vancouver I., British Columbia, tree species selected all dead, included western white pine and hemlock (Joy 2000). In another British Columbia sample, 38 of 69 nests in dead trees (Campbell et al. 1990). In w. Oregon, most birds (18 of 20) nested in snags with >48 cm dbh, with preference for snags in more advanced class of decay (Mannan 1977). In nw. California, 46 of 49 nests in snags or dead portions of live trees (Raphael and White 1984). Tree species used include quaking aspen (central British Columbia; Zimmerman

Table 1. Characteristics of nest trees of Red-breasted and Red-naped sapsuckers. Data shown as mean ± SD (*n*) or mean (range, *n*).

Species/location Tree species[2]	Tree height (m)	DBH[1] (cm)	Nest height (m)	Reference
RED-BREASTED SAPSUCKER				
British Columbia				
Western white pine	32.5 ± 13.4 (31)	93.3 ± 25.6 (31)	17.2 ± 8.5 (32)	Joy 2000
Broadleaf maple (5/10)	19.4 ± 8.0 (10)	72.8 ± 28.2 (9)	13.4 ± 5.0 (10)	Kelleher 1963
Deciduous species (45/69)			(1.8–24.3, 72)	Campbell et al. 1990
Quaking aspen (16/16)		(25–36.6, 16)		Zimmerman 1998
Oregon				
Douglas-fir		93 (36–216, 20)	20.6 (6.1–43.3, 20)	Mannan 1977
RED-NAPED SAPSUCKER				
British Columbia				
Quaking aspen (55/56)	17.2 ± 5.9 (56)	28.8 ± 7.1 (56)	5.67 ± 3.50 (155)	Walters 1996, EHM, ELW
Quaking aspen		22.9 (14)[3]	(1.37–9.91, 60)	Erskine and McLaren 1972
Quaking aspen	18.4 ± 5.0 (159)	32.8 ± 7.6 (159)	8.0 ± 3.8 (159)	Harestad and Keisker 1989
Quaking aspen (134/273)		(15–64, 27)	(0.5–22.9, 284)	Campbell et al. 1990
Montana				
Western larch (84/125)	24.8 (3.5–50.6, 125)	59 (23–119, 125)	17.9 (1.4–42.7, 125)	McClelland and McClelland 2000
Nevada				
Quaking aspen (89/93)	11.9 ± 4.3 (85)	30.4 ± 8.7 (85)	4.4 ± 2.6 (87)	S. A. Fleury pers. comm.
Oregon				
Quaking aspen	14.6 ± 2.5 (25)	27.4 ± 8.0 (25)	4.2 ± 1.5 (25)	Dobkin et al. 1995
Colorado				
Quaking aspen (51/51)		23.3 (17.3-31.0, 40)	2.9 (1.1–5.3, 40)	Crockett and Hadow 1975
Arizona				
Quaking aspen (20/20)		37.1 ± 5.83 (20)	13.3 ± 3.62 [sic] (20)	Li and Martin 1991

[1]DBH = diameter at breast height.
[2]Tree species of most frequent nest tree identified; numbers indicate frequency of most common species out of total number of trees.
[3]Diameter of trunk at cavity.

1998); broadleaf maple, Douglas-fir, western hemlock, cottonwood, Engelmann spruce (*Picea engelmanni*; sw. British Columbia; Kelleher 1963); white fir, lodgepole pine, red fir, quaking aspen, Douglas-fir, and Pacific madrone (*Arbutus menziesii*; nw. California; Raphael 1987, Raphael and White 1984).

Considerable overlap in characteristics of nest sites among Red-breasted and Red-naped sapsuckers nesting in hybrid zone in central Oregon; same-species pairs did not differ from interspecific or hybrid pairs in nest-site selection (n = 80), but interspecific pairs showed tendency to select shorter trees than did same-species pairs (n = 42; Trombino 1998).

RED-NAPED SAPSUCKER. Nest cavities in both dead and live trees. In areas abundant with quaking aspen, most nests in live trees (30 of 33 [Daily 1993], 46 of 56 [Walters 1996], 16 of 20 [Li and Martin 1991]). Dead trees more often used in conifer-dominated forests (McClelland and McClelland 2000). Prefers trees infected with heartwood decay fungus (*Phellinus tremulae* [= *Fomes igniarius* var. *populinus*): all of 21 in Colorado (compared with only 8 of 20 trees infected adjacent to nest trees; Daily 1993); 54 of 55 in British Columbia (but only 10 trees exhibited conks [fungal fruiting body] on trunk; Walters 1996); 33 of 51 in Colorado and Wyoming (Crockett and Hadow 1975); all of 125 in Montana (external evidence in 73 of 84 larch and 26

of 30 birch; McClelland and McClelland 2000). Heart rot enters quaking aspen at base of tree; sapsucker holes tend to be higher in tree each successive season as heart rot moves up tree: mean cavity height 2.7 m (n = 11) if only cavity in tree, if >1 cavity in tree, mean height of active cavity 6.0 m (n = 22; Daily 1993). At Hat Creek, British Columbia, however, only 18 of 48 nests (where >1 cavity in tree) in highest cavity; when nest tree used in subsequent year, only 16 of 28 nests higher than previous nest (EHM, ELW). Heartwood decay in larch enters near broken top of snags, and sapsuckers consequently excavate progressively lower in successive seasons (McClelland and McClelland 2000). Quaking aspen most frequently listed nest tree (Crockett and Hadow 1975, Harestad and Keisker 1989, Daily 1993, Walters 1996, Table 1); other species include western larch (*Larix occidentalis*), lodgepole pine, Douglas-fir, grand fir (*Abies grandis*), ponderosa pine, paper birch (*Betula papyrifera*), Engelmann spruce, subalpine fir, western hemlock, western red cedar, and black cottonwood (Bull 1980, Tobalske 1992, McClelland and McClelland 2000).

Site characteristics. *Red-breasted Sapsucker.* On n. Vancouver I., British Columbia, nest trees taller and with greater diameter than trees not used (Joy 2000). Of 25 nests in snags found on East Limestone I., Queen Charlotte Is., British Columbia, median nest height 30 m (range 15–50; A. J. Gaston pers. comm.). In nw. California, most nests (48 of 50) >5 m high (Morrison et al. 1983). See also Table 1.

Red-naped Sapsucker. Diameter of nest tree varies according to location, usually larger-diameter trees selected for nesting; tends to avoid trees <25–29 cm dbh class, preferring 30–34 cm dbh class (Harestad and Keisker 1989); but in areas where available aspen were smaller (mean dbh 22.6 cm ± 1.56 SD; n = 2,528), nested in trees with mean dbh 28.8 cm ± 9.43 SD (range 17.2–45.1, n = 56; Walters 1996). Cavity heights ranged from 0.7 m to 22.9 m (n = 155; EHM, ELW). Minimum tree sizes (dbh) for sapsucker nests reported: 17.2 cm (n = 56; Walters 1996), 17.3 cm (n = 51; Crockett and Hadow 1975), 20.1 cm (n = 159; Harestad and Keisker 1989), and 23 cm (n = 125; McClelland and McClelland 2000). See Table 1.

NEST

Construction process. Male does most of cavity excavation; female often sits at cavity entrance facing cavity and may preen while male is away. In some cases, each member of pair excavates in separate trees and each may start several cavities before one site finally selected; mechanism of selection unknown. Female participation in excavation increases as season progresses; construction any time between dawn and dusk (EHM, ELW). Period of excavation varies from 6 d to 2 wk (Howell 1952) to at least 3–4 wk (EHM, ELW).

Structure and composition matter. Eggs laid on bed of wood chips created by pecking sides and bottom of cavity (EHM, ELW).

Dimensions. *Red-breasted Sapsucker.* For 22 nests in British Columbia, mean width of cavity entrance 4.6 cm ± 0.5 SD (range 3.9–5.7), mean height 4.7 cm ± 0.5 SD (range 4.3–5.4), mean depth of cavity 24.8 cm ± 4.5 SD (range 14.1–34.2; Joy 2000, J. Joy pers. comm.). For 13 nests in California, mean diameter of cavity entrance 3.8 cm ± 0.47 SD, mean cavity depth 17.9 cm ± 3.5 SD, inside width 10.7 cm ± 2.7 SD (Raphael and White 1984).

Red-naped Sapsucker. For 14 nests in Cariboo Parklands of British Columbia, mean entrance width 3.8 cm, mean height 4.1 cm, mean cavity depth 16.5 cm, mean inside width 12.1 cm (Erskine and McLaren 1972). For nests at Hat Creek, British Columbia, mean entrance width 3.8 cm ± 0.4 SD (range 3.2–4.7, n = 42), mean height 4.2 cm ± 0.6 SD (range 3.3–5.7, n = 16; EHM, ELW). For 25 nests in Oregon, mean entrance width 4.0 cm ± 0.5 SD, entrance height 4.6 cm ± 0.5 SD (Dobkin et al. 1995). For 22 nests in Nevada, inside cavity depth 10.6 cm ± 2.2 SD, internal width 11.7 cm ± 2.3 SD (S. A. Fleury pers. comm.). Entrance hole often just large enough for adult sapsucker; e.g., radio-transmitter only 5 mm in thickness, attached interscapularly, prevented adult sapsucker from exiting nest cavity (ELW).

Microclimate. *Red-breasted Sapsucker.* No information on degree of exposure or insulative value of nest. Large snags may provide greater insulation when night temperatures <0°C during breeding season. On Vancouver I., nest orientation not different from random (n = 32; Joy 2000).

Red-naped Sapsucker. At Hat Creek, British Columbia, all cavities (n = 14) on noticeably leaning trees faced direction of lean (Walters 1996); in se. Oregon, 9 of 11 cavities similarly on underside of lean (Dobkin et al. 1995). Cavities may tend to southern orientation (British Columbia, 222.6° ± 83.75 SD [n = 71; Walters 1996]; Colorado, 170° [n = 36; Inouye 1976]; sw. Saskatchewan, 169.4° ± 16.23 SD [n = 27; Kalcounis and Brigham 1998]); and most face southward (Colorado and Wyoming; Crockett and Hadow 1975), east or southwest (se. Oregon [n = 25; Dobkin et al. 1995]), or show no directional preference (Arizona [n = 20; Li and Martin 1991]; Montana [n = 135; McClelland and McClelland 2000]). No information on insulative value of nest.

Maintenance or reuse of nests. *Red-breasted Sapsucker.* Nest cavity not reused (n = 17; Joy 2000); trees that harbor cavities from previous years are used (Kelleher 1963).

Red-naped Sapsucker. In quaking aspen habitat in British Columbia, 15 of 56 nests in old cavities (Walters 1996); in Nevada, 30 of 86 in old cavity in subsequent year (S. A. Fleury pers. comm.); in Colorado, 3 of 33 cavities reused (Daily 1993); in Montana, 6 of 42 in same cavity in subsequent year (McClelland and McClelland 2000).

Nest tree often used in successive years but new cavity excavated (see Nest site, above). In Montana, 22 of 42 nest trees reused in successive year; as consequence of tree reuse, larch trees had up to 40 sapsucker cavities (mean 4.0 cavities / tree ± 5.96 SD; n = 84) and birch trees up to 10 cavities (mean 2.0 cavities / tree ± 1.92 SD [n = 30]; McClelland and McClelland 2000). In Nevada, 13 of 36 males and 10 of 31 females reused same nest tree (Fleury 2000; see also Demography and populations: range, below).

Nonbreeding nests. *Red-breasted Sapsucker.* No information.

Red-naped Sapsucker. Typically several excavations started before settling on final cavity. At Hat Creek, British Columbia, within eventual nest tree, mean of 1.7 new excavations (range 0–6, n = 71) besides nest excavation; of new excavations, mean 0.8 (range 0–2, n = 55) functional cavities; within territory, 0–14 (n = 57) other new excavations, among which 0–3 (n = 54) functional cavities (EHM, ELW). In Colorado, 67% (n = 33) of nests in trees with nest cavities of previous years (Daily 1993). In British Columbia, 91% (n = 55) of nest trees had other cavities present (Walters 1996). Many sapsucker cavities remain empty in subsequent years or occupied by other bird and mammal species (Erskine and McLaren 1972).

EGGS

Shape. *Red-breasted Sapsucker.* Ovate to elliptical-ovate or rounded-ovate (Bent 1939).

Red-naped Sapsucker. Ovate to elliptical-ovate or rounded-ovate (Bent 1939).

Size. *Red-breasted Sapsucker.* For 100 eggs from 20 clutches of *S. r. ruber*, mean size 23.6 (range 21.3–25.7) × 18.0 mm (range 16.4–19.9); for 95 eggs from 20 clutches of *S. r. daggetti*, mean size 23.2 (range 20.6–25.9) × 17.6 mm (range 16.6–18.8; Western Foundation of Vertebrate Zoology [WFVZ] data).

Red-naped Sapsucker. For 110 eggs from 22 clutches, mean size 22.7 (range 20.2–26.8) × 17.2 mm (range 15.7–18.2; WFVZ data).

Mass. *Red-naped Sapsucker.* Mass of fresh egg approximately 3.8 g (Schönwetter 1967); full clutch about 26–61% of female's body mass (Fleury 2000).

Color. Pure white (Howell 1952).

Surface texture. *Red-breasted Sapsucker.* Little or no gloss (Bent 1939).

Red-naped Sapsucker. Moderately glossy (Bent 1939).

Eggshell thickness. *Red-breasted Sapsucker.* No information on thickness. Mean mass of empty shell for *S. r. ruber*, 0.28 g (range 0.20–0.34, n = 100); for *S. r. daggetti*, 0.25 g (range 0.20–0.30, n = 95; WFVZ data).

Red-naped Sapsucker. No information on thickness. Mean mass of empty shell 0.24 g (range 0.20–0.29, n = 110; WFVZ data).

Clutch size. *Red-breasted Sapsucker.* Mean clutch size 4.69 ± 0.72 SD (n = 42); not correlated with latitude (Koenig 1986). Range 4–7 (Short 1982).

Red-naped Sapsucker. Mean clutch size 4.77 ± 1.09 SD (n = 17); not correlated with latitude (Koenig 1986). In Nevada, mean clutch size 4.8 ± 0.13 SE (range 3–7, n = 54; S. A. Fleury pers. comm.). At Hat Creek, British Columbia, mean clutch size 4.82 ± 0.75 SD (range 3–7, n = 55); mean clutch size in old holes (5.15 ± 0.99 SD; range 4–7, n = 13), significantly larger (p = 0.04) than mean clutch size in new holes (4.61 ± 0.69 SD [range 3–6, n = 28]; EHM, ELW).

Egg-laying. *Red-breasted Sapsucker.* Eggs laid after cavity excavation completed (Howell 1952); no specific information, likely similar to Red-naped Sapsucker.

Red-naped Sapsucker. For 42 clutches at Hat Creek, British Columbia, eggs laid 1 egg / d in 29 clutches; among remaining 13 clutches, 13 occurrences in 12 clutches of 2- to 4-d laying interval, and 6 occurrences in 6 clutches of 2 eggs laid within 24-h period; clutch may be replaced if lost, but individual eggs are not (EHM, ELW). Adults quiet and often away from nest during beginning of egg-laying period. No evidence of intraspecific egg-dumping (EHM, ELW; but see Behavior: sexual behavior, above).

INCUBATION

Onset of broodiness and incubation in relation to laying. Adult Red-naped Sapsuckers frequently observed in cavity for extended periods on or after day that second egg laid (EHM, ELW); point at which incubation actually begins unknown.

Incubation patch. Both sexes have well-developed brood patch (Howell 1952).

Incubation period. *Red-breasted Sapsucker.* At 1 nest attended by hybrid (but close to Red-breasted Sapsucker) adults, incubation at minimum 11 d; this observation likely basis for general statement of "approximately" 14 d (Howell 1952: 248); 14–15 d (Short 1982).

Red-naped Sapsucker. At Hat Creek, British Columbia, assuming incubation begins on day last egg laid, mean incubation period 10.3 d ± 0.98 SD (range 8–12, n = 33; EHM, ELW).

Parental behavior. Nest rarely unoccupied during incubation; adults reluctant to leave nest even when objects placed in cavity or tree struck (Howell 1952, EHM, ELW). Both sexes incubate at intervals of 5–90 min, vocalizations mark changeover (see Sounds: nonvocal sounds, above); male stays in cavity from dusk to dawn and presumably incubates (Short 1982).

Hardiness of eggs against temperature stress; effect of egg neglect. No information. Loss of adult usually results in nest failure (EHM, ELW).

HATCHING

Preliminary events and vocalizations. Young sapsuckers <1 d old capable of faint cheeping (Howell 1952, EHM, ELW; see Sounds: vocalizations, above).

Shell-breaking and emergence. Red-naped Sapsucker clutches hatch within 24-h period (EHM, ELW). One case of egg capping where shell of hatched egg covered over another egg that did not hatch (S. A. Fleury pers. comm.).

Parental assistance and disposal of eggshells. Little information. Adults remove eggshells and unhatched eggs, usually within few days of hatching. At Hat Creek, British Columbia, all eggs of 1 clutch removed from cavity and thrown to ground at base of nest tree 6 d after clutch completion; embryonic development appeared retarded (EHM, ELW; see also Parental care, below).

YOUNG BIRDS

Condition at hatching. Altricial and nidicolous; pink in color (Howell 1952).

Growth and development. *Red-breasted Sapsucker*. At 7 d, eyes not open and unopened pinfeathers appear in major feather tracts; at 10 d, eyes half open; at 14 d, fully feathered (Howell 1952). No information on control of body temperature.

Red-naped Sapsucker. At Hat Creek, British Columbia, for young 12–17 d old, mean mass 41.9 g ± 5.0 SD (n = 40); for young 20–24 d old, mean mass 46.8 g ± 5.3 SD (n = 77; EHM, ELW). No information on control of body temperature.

PARENTAL CARE

Brooding. Both sexes brood and remain brooding until relieved by mate from hatching until 6 d; after 6 d, parents rarely brood (Howell 1952).

Feeding. Summarizing observations in ne. California (Howell 1952): both adults feed young, but no coordination exists between parents; from hatching until 6 d, adult always enters cavity to feed; from 6 to 16 d, adult enters cavity to feed young but exits without waiting for mate; after 16 d, adults do not enter cavity to feed young but male enters to remove fecal material and to roost over night; food of young identified as primarily insects (ants, plus caterpillars and mayflies) and spiders. Feeding visits every 7 min for first 5–6 d; afterward, feeding visits up to every 2 min from dawn until dusk.

Nest sanitation. Chicks defecate in nest, presumably in response to prodding by male, who removes fecal sacs, usually to particular tree near nest (Howell 1952, Wible 1960); this tree (sanitation post) used for duration of nesting period and may be used by same male in subsequent year (ELW). Hippoboscid flies frequently associated with Red-naped Sapsucker nests (EHM, ELW; see also Demography and populations: disease and body parasites, below).

Carrying of young. Not known to occur. Red-naped Sapsuckers observed carrying eggs, but context of behavior indicates eggs were food source rather than as nest-moving behavior: 1 individual fed upon sapsucker egg wedged into bark of tree; unknown if egg came from sapsucker's own nest or from that of another (Cooper 1992, EHM); adult removed egg from its own damaged cavity and ate it (Flanagan 1911); adult carried unidentified egg to tree (Wible 1960).

COOPERATIVE BREEDING

Only 2 incidents of helping behavior documented. Nest observed 42 h over 38 d attended by 3 adults (male Red-breasted Sapsucker, female Red-naped Sapsucker, and female hybrid [appearance close to Red-breasted Sapsucker]) in ne. California; at least 8 eggs and reared 5 young (all males; 1 Red-breasted Sapsucker, 1 Red-naped Sapsucker, 3 intermediate plumage; Howell 1952). Also, 3 Red-breasted Sapsucker adults observed feeding young at Oregon nest (Trombino 2000).

BROOD PARASITISM

Not known to occur.

FLEDGLING STAGE

Departure from nest. *Red-breasted Sapsucker*. Leaves nest at age 23–28 d (n = 4); fully feathered and capable of limited, gliding, flight when first departing nest (few to 70 m); during last week in nest, nestlings frequently make clapping sound (produced by opening and closing beak rapidly); during 2–3 d before fledging, young give occasional calls (likely *Waa* Calls; see Sounds: vocalizations, above) similar to those of adults and frequently extend one-half to two-thirds of their bodies out of nest; young leave nest individually and often spread out over a few days (Howell 1952).

Red-naped Sapsucker. At Hat Creek, British Columbia, last chick leaves nest at 28.3 d ± 1.74 SD

(range 23–32, $n = 31$) of age; among 39 broods, all young fledged on same day in 13 broods; over 2 d for 22 broods; and over 3 d for 4 broods (EHM, ELW).

Growth. *Red-breasted Sapsucker.* Young usually within 1–2 g of adult mass when fledging, but wings and tails much shorter than adults' (Howell 1952). No information once young leave nest.

Red-naped Sapsucker. No information.

Association with parents or other young. Once fledged, parental behavior variable; some adults very attentive to young birds while others appear indifferent. Parents appear to try to lead just-fledged offspring to higher elevations or to vicinity of sap wells. Parents continue to feed young that still remain in nest while attending to fledged individuals (Howell 1952). In Red-naped Sapsucker, family group remains together for at least a week in vicinity of nest after fledging (Hadow 1977).

Ability to get around, feed, and care for self. *Red-breasted Sapsucker.* Young fed by parents after fledging but not regularly; young try to feed on their own almost immediately (Howell 1952).

Red-naped Sapsucker. Young frequently observed at sap wells within 2 wk of fledging; often observed being fed insects by adults (ELW). Juveniles able to forage on own soon after leaving nest (Tobalske 1992).

IMMATURE STAGE

No information.

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding; intervals between breeding. Red-naped Sapsucker, and presumably Red-breasted Sapsucker also, can first breed at 1 yr and annually thereafter; some individuals do not reproduce until 2 yr old (Fleury 2000, EHM, ELW). One female at Hat Creek, British Columbia, at least 5 yr old, appeared to be post-reproductive; she paired with male, but no eggs laid in his roosting cavity (EHM, ELW).

Clutch. Clutch size usually 4 or 5 eggs. See Eggs: clutch size, above.

Annual and lifetime reproductive success. At Hat Creek, British Columbia, for 196 eggs laid in 41 Red-naped Sapsucker nests, 122 young survived to 12 d of age (EHM, ELW). In 3-yr Nevada study, for 266 eggs laid in 56 nests, 214 hatched and 34 young survived to leave the nest (Fleury 2000, S. A. Fleury pers. comm.).

Losses of eggs or young due to infertile eggs, predation, loss of parent, unusually cold weather, and lack of arthropods to feed young (EHM, ELW). Also see Causes of mortality, below.

Number of broods normally reared per season. One; except if first brood fails, replacement clutch sometimes laid (EHM, ELW).

Proportion of total females that rear at least one brood to nest-leaving or independence. Over 3 yr in Nevada, 63 of 85 Red-naped Sapsucker nests fledged ≥1 young; nesting success 77% ($n = 24$ for 1-yr-olds) to 92% ($n = 22$ for 3-yr-olds; S. A. Fleury pers. comm.). Over 3 yr at Hat Creek, British Columbia, 58 of 67 Red-naped Sapsucker nests produced young (Walters 1996).

LIFE SPAN AND SURVIVORSHIP

Red-breasted Sapsucker. In s. Oregon, 27 of 51 Red-breasted and 17 of 29 Red-naped sapsuckers returned in following year with average longevity 2–3 yr; return rate of hybrid individuals lower, only 11 of 51 individuals returned (Trombino 1998); failure to return, however, not necessarily indicative of mortality.

Red-naped Sapsucker. Maximum longevity at least 6 yr; estimated survival for first year (from fledge date to 1 yr old), 0.02–0.27; survival for third year (from 2 to 3 yr old), 0.46–0.71; and survival for fourth year (from 3 to 4 yr old), 0.40–0.60 (Fleury 2000). In Nevada, 56 of 131 adults and 1 of 82 young returned in following year (Fleury 2000); at Hat Creek, British Columbia, 34 of 72 adults and 8 of 141 young returned in following year (EHM, ELW). Most adults that survive migration presumed to return to previous breeding locality; individuals dispersing beyond study areas not recorded, making estimates of survivorship difficult. No information on dispersal rate of young, but few return to natal areas (EHM, ELW; see also Range, below).

DISEASE AND BODY PARASITES

Diseases. No information.

Body parasites. Recorded ectoparasites include mite *Pteronyssoides simplex* (Acari) from Red-breasted Sapsucker (Banks 1905), bird flea *Dasypsyllus gallinulae perpinnatus* (Siphonaptera) from Red-breasted Sapsucker (Holland 1984), biting lice *Penenirmus auritus* (Phthiraptera) from both Red-breasted and Red-naped sapsuckers (Emerson 1972, D. C. Arnold pers. comm.), and louse fly *Ornithomyia fringillina* (Diptera: Hippoboscidae) from both Red-breasted and Red-naped sapsuckers (Bequaert 1954). Also unidentified tick (4 mm diameter; Acarina) from Red-naped Spasucker (EHM, ELW). One Red-breasted Sapsucker examined for haematozoa, but none found (Williams 1978).

CAUSES OF MORTALITY

Exposure. Red-breasted Sapsuckers may be susceptible to very low ambient temperatures during winter months. Populations reduced following

extremely cold winters in Queen Charlotte Is., British Columbia (Guiguet 1954). Some Red-naped Sapsucker nests lost when tree falls or breaks at cavity entrance (McClelland 1977).

Predation. See Behavior: predation, above. Predation losses at Red-naped Sapsucker nests in Arizona ranged from 0 (n = 18; Martin and Li 1992) to 3.4% (Martin 1995), and at Hat Creek, British Columbia, from 12% (n = 25) to 20% (n = 30) for years with daily monitoring of nests (Walters and Miller 2001).

Competition with other species. House Wren may kill Red-naped Sapsucker nestlings to acquire nest cavity (Walters and Miller 2001).

RANGE

Initial dispersal from natal site. In Nevada, distance between site of fledging and first breeding for 2 returning juvenile male Red-naped Sapsuckers, 1,456 and 3,129 m; for juvenile females, 1,746 m ± 814 SD (range 864–3,061, n = 5; Fleury 2000). At Hat Creek, British Columbia, dispersal distance for 4 returning juvenile male Red-naped Sapsuckers, 1,450 m ± 800 SD (range 750–2,350), for 4 juvenile females, 2044 m ± 1,572 SD (range 350–4,150; EHM, ELW). Most studies biased because researchers rarely search outside of their study areas.

Fidelity to breeding site and winter home range. In Nevada, all marked Red-naped Sapsuckers that returned to study site returned to <3 km of their adult banding site; 13 of 36 males and 10 of 31 females returned to same nest tree; 16 of 36 males and 13 of 31 females returned to <50 m of nest tree; 35 of 36 males and 30 of 31 females to same canyon (Fleury 2000). At Hat Creek, British Columbia, all marked Red-naped Sapsuckers that returned to study site, returned to <1 km of their adult banding site; 7 of 29 males and 7 of 27 females returned to same nest tree; 16 of 29 males and 11 of 27 females returned to <50 m of nest tree (EHM, ELW).

Dispersal from breeding sites. In Nevada, dispersal distance for returning breeding adult Red-naped Sapsucker males was 229 m ± 516 SD (range 0–2,685, n = 36); for females 246 m ± 523 SD (range 0–2,685, n = 31; Fleury 2000); and at Hat Creek, British Columbia, dispersal distance for males was 125 m ± 182 SD (range 0–600, n = 29) and for females 219 m ± 222 SD (range 0–650, n = 27; EHM, ELW).

Home range. See Behavior: spacing, above.

POPULATION STATUS

Numbers. *Red-breasted Sapsucker.* Breeding Bird Survey (BBS) census data for routes with highest counts were 26.3 birds/route in Masset, Queen Charlotte Is., British Columbia; 20.3 in Mitkof I., AK; and 5.7 in Los Angeles Co., CA (Price et al. 1995). Estimated population, prior to European settlement, in Douglas-fir forests of nw. California 49,400 birds; estimate in 1988 for same area approximately 15% less, and populations expected to decrease with continued timber harvest (Raphael et al. 1988). Maximum potential density in Douglas-fir forests of Coast Range of Washington and Oregon modeled as 11.3 pairs/40 ha (Neitro et al. 1985). In w. Oregon, density estimates in winter in managed Douglas-fir forests 2–4 birds/40 ha and in riparian areas 4 birds/40 ha; during breeding season, these values 3–5 birds/40 ha and 22 birds/40 ha, respectively (Mannan 1977; despite Neitro et al.'s [1985] projection). In central Oregon, density estimates 0.44–1.16 birds/40 ha (Bate 1995). In Douglas-fir forests of nw. California, densities range from 1.3 to 2.0 birds/40 ha depending on age of forest (Raphael et al. 1988).

Red-naped Sapsucker. BBS census data for routes with highest counts were 9.1 birds/route in Grand Forks, British Columbia, 7.6 in Oliver, British Columbia, and 7.0 in Valley Co., ID (Price et al. 1995). At Hat Creek, British Columbia, density estimated at 4 birds/40 ha in riparian areas of suitable habitat (EHM, ELW). In n.-central British Columbia, Red-naped Sapsucker second-most abundant cavity-excavating species (68 of 201 cavities surveyed; Martin and Eadie 1999).

Trends. Trends measured by BBS data suggest no changes in population from surveywide data for *varius* superspecies for 1966–2000, but statistically significant trends noted for 2 states for period 1966–2000: Red-breasted Sapsucker—Oregon with a positive trend: +3.6%/yr, n = 63 routes, p = 0.03; California with negative trend: –2.9%/yr, n = 62 routes, p = 0.02 (Sauer et al. 2001). No Red-naped Sapsuckers present in Toiyabe Range, NV, for period before 1940 to 1950 (Dobkin and Wilcox 1986; see also Conservation and management: effects of human activity, below); now this species second most abundant woodpecker in Toiyabe Range (Fleury 2000).

POPULATION REGULATION

Little information. Pair of Red-breasted Sapsuckers in sw. British Columbia collected during excavation on 14 May was replaced by another pair by 3 Jun (Kelleher 1963). Red-breasted Sapsuckers fluctuate greatly in numbers, being the most numerous species in one year and almost absent in another (Guiguet 1954). Large numbers of sapsuckers may die in British Columbia during exceptionally cold winters when sap of coniferous trees freezes (Ziller and Stirling 1961). See Causes of mortality, above.

In extreme drought conditions, Red-naped Sapsuckers absent from breeding areas in Utah and s. Idaho (Smith 1982a).

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Red-breasted Sapsucker. Little information. See Demography and populations: population status, above. Historically considered a pest in orchards, and shot as a result (McAtee 1911); no longer the case.

Red-naped Sapsucker. Historically considered pest in orchards; in Washington, "whole orchards of young apple trees [*Malus* sp.] have been destroyed" (McAtee 1911: 20). No sapsuckers present in Toiyabe Range, NV, for period before 1940 to 1950 or later (see Demography and populations: population status, above) due to quaking aspen cut for mining purposes and creation of extensive logging roads (Dobkin and Wilcox 1986). Habitat degradation of riparian areas over past decades due to livestock grazing and fire suppression reduced available habitat in Intermountain West for sapsuckers because of habitat loss and degredation (Dobkin et al. 1995). Recent harvesting of quaking aspen for furniture and chopsticks has further reduced available habitat (ELW). Nest trees have been cut down for firewood during breeding season, especially snags (McClelland 1977, Mills et al. 2000). Little affected by vehicle traffic when nesting alongside roads; some breeders abandon nests if banded early in nesting cycle, but once feeding young there is low probability of abandonment because of banding; otherwise little disturbed by investigators' presence (EHM, ELW).

MANAGEMENT

Protected under Migratory Bird Treaty Act in U.S. and Canada. Willamette National Forest Plan includes provision to manage forests for 40% of potential maximum population densities of Red-breasted Sapsucker with range of 15.8–19.8 birds/100 ha (Bate 1995). Estimate 112 snags needed to manage Douglas-fir habitat for maximum density of 28 pairs of Red-breasted Sapsuckers/100 ha (Neitro et al. 1985).

APPEARANCE

MOLTS AND PLUMAGES

Plumage and molt descriptions based on Ridgway 1914, Short 1982, Kaufman 1990, Pyle and Howell 1995, Pyle 1997, and examination of specimens.

Hatchlings. Naked at hatching.

Juvenal plumage. Acquired by complete Prejuvenal (postnatal) molt. No information on timing and sequence of Prejuvenal molt except occurs before fledging.

In both species, wing and tail as in Definitive Basic (adult) plumage, except outer primaries (P6–P9) more tapered, outermost primary (P10) longer and broader, rectrices more pointed, and tail with more barring than in adults.

RED-BREASTED SAPSUCKER. Body plumage overall appearance dark or olive-brown; back more black, often with black-and-white mottling; rump with more barring on white areas; and sides and flanks with more extensive dark or olive-brown markings. Underparts mainly or completely dark brown or black. No white in throat; red tint over breast and throat. Sexes similar. Plumage of *S. r. ruber* darker above than *S. r. daggetti.*

RED-NAPED SAPSUCKER. Body plumage overall appearance dark or olive-brown; back more black, often with black-and-white mottling; rump with more barring on white areas; and sides and flanks with more extensive dark or olive-brown markings. Belly unmarked, pale yellowish white in midline; flanks dull brownish with dark or olive-brown barring. Lower throat, neck, and breast pale brown with scallop-shaped dusky bars. Head brown with dark-brown to slate crown, ear-coverts and throat; narrow buffy-white lines above and below eye usually present, throat paler than in adults. Males may have some red feathers in chin, forehead, and crown.

Basic I plumage. Molt pattern for both species similar except for timing. Acquired by incomplete Prebasic I (Postjuvenal) molt primarily on summer grounds. None to a few inner lesser and medium wing-coverts replaced. All other feathers replaced. Occasional individuals (hybrids with *S. varius*) may retain a few Juvenal body feathers. Red-breasted Sapsucker molts Jun–Sep, Red-naped Sapsucker Jun–Oct.

RED-BREASTED SAPSUCKER. Basic I plumage similar to Definitive Basic plumage except for presence of retained Juvenal feathers.

RED-NAPED SAPSUCKER. Similar to Definitive Basic plumage, except for presence of retained Juvenal feathers.

Basic II plumage. Molt pattern for both species similar, except for timing. Acquired by incomplete Prebasic II molt. Includes all wing-coverts and primaries, all or most rectrices, and 0–outermost 1 or 2 primary-coverts; 1–6 secondaries retained, usually in a block among S1–S6, and often symmetrically on both wings. Red-breasted Sapsucker molts Jun–Sep, Red-naped Sapsucker Jun–Oct.

Similar to Definitive Basic plumage, except that feathers of earlier plumages retained.

Definitive Basic plumage. Molt pattern for both species similar except for timing. Definitive Prebasic molt seldom (if ever) complete; 1–5 secondaries often retained among S1–S8, seldom in a block and less often symmetrically on both wings. Red-

breasted Sapsucker molts Jun–Sep, Red-naped Sapsucker Jun–Oct (Fig. 4).

Red-breasted Sapsucker. S. r. ruber: Head, neck and breast vermilion red (few if any black markings present), except eye narrowly bordered in front and on lower half with black; short, dull yellowish white or pale dull buffy mustachial stripe extends from nasal tufts back through anterior portion of lores and under front and middle portion of black band (this stripe sometimes continues more distally but distal portion is whitish red in color); and base of lower mandible narrowly bordered with black feathers. Back, scapulars, and rump black, except both sides of upper back (sometimes extending to inner scapulars) sparsely, and irregularly marked with dull yellowish white bars; lower back similarly marked but markings white; and center of rump heavily marked with white. Upper tail-coverts black, except inner web and distal portion of outer web (including tip) white; and white area greatest on innermost feathers. All rectrices pointed; R1 slightly pointed, but R2–R5 with attenuated tips which increase in extent inwardly. Rectrices black except inner webs of central pair (R1) barred with white, and outermost 2 pairs (R4, R5) tipped and edged on outer web with cinnamon buff, and occasionally with small cinnamon buff subterminal spots. Wings black except as follows. Middle and distal portions of median-coverts, and outer webs of inner greater-coverts (but restricted to tips of innermost feathers) white, forming an elongated white patch on the wing; all primaries (except P9 and vestigial P10) and outermost secondaries barred on outer web with white; primaries and secondaries edged at tip with white; and distal portion of tertials variably white along shaft and at tip. Remaining underparts straw yellow or yellowish white, except sides, flanks, and under tail-coverts with dark gray V-shaped bars, although in some individuals dark markings on proximal sides are streaks rather than V-shaped bars.

S. r. daggetti similar to *S. r. ruber* except as follows. Red markings average slightly paler; black head markings like in other sapsucker species may be evident on ear-coverts, sides of crown, and elsewhere; pure white portion of mustachial streak sometimes extends more distally to beyond rear of eye; yellowish white underparts paler (this character not always evident in faded specimens); red of breast extends as reddish wash onto upper belly so that red and yellowish white underparts not as cleanly separated as in *S. r. ruber*; back, and rump with heavier pale markings and these tend to be white not yellowish (although some individuals clearly yellowish white), and white markings on wings greater in extent, including tertials which are often barred with white.

Sexual differences. Sexes alike in both subspecies except pale markings on tail average more extensive in females than in males, but sexes overlap. In females with greatest amount of pale markings on tail, inner webs of central pair (R1) largely white, becoming cinnamon buff distally, and narrowly barred black (except attenuated tip entirely black); attenuated tip of R3 cinnamon buff; outermost 2 rectrices (R4, R5) margined distally with cinnamon buff and with a one or more subterminal bar-like spots of same color on distal portion of inner web and any portion of outer web. Some females of *S. r. daggetti* (and perhaps occasionally *S. r. ruber*) also have white mottling at center of outer rectrices. Female tail variable and some may show almost entirely black outer rectrices, but males apparently do not show the extensive pale subterminal markings on outer rectrices exhibited by some females (Pyle 1997).

Red-naped Sapsucker. Male forehead and crown bright poppy red or crimson, bordered by occipital crescent of glossy blue-black, extending laterally to above middle of eye; hindcrown black; red patch on nape; chin, malar region, and throat bright poppy red (feathers with white bases). Band of white from nasal tufts extending below eye to side of neck; narrower band of white from behind eye to red patch on nape; red malar region bordered along proximal portion with black. Back and scapulars black faintly glossed with greenish blue, broken by heavy spotting of white or brownish white, white prevailing on sides of back, black prevalent in center of back; rump and upper tail-coverts mostly black on sides and mostly white in center; tail black, inner web of central pair of rectrices (R1) white with several oblique black spots or bars, terminal margins of outer rectrices white; wings black; median-coverts (except at base), and outer webs of inner greater-coverts (but restricted to tips of innermost feathers) white, forming conspicuous patch; all primaries (except P9 and vestigial P10) and outermost secondaries barred on outer web with white; primaries and secondaries edged at tip with white; tertials barred mainly on inner web with white. Red throat bordered distally by crescent-shaped black patch whose apex ends on center of lower breast. Underparts (posterior to black crescent-shaped patch) pale yellow; sides and flanks dull white or brownish white with black V-shaped marks. Under tail-coverts white.

Female similar to male, except usually (90% of females) chin and upper throat white (but sometimes with red mottling) and malar region with little to no red; some females have completely red chin and throat, but rare; outer rectrices usually with pale tip and some pale mottling.

Table 2. Linear measurements (mm) and mass (g) of representative samples of adult Red-breasted Sapsuckers (*S. r. ruber*) from population on Queen Charlotte Is., British Columbia (EHM), and Red-naped Sapsuckers from population at Hat Creek, British Columbia (EHM, ELW), except tail-length measurements (from Ridgway 1914 for Red-breasted Sapsucker and Short and Morony 1970 for Red-naped Sapsucker). Data shown as mean ± SD (*n*) or mean (range, *n*).

	Red-breasted Sapsucker	Red-naped Sapsucker
Bill length[1]		
Male	25.1 ± 2.15 (20)	22.5 ± 1.20 (50)
Female	23.7 ± 2.06 (21)	22.6 ± 1.21 (51)
Wing length		
Male	131 ± 3.67 (20)	126 ± 4.16 (27)
Female	131 ± 3.21 (21)	128 ± 2.55 (26)
Tail length		
Male	78.9 (72–81.5, 10)	74.5 (69.7–78.9, 24)
Female	81.5 (78.5–85, 10)	76.7 (74.0–82.5, 11)
Tarsal length		
Male	21.6 ± 0.56 (14)	21.4 ± 1.55 (25)
Female	21.5 ± 0.51 (18)	21.2 ± 0.61 (26)
Body mass		
Male	58.3 ± 5.23 (23)	50.5 ± 4.71 (48)
Female	57.7 ± 4.50 (22)	49.2 ± 4.27 (49)

[1]Exposed culmen.

BARE PARTS

Bill and gape. Black (EHM, ELW).

Iris. Red-breasted Sapsucker, dark brown; Red-naped Sapsucker, brown (Short 1982).

Legs and feet. Red-breasted Sapsucker, grayish; Red-naped Sapsucker, greenish gray (Short 1982).

MEASUREMENTS

LINEAR

See Table 2. No sexual dimorphism for Red-breasted Sapsucker except for populations on Queen Charlotte Is., British Columbia (see Systematics: geographic variation; subspecies, above); northern subspecies *S. r. ruber* larger than southern subspecies *S. r. daggetti*. No geographic variation in size and no sexual dimorphism evident in Red-naped Sapsucker (Pyle 1997).

MASS

See Table 2. In Red-naped Sapsucker, adult mass decreases during breeding cycle when feeding young (EHM, ELW), but overall seasonal variation not described.

PRIORITIES FOR FUTURE RESEARCH

Nothing is known of sapsucker physiology. At times, sap may constitute 100% of the diet for these species. The criteria by which trees are chosen for sap wells is not known. Trees may be selected because they are entering senescence and sapsuckers can take advantage of additional amino acid content of their sap (L. S. Eberhardt pers. comm.). Interaction between tree and sapsucker is understood only generally. Red-breasted Sapsucker, especially, is in need of more study for most aspects of its life history. Most studies of sapsuckers have been made during the breeding season, with only limited observations on behavior within nest cavities of either species. Much remains to be learned about behavior and ecology of these species during other times of the year. Little is known about dispersal of young from their natal area (and researchers' study sites). Studies using color-banded individuals would help gain better insight into dispersal and survivorship. Likewise, travels of migrating individuals are not known. Future studies should also build upon earlier work to examine changing dynamics of hybrid zones among all species in the *S. varius* sapsucker complex. More studies that examine population trends, especially on regional scales, are needed.

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