

Habitat and space use of the Red-naped Sapsucker, *Sphyrapicus nuchalis*,
in the Hat Creek valley, south-central British Columbia.

by


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B.Sc., University of Victoria, 1990

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We accept this thesis as conforming
to the required standard



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ABSTRACT

As a double keystone species, Red-naped Sapsuckers (*Sphyrapicus nuchalis*) play a crucial role within the communities they are found, yet overall habitat use is poorly known. A study of habitat and space use of Red-naped Sapsuckers was undertaken in the Hat Creek valley of south-central British Columbia, Canada. Individual adult birds were radiotagged and then tracked to measure site fidelity, habitat use, and overall movements. Sapsuckers were shown to exhibit a home range both on a daily and multiday level and thus, home ranges were determined by the minimum convex polygon method ($\bar{x} = 13.23$ ha \pm 3.767 SE, n=10).


Willow (*Salix bebbiana*, *S. prolixa*, *S. drummondiana*, *S. scouleriana*) was found to be an important habitat for sap feeding, live heart rot (*Phellinus igniarius*)-infected Trembling Aspen (*Populus tremuloides*) was important for nesting, and large (>30 cm diameter at breast height) Douglas-fir (*Pseudotsuga menziesii*) for insect gleaning.

Birds nested among significantly larger and denser aspen relative to availability. Nests were usually excavated in the year they were used, tended to face southwest, and were usually in a tree that harboured several other cavities

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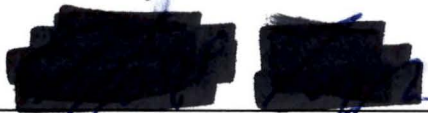
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DEDICATION

To my parents, Karen and Larry Walters, whose appreciation of the outdoors was instilled in me at a very young age. They have given me the opportunity to explore the natural world, through their unending belief in me and my abilities.

This thesis is also dedicated to two very special people, Catherine Mutter and Michelle Wardley: their love, support, and friendship will not be forgotten.

INTRODUCTION

We live in a time when conservation issues and maintenance of biodiversity are of paramount concern. At the current rate of species extinctions, we can expect 50% of the world's species to go extinct by the year 2100 (Scudder, 1993). Because forests provide habitat for roughly half of the estimated 10-80 million forms of life on Earth (Ryan, 1992), loss of forested areas will result in loss of species. Since preagricultural times, temperate forests have lost 32-35% of their area (W.R.I., 1990). To combat continued loss of species because of forestry practices, regulations such as the Forest Practices Code (Ministry of Forests, 1995) have been created. Forest managers find themselves maintaining a delicate balance between species conservation and timber production. In order that these land managers can make informed decisions, it is imperative that they are provided with basic information concerning the species to be managed. This information can take the form of life-history traits, habitat requirements, or other baseline data.

Recently there has been a movement toward managing species, by managing the communities in which they are found, at the landscape level (*e.g.* Forest Practices Code of British Columbia Act) rather than on a species-by-species basis. One method, within this context, has been the use of vertebrates as indicators of habitat quality for other species (Landres *et al.*, 1988). Some authors (*e.g.* Burkey, 1989) have suggested that by managing for keystone species (*sensu* Paine, 1969), we can maximize biodiversity protection (*cf.* Mills *et al.*, 1993). A keystone species is defined as “one whose impact on its community or ecosystem is large, and disproportionately large relative to its

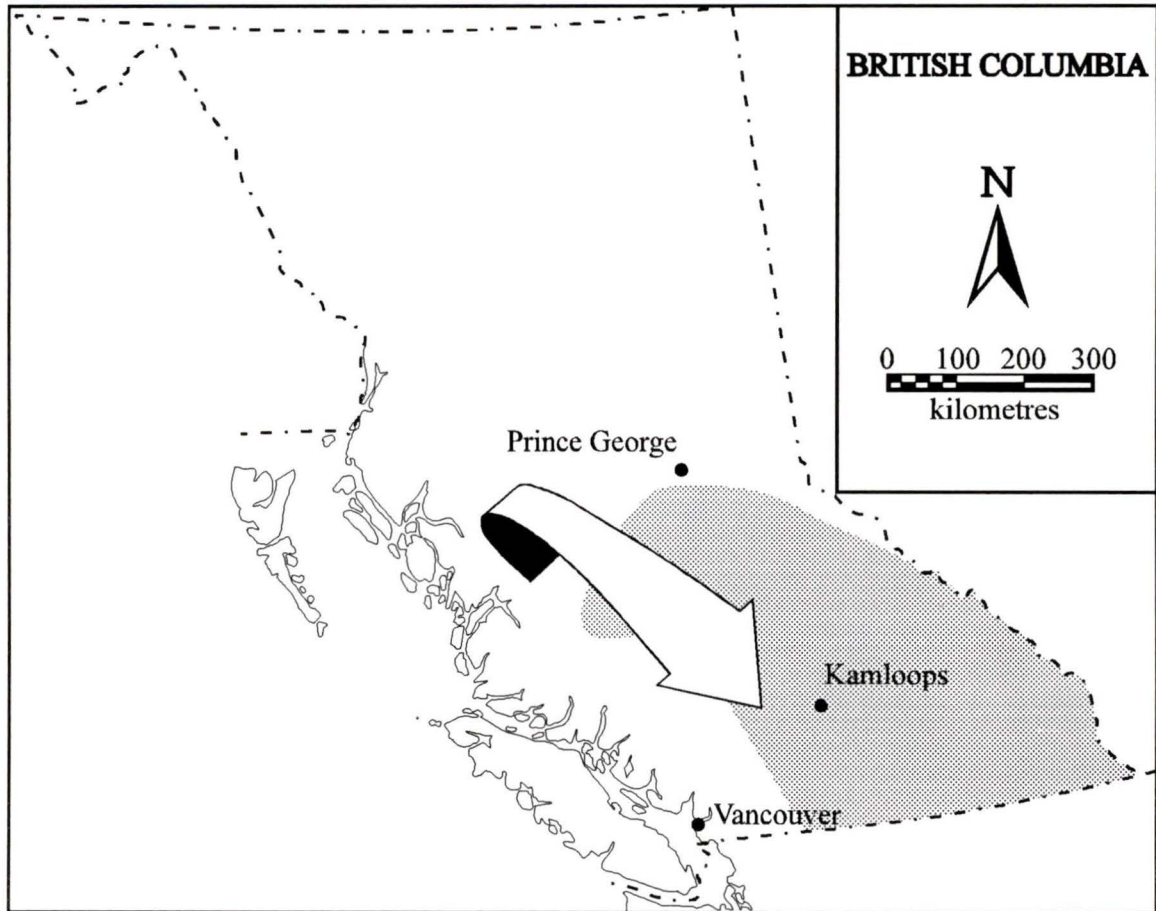
abundance” (Power *et al.*, 1996, p. 609). Sometimes the impact is so large that communities may be dominated by these keystone species (Menge *et al.*, 1994).

Two avian species have been classified as keystone within the communities in which they are found: the Lesser Snow Goose (*Chen caerulescens*) was first recognized as such by Kerbes *et al.* (1990) and subsequently the Red-naped Sapsucker (*Sphyrapicus nuchalis*) was labelled a “double keystone bird in a keystone species complex” by Daily *et al.* (1993, p. 592). The latter was considered to be a keystone species because of its nesting and foraging habits (Daily *et al.*, 1993).

During the spring (March - April) Red-naped Sapsuckers migrate northwards from their wintering grounds in northern Mexico and the southwestern United States (Howell, 1953). They breed primarily in the Rocky Mountain region in forests containing aspen in pure stands or mixed with conifers, rarely breeding in predominantly coniferous forests (Howell, 1952). Within British Columbia, *S. nuchalis* breeds chiefly south of Prince George and east of the Fraser River (Figure 1-A). Fall migration takes place in the early part of September and may continue into October (Howell, 1952).

Upon arrival at the breeding grounds pairs establish and set about excavating a cavity (*i.e.* they are primary cavity nesters), usually in live aspens (*Populus tremuloides*) that are infected with the heart rot fungus, *Phellinus igniarius* (Kilham, 1971). Cavities made by

Figure 1-A. Breeding distribution of Red-naped Sapsuckers in British Columbia (after Campbell *et al.*, 1990) showing location of Hat Creek study site.



sapsuckers usually outnumber all those made by other primary cavity nesters by an order of magnitude (Daily *et al.*, 1993). Secondary cavity nesters, by definition, usually do not excavate their own cavity (*e.g.* bluebirds, starlings, swallows) because they lack the morphological characteristics necessary. Most of the secondary cavity nesters use natural (*i.e.* not created by an excavator) cavities or those excavated by woodpeckers (Cunningham *et al.*, 1980). Thus, sapsuckers provide nest cavities for secondary cavity-nesting species (*i.e.* the first purported keystone role). It has been demonstrated that two obligate secondary cavity nesters (Tree Swallows, *Tachycineta bicolor* and Violet-green Swallows, *Tachycineta thalassina*) are dependent upon a co-occurrence of sapsuckers (Daily *et al.*, 1993). The alleged keystone complex thus consists of aspens, heartwood fungus, and sapsuckers. Daily *et al.* (1993) firmly believe that the disappearance of any one element would result in local extinction of the swallow species.

Taxonomically, sapsuckers are a specialized group of four species (Williamson's, *S. thyroideus*,; Red-breasted, *S. ruber*; Yellow-bellied, *S. varius*, and Red-naped) within the family Picidae. They have evolved an ability to procure sap from trees (Tate, 1973). This habit of extracting sap by incision of plants is not very common among vertebrates. Only 8 other vertebrate species are known to extract sap in this manner (Eberhardt, 1994). Potential host trees are examined and some are then actively pecked at to facilitate sap flow (Foster and Tate, 1966; Eberhardt, 1994) but the criteria used by the birds to ultimately determine which tree will be used to create wells within is unknown. The birds must return to this food source throughout the day to ensure that the conductive tissues are disrupted because plants will normally stop flow (*i.e.* heal) within several hours of

injury (Ehrlich and Daily, 1988; *cf.* Eberhardt, 1994). No fewer than 48 species of birds, 30 groups (species and families) of insects, and 6 species of mammals have been associated with sapsucker wells (Foster and Tate, 1966; Tate, 1973; Ehrlich and Daily, 1988; Rissler *et al.*, 1995). This resource can play an important role in the life histories of the organisms feeding upon the wells, especially during times of reproduction or fat storage prior to migration or hibernation. Some species (*e.g.* Ruby-throated Hummingbird, *Archilochus colubris*, and Rufous Hummingbird, *Selasphorus rufus*) appear to be limited in terms of distribution and timing of migration based on the availability of sapsucker sap wells (Miller and Nero, 1983). Thus, these sap wells (*i.e.* sapsuckers' second alleged keystone role) form another part of the so-called keystone complex to which sapsuckers belong (Daily *et al.*, 1993).

It appears that sapsuckers may play a large role with respect to species composition within the communities they are found. Elucidating habitat needs of sapsuckers both to manage this species and understanding the role they play within communities (*i.e.* their interactions with others species, both directly and indirectly) is important. This keystone species management approach to maintain biodiversity may be attractive because of its inherent cost effectiveness (*i.e.* we essentially manage for a community of species at the cost of managing for one) and its ability to unite the best features of single-species and ecosystem management (Simberloff, In Press).

A second approach to maintaining biodiversity within forests has been developed. Stand-level planning focuses on, but is not limited to, plant species composition and stand

structure through the retention of so-called “wildlife trees” (Fenger, 1996). Wildlife trees are defined, for example, by the Wildlife Tree Committee of British Columbia (1997, p. 1-3) as any “standing dead or live tree with special characteristics that provide valuable habitat for the conservation or enhancement of wildlife”. Many studies have shown the importance of wildlife trees, especially for birds (*e.g.* Raphael and White, 1984; Li and Martin, 1991). In British Columbia, wildlife trees support 16% of the province’s vertebrate fauna (Steger *et al.*, 1996). Sapsuckers are considered users of wildlife trees based on their habit of excavating cavities within dying aspens.

One could suggest that sapsuckers may play an important role in the maintenance of biodiversity within forested communities, based on either a keystone species or wildlife tree approach. Until recently (1983), *S. nuchalis* was considered as a subspecies of *S. varius* (A.O.U., 1983). Most studies have concentrated on the latter; thus, very little is known about the life-history traits of *S. nuchalis*. Effective conservation of species requires identification of specific habitat features and associated resources that directly influence reproduction or survival (Martin, 1992). This study examines the space used by breeding sapsuckers and then relates these findings to relative habitat use. Specific habitat associated with foraging and nesting are determined. Knowing whether or not Red-naped Sapsuckers are keystone species is important if we are going to manage forests within which sapsuckers are found using a keystone species management approach. This study merely assumes that sapsuckers are keystone species and makes no attempt at confirming or refuting this classification. Determining the strength of species interactions within the communities in which sapsuckers are found is beyond the scope of this thesis.

Organisms select habitat on several levels of spatial scale (Schneider, 1994). Johnson (1980) coined the terms *first-, second-, third-, and fourth-order selection*; to reflect some of these levels. He defined *first-order* habitat selection as the overall physical or geographical range of a species. Within that range, *second-order selection* refers to the distribution of an individual or social group. *Third-order selection* is the use of habitats within the range of an individual or social group. *Fourth-order selection* applies to highly selective local use of a site (*e.g.* the procurement of food items at a particular location). Thus, there is a continuum of scales to which habitat use can be measured against. In this study, I investigate habitat use by sapsuckers in terms of the overall nesting habitat available (*i.e.* by pooling the habitat found around each nest across all nests; analogous to Johnson's second-order selection) and in terms of the within-nest habitat available (analogous to third-order selection).

Chapter One of this thesis addresses the question of home range and space use. To determine habitat needs at the within-nest site scale, it is necessary to know if a species uses particular areas repeatedly and to what extent those areas are used. Such an area can loosely be termed a "home range", an area that can both be measured spatially and characterized ecologically.

Chapter Two examines in detail the habitats used by sapsuckers within and across nests. Information collected by following individuals with mounted radiotags is documented. The movement data are then analyzed by comparing habitat use with habitat availability. Foraging activity within each habitat type is discussed.

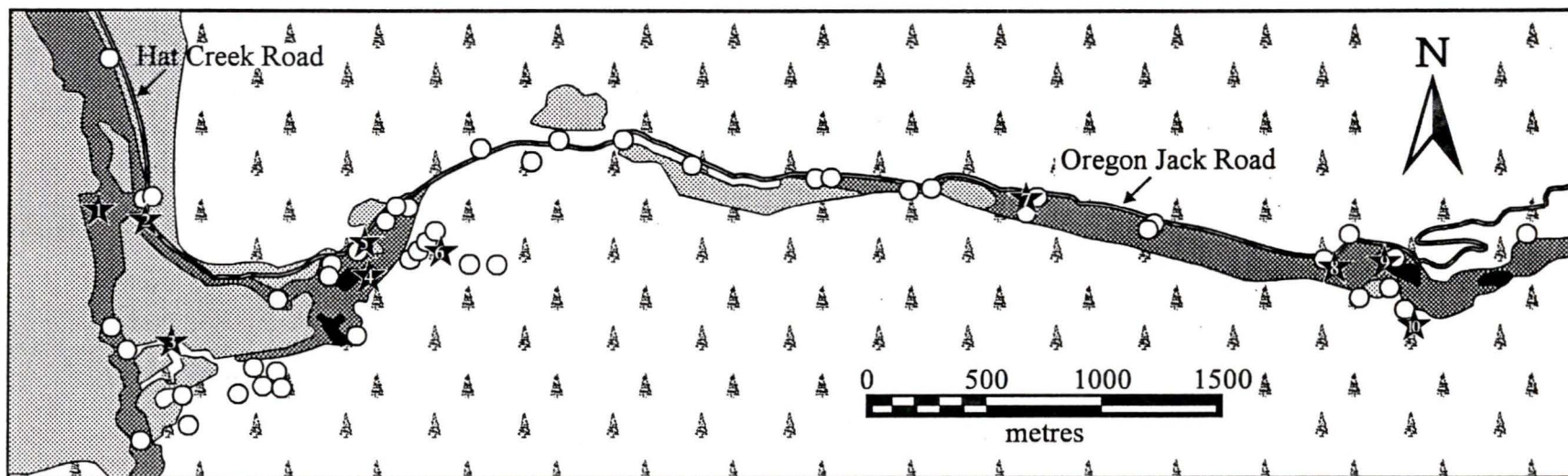
Chapter Three treats nesting habitat. The nest tree is quantified and compared with available habitat within the territory (*i.e.* the defensible area around a nest). Other factors that could influence nest site selection are examined, including tree health, cavity orientation, and nest placement.







Study Site

This study was conducted in the Hat Creek valley (centered at 50°38'N 121°32'N), approximately 23 km SW of Ashcroft, British Columbia at an elevation of approximately 1,158 m (Figure 1-A). The study site is located in the Hat Creek and Oregon Jack valleys in the Interior Douglas-fir biogeoclimatic zone and consists of approximately 1,350 hectares (Figure 1-B). The valley bottoms are quite narrow (approximately 500-1,000 m wide) with riparian areas running most of their lengths. At several locations the creek has been dammed by beavers (*Castor canadensis*) and forms both large and small ponds. The slopes of the valleys consist of open forests dominated by Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*) and, to a lesser extent, by lodgepole pine and trembling aspen. Pine grass (*Calamagrostis rubescens*) grows under most of the trees on the slopes because there is little understorey due to cattle grazing. The valley bottoms contain mainly shrubby deciduous thickets interspersed with forested and open areas. Vegetation of the valley bottoms consists mainly of willow (*Salix bebbiana*, *S. prolixa*, *S. drummondiana*, *S. scouleriana*), trembling aspen, hybrid white spruce (*Picea engelmannii* x *glauca*), Rocky Mountain juniper (*Juniperus scopulorum*), lodgepole pine (*Pinus contorta*), black cottonwood (*Populus trichocarpa*), swamp birch (*Betula pumila*), water birch (*Betula occidentalis*), choke cherry (*Prunus virginiana*) and mountain alder (*Alnus tenuifolia*).

Within the study area, many species of vertebrates use tree cavities for protection and to raise young within. Such avian species include Barrow's Goldeneye (*Bucephala*

Figure 1-B. Map of study site showing locations of all nest trees from 1992-1994 (white circles), nest sites of radiotagged birds (black stars) and habitat types (open field, riparian, forest, and beaver pond).



- | | |
|---|--|
|  open field |  sapsucker nest site |
|  riparian |  sapsucker nest site (radiotelemetry) |
|  forest | |
|  beaver pond | |

islandica), Bufflehead (*Bucephala albeola*), Common Merganser (*Mergus merganser*), American Kestrel (*Falco sparverius*), Flammulated Owl (*Otus flammeolus*), Northern Saw-whet Owl (*Aegolius acadicus*), Northern Flicker (*Colaptes auratus*), Red-naped Sapsucker, Downy Woodpecker (*Picoides pubescens*), Hairy Woodpecker (*Picoides villosus*), Pileated Woodpecker (*Dryocopus pileatus*), Tree Swallow, Violet-green Swallow, Mountain Chickadee (*Parus gambeli*), Black-capped Chickadee (*Parus atricapillus*), Red-breasted Nuthatch (*Sitta canadensis*), House Wren (*Troglodytes aedon*), Mountain Bluebird (*Sialia currucoides*), European Starling (*Sturnus vulgaris*), and House Sparrow (*Passer domesticus*). Besides birds, several mammals also use cavities at Hat Creek and these include Red Squirrel (*Tamiasciurus hudsonicus*), Northern Flying Squirrel (*Glaucomys sabrinus*), and *Myotis* spp.

CHAPTER 1

The use of space by Red-naped Sapsuckers in the Hat Creek valley, British Columbia.

Introduction

The concept of “home range” was popularized by Burt (1943), who defined it as “that area traversed by the individual in its normal activities of food gathering, mating and caring of young” (*Ibid*, p. 351). The notion of home range has some limitations because it cannot be easily defined operationally or characterized (Cooper, 1978; Spencer *et al.*, 1990). For this reason, a better definition has been proposed by Spencer *et al.* (1990) who define a home range as the planar region that an individual exhibits fidelity toward.

The concept is used extensively in wildlife biology because it embraces ecologically important aspects of habitat use and resource selection, population density, feeding and reproductive behaviour, etc. (Krebs, 1971; Schoener, 1968; Harris *et al.*, 1990). Some authors have been very critical of the term *home range* because it has been misused (*e.g.* Larkin and Halkin, 1994). Nevertheless, it has a common-sense flavour to it, and is heuristically valuable.

The area within which an individual or group moves, within some biologically relevant time frame (*e.g.* a breeding season, or a lifetime), can be quantified. Many analytic tools are available for estimating this area (Larkin and Halkin, 1994). This is the sense in which

the term “home range” is used hereafter. In this study, home range was estimated by use of radiotelemetry, a technique that was introduced in the late 1950s (LeMunyan *et al.*, 1959). Home range, using telemetry, typically describes two types of movements: the basic map of locations produced from tracking an individual and the numerical estimate of the area used by that same individual (White and Garrott, 1990).

Space use of Red-naped Sapsuckers is largely unknown. This study first attempted to determine whether site fidelity existed on a daily and multiday level, based on the definition provided by Spencer *et al.* (1990) mentioned above. If this fidelity was shown to exist then an estimate of home range was calculated.

Methods

In order to obtain an unbiased estimate of sapsucker movements during the nesting season I used the technique of radiotelemetry. Sapsucker nests were found by routine searches of the study site from late April until early June 1994. Once nest locations were determined, the sex and nest location of sapsuckers to be fitted with transmitters were chosen at random from those found. A net (made of plastic mesh attached to a conical wire frame) was suspended above the nest cavity using several nails and a length of fishing line which extended to the ground. The trap was lowered once the bird had entered the cavity by releasing the fishing line. This method involves both climbing the tree prior to capture to position the net and afterwards to remove the bird from the net. Only those individuals

which had laid full clutches were captured to reduce the probability of nest desertion. Trees that were not climbable were excluded because I could not confirm the stage of nesting nor could I capture the birds. Thus, my observations of birds carrying radiotags were restricted to 4 June - 21 July 1994.

Captured sapsuckers were fitted with radiotransmitters (BD-2G Holohil Systems Ltd, Woodlawn, Ontario) attached interscapularly (Hooge, 1991). The feathers of the *pteryla spinalis* were trimmed to 2-3 mm in the anterior region so as to maximize feather surface area, posterior to the nape of the neck. Cyanoacrylic glue (Superglue[®]) was placed on the ventral surface of the transmitter base and attached firmly to the trimmed feathers. Glue was placed on the dorsal surface of the transmitter base to allow the feathers of the *pteryla capitalis*, located on the nape region, to adhere and cause the transmitter to be hidden beneath the feathers. The transmitter was oriented such that the antenna followed the vertebral column to the distal tip of the two central tail retrices. Transmitters had a battery life of 4 months and fell off the bird 1-6 weeks after attachment. The transmitters weighed 1.9 g, so were <5% of adult body mass, which is commonly viewed as acceptable (see Caccamise and Hedin, 1985). This should result in <2.5% reduction in surplus power (the difference between power available for flight and the power required to fly at the most efficient velocity), based on a mass of 50 g (typical mass of nesting Red-naped Sapsuckers, unpubl. data) and thus is an acceptable experimental impact (Caccamise and Hedin, 1985).

After being fitted with transmitters, birds were not disturbed for at least 24 hours. Ten breeding individuals (5 males, 5 females) were each observed for 1-11 1-hour sampling periods ($\bar{x} = 5.3 \pm 1.01$ SE). Start times of the sampling periods were chosen by drawing times out of a hat. Initially, 17 sampling start times (rounded to the top of the hour) ranging from 0500 hrs PDT (approximate time that birds become active) until 2100 hrs PDT (1 hr before darkness when birds begin roosting) were placed in the hat. I chose these without replacement for the birds that were available (*i.e.* those with mounted radiotags) until no times remained. When the available start times were exhausted I put a second set of 17 times back in the hat. Birds were chosen in sequence so that all birds would be equally sampled. If times conflicted (*i.e.* there was not enough time to prepare for the next bird to be sampled) then I drew another start time. I had to allow time to travel to the nest, time to locate the bird, and time to label trees and take notes after the sampling period for each 1-hr sample. Thus, the actual time to obtain a 1-hr sample took about 3 hours when I factored in all the pre- and post-sampling activities. Typically, no more than 3 birds were sampled in any one day due to time constraints. Two observers tracked the birds simultaneously, using 3-element Yagi antennas and Wildlife Materials TRX-2000s receivers. The observers communicated with one another by walkie-talkies and hand signals. Typically one person would be located in the vicinity of the nest and the other would be near the foraging sites. However, this varied according to the bird's behaviour and our knowledge of its movement patterns. Bird locations were plotted every 10 minutes during the 1-hour sampling period. Special effort, however, was made to record locations continuously between the 10-minute sampling intervals to aid in more accurate estimates of home range. Visual contact was maintained wherever possible to

avoid biases associated with triangulation (Nams, 1989). When birds were not visible at the 10-minute intervals, their locations then were estimated by triangulation (if a signal was received) or by taking the midpoint of the nearest locations, before and after the 10 minute point. I marked trees with flagging tape during data collection and later measured distance of locations from the nest tree (*i.e.* I ignored the height of the bird above the ground). Distance measurements were made (± 1 m) using a 50 m Sokkia fiberglass tape measure. All data points were measured relative to the nest and converted to a cartesian system using a computer program (Microsoft Excel[®] spreadsheet) where the nest was considered the origin.

To determine the strength of site fidelity, I used a procedure developed by Munger (1984) modified by Danielson and Swihart (1987) and Spencer *et al.* (1990). A random path was generated for each individual, based on the observed distances between successive locations, on both a daily and multiday scale. For each individual, distances travelled between the 10-minute observations were calculated, then randomly chosen without replacement until none remained. In this way, the distances between locations remained the same, but the sequence of distances was different (*i.e.* I shuffled the distances). Each selected distance was associated with a randomly generated angle over the interval 0° to 359° to calculate the x and y coordinates for a random location. Taken in sequence, these random locations generate a random movement path. This procedure was repeated to yield 100 random movement paths for each daily and multiday period, for each individual.

Two measures were used to test for site fidelity. The first, mean squared distance (MSD) measures dispersion around the home range centroid (Calhoun and Casby, 1958; Schoener 1981). It is a measure of movement concentration and is defined as r^2 .

$$r^2 = [1 / (n - 1)] \sum_{i=1}^n r_i^2,$$

where n is sample size, and r_i is the i^{th} geometric distance to the centre of gravity.

$$r_i = [(x_i - \bar{x})^2 + (y_i - \bar{y})^2]^{1/2},$$

where (\bar{x}, \bar{y}) is the geometric centre.

$$\bar{x} = \sum x_i / n, \bar{y} = \sum y_i / n$$

The second measure of site fidelity used was the Linearity Index (LI). The LI = linear distance between the starting and end points of an animal's path / total distance travelled. Thus, a linear path would be equal to 1 and nonlinear meandering paths would be less than 1 (Bell and Kramer, 1979). MSD and LI were calculated for the actual path traversed by an animal for movement over daily and multiday periods.

For MSD and LI, the 100 values were ordered (from smallest to largest), thus forming an empirical sampling distribution with which observed values could be compared. Statistical significance was achieved if observed values were smaller (or larger) than the tenth (or ninetieth) percentile of the randomized distributions (see Danielson and Swihart, 1987). This value was chosen to balance type I and type II errors (Danielson and Swihart, 1987; Swihart and Slade, 1986; Toft and Shea, 1983). Because some of the random distributions did not meet the requirements of normality (Shapiro-Wilks, $p < 0.05$; SPSS), this ranking method seemed appropriate. The test was 2-tailed in order to test significance at both ends of the distribution. If, for example, observed values for LI were all significantly higher than those obtained for the random paths, this might bring in to question the methods being used to test for site fidelity.

The “shape” or symmetry of a home range was described by its eccentricity (ECC).

$$ECC = \sqrt{\lambda_1 / \lambda_2},$$

where λ_1 and λ_2 are the eigenvalues of the variance-covariance matrix of X and Y coordinates (Sokal and Rohlf, 1981; Bergstrom, 1988). For a circular range the ECC would be equivalent to 1 and values will increase as the home range becomes more elongate (Spencer *et al.*, 1990). As above, 100 simulation paths for both daily and multiday data were generated and compared with actual.

Locational data were tested for serial correlation to avoid pseudoreplication (*sensu* Hurlbert, 1984) using Schoener's ratio (t^2/r^2) where t^2 is the squared distance between two successive observations and r^2 is a measure of movement concentration as previously discussed (Swihart and Slade, 1985b). If Schoener's ratio departs significantly from 2 then data are said to be serially correlated (Schoener, 1981). A t-test was used to test Schoener's ratio obtained for each of the 10 radiotagged birds against the expected value (2) if data points are independent.

Home range was determined for individuals tracked based on the minimum convex polygon (MCP) method (Mohr, 1947). The polygon is constructed by connecting the outer locations to form a convex polygon and the area of this polygon is calculated. This method was chosen because it is known to be less sensitive to serially correlated data than probabilistic models of home range (Swihart and Slade, 1985a). Differences in the size of the polygon estimate between males and females was tested with a t-test (assuming unequal variances).

Results

Differences between observed and simulated movements for each individual were tested for each day (n=10 individuals, 53 1-hr samples) and each multiday period (n=9 individuals). About half of observed movements within days were smaller than simulated values (Table 1-A). Of those individuals whose movements were less than simulated values, none were consistently less in terms of MSD for *all* days and only 2/10 were consistently less with respect to LI (*i.e.* birds show variation in movement patterns across days). For multiday movements, 89% of empirical MSD values and 67% of LI values were less than simulated movement values. Under the criterion used to test the null hypothesis of random movement, only 10% of all animals should deviate from randomness by chance. Thus, these results are highly significant and indicate that movements are localized, both within and across days.

ECC for actual movements were significantly larger than simulated movements within days (27.1%) and across days (44.4%). Similar to the findings with respect to MSD and LI, no individual had actual home range shape (ECC) indistinguishable from that resulting from random movement for *all* days tracked, indicating that home range shape varied among days for each individual. When within-day movement patterns were compared with those across days, I found that 74% (37/50) of MSD and 52% (26/50) of LI values were less than multiday values. The opposite was true for ECC, where 59.6% (28/47) of within-day values were larger than those obtained across days.

Table 1-A. Measurement of mean squared distance (MSD, m²), linearity index (LI), and eccentricity (ECC) for each bird from actual movement patterns for within-day and across-day time periods with expected probability based on the simulated sampling distribution.

Bird	Within Days						Across Days					
	MSD	p	LI	p	ECC	p	MSD	p	LI	p	ECC	p
1a ^o	41156	0.01	0.33	0.31	1.06x10 ⁸	1.0	22227	0.01	0.22	0.01	3.28	0.54
1b	2489	0.37	1.00	-**	-	-***						
1c	2981	0.05	0.02	0.02	1.17	0.07						
1d	8303	0.04	0.17	0.13	3.00	0.59						
1e	2509	0.01	0.11	0.06	2.67	0.83						
1f	4093	0.60	0.25	0.20	5.27	0.90						
1g	40425	0.02	0.33	0.31	23.23	1.0						
1h	33315	0.01	0.07	0.05	4.64	0.85						
1i	64240	0.32	0.08	0.04	6.93	0.85						
1j	2234	0.83	0.92	0.96	4.98	0.79						
1k	457	0.02	0.25	0.02	91.71	1.0						
2a	1071	0.09	0.00	0.01	49.20	1.0	28851	0.01	0.08	0.01	2.52	0.93
2b	3870	0.01	0.14	0.04	3.27	0.60						
2c	3478	0.01	0.09	0.05	1.99	0.33						
2d	15455	0.17	0.18	0.09	2.14	0.27						
2e	6953	0.01	0.12	0.04	6.57	0.78						
2f	32960	0.02	0.06	0.04	2.82	0.76						
2g	10078	0.01	0.00	0.01	3.23	0.79						
3a	19409	0.82	0.72	0.46	16.46	0.96	205373	0.10	0.32	0.03	26.18	0.90
3b	24304	0.23	0.10	0.03	3.17	0.68						
3c	12739	0.21	0.00	0.01	5.26	0.84						
3d	53977	0.06	0.24	0.17	1.75	0.29						
3e	66975	0.01	0.16	0.18	4.64	0.91						
3f	3.51x10 ¹¹	0.38	0.28	0.22	8.87	0.99						
3g	-	0.71	-	-**	-	-***						
3h	-	-*	-	-*	-	-***						
4a	9858	0.39	1.00	-**	-	-	25083	0.01	0.27	0.01	2.89	0.80
4b	2002	0.04	0.19	0.17	1.94	0.52						
4c	9906	0.06	0.16	0.11	3.47	0.57						
4d	11960	0.20	0.00	0.01	4.96	0.74						
4e	41608	0.02	0.24	0.20	2.72	0.68						
4f	7829	0.01	0.00	0.01	1.31x10 ⁸	1.0						
4g	17706	0.82	0.96	0.76	10.85	0.75						
5a	9947	0.02	0.10	0.07	4.43	0.85	11220	0.01	0.44	0.11	4.75	1.00
5b	2278	0.02	0.26	0.15	2.86	0.67						
5c	13590	0.36	1.00	-**	-	-***						
5d	20689	0.82	0.97	0.84	11.00	0.85						
6a	8371	0.15	0.00	0.01	4.63	0.84	N/A	N/A	N/A	N/A	N/A	N/A
7a	5436	0.03	0.22	0.16	1.38	0.11	7154	0.02	0.30	0.21	2.05	0.57
7b	8927	0.21	0.41	0.36	11.28	0.99						

Table 1-A (cont'd).

Bird	Within Days						Across Days					
	MSD	p	LI	p	ECC	p	MSD	p	LI	p	ECC	p
8a	25176	0.22	1.00	-**	-	-***	72661	0.01	0.24	0.01	1.20	0.08
8b	39456	0.09	0.17	0.13	5.56	0.88						
8c	15659	0.25	0.48	0.68	3.00	0.63						
8d	56006	0.09	0.31	0.28	2.43	0.53						
8e	60702	0.03	0.00	0.01	5.81	0.99						
8f	24174	0.08	0.26	0.28	7.41	0.94						
8g	7729	0.07	0.31	0.22	2.58	0.57						
9a	380	0.60	0.73	0.43	2.95	0.31	41683	0.41	0.59	0.19	5.28	0.27
9b	55782	0.50	0.58	0.19	4.89	0.32						
10a	6728	0.06	0.32	0.33	10.70	1.0	13188	0.01	0.22	0.02	5.25	1.00
10b	9135	0.01	0.00	0.01	-	-***						
10c	17128	0.35	0.49	0.67	7.43	1.0						
10d	22634	0.01	0.16	0.03	4.62	0.88						
% sig. τ (p<0.10)		48.1		41.7		1.0	88.9		66.7		11.1	
% sig. τ (p>0.90)		0.0		0.0		27.1	0.0		0.0		44.4	

ω = bird identity with associated day (e.g. 1a refers to bird 1, day a)

ξ = 131210219.32

ψ = 106362225.04

* bird did not move during sampling period

** bird moved once hence all values = 1

*** bird moved once or not at all hence ECC could not be calculated

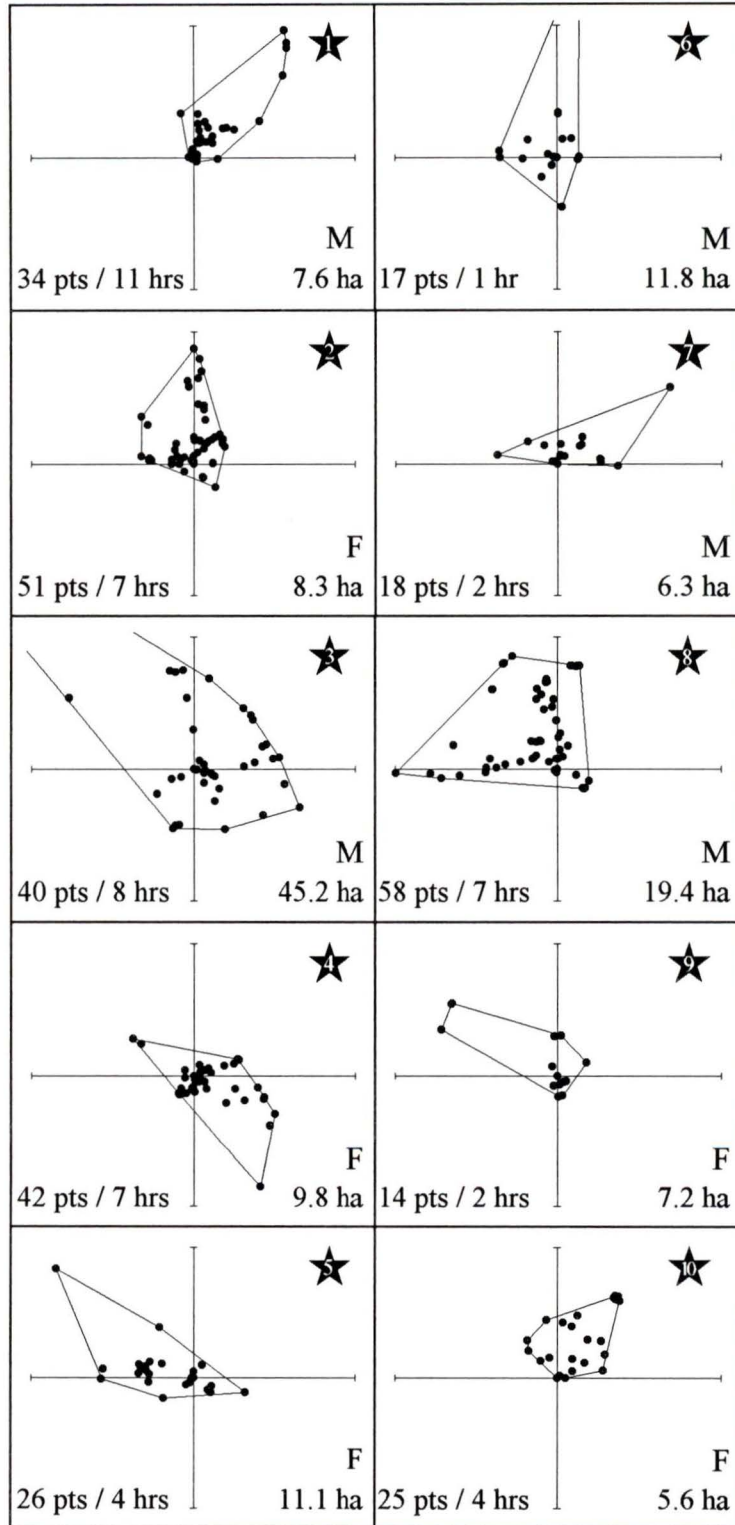
τ = overall significance (second-order mean) is calculated based on the mean % significant for each bird.

Given that home range existed (*i.e.* site fidelity was demonstrated), I calculated home range size estimates for all individuals (n=10). The MCP method was used because data points were found to be serially correlated ($\bar{x}_{r^2/r^2} = 1.27 \pm 0.140$ SE, $p < 0.001$, $t = 5.199$, $df = 9$). Data used for the calculation of MCPs included all locations observed (not just the 10-minute interval locations used for calculating MSD, LI, and ECC). The largest distance from the nest recorded was 1.4 km and >95% (325/332) of unique locations were within 500 meters of the nest. Home range size varied from 5.6 - 45.2 ha with mean of $13.23 \text{ ha} \pm 3.767$ SE (Figure 1-C). The range estimate for males ($\bar{x} = 18.06 \text{ ha} \pm 7.159$ SE) did not differ significantly ($p = 0.252$, $t = 1.33$, $df = 4.1$) from that of females ($\bar{x} = 8.40 \text{ ha} \pm 0.963$ SE).

Discussion

Red-naped Sapsuckers exhibited significant daily and multiday site fidelity, indicating that they had a home range at both scales. These results confirm what one would expect of a central place forager (*sensu* Orians and Pearson, 1977). That is, a bird caring for its young in the nest and, thus, using the nest as a centre of activity, should exhibit site fidelity on both daily and multiday time scales. Sapsuckers invest heavily in maintaining sap wells in willow and other tree species (Ehrlich and Daily, 1988; Eberhardt, 1994) and, hence, remain closely associated with the area around these investments. This fidelity would explain, too, the significant finding that MSD and LI were less than would be expected

Figure 1-C. Minimum convex polygon plots based on radiotelemetric locations for each bird monitored. Nests are located at the origin of the plot and locations within 500 m of nest, nest number, sex, number of unique points, hours observed, and size of polygon are indicated.



through random movement patterns. Lower MSD indicates more concentrated movement; lower LI indicates a tendency to meander off a linear path. If birds are attending young and visiting sap wells frequently one would expect lower MSD and LI. This too probably explains why so few unique points were found when tracking (Figure 1-C). Birds often returned to the same area during sampling observations, and sometimes even to the same individual tree or shrub. For example, most pairs actively maintained sap wells in certain willow clumps for several months (unpub. data).

All birds were shown to exhibit site fidelity but variation existed within birds among the days. These deviations could reflect innate differences among individuals or the influence of environmental factors (Spencer *et al.*, 1990). Nest placement within the study area relative to neighbouring pairs and proximity to potential foraging areas were probably factors affecting the measures obtained. This seemed particularly evident with respect to ECC values obtained for multiday samples. For example, the highest multiday ECC measurements came from nests where birds foraged far from their nests (*e.g.* bird 3 had a willow well 1.4 km away from the nest), where nests were located on the perimeters of large open spaces (*i.e.* non-utilized habitat - see Chapter 2; *e.g.* birds 1, 2 and 4), or where nesting territories were adjacent to nearby pairs resulting in the birds using foraging sites that favoured one particular direction (*e.g.* birds 5 and 9). Given that sapsuckers nested in patchy habitat, one would expect ECC to be greater than 1. Ford (1983) has shown that optimal range shape among central place foragers in patchy environments tends to be more elongate, but this surely depends on the juxtaposition of habitat. Nonetheless, my findings tend to agree with the predictions of Ford's model.

Comparison of daily with multiday values also shows that daily movement was more concentrated (lower MSD), slightly more meandering (lower LI), and more elongate (higher ECC) than corresponding multiday movement. This suggests that birds exhibit a slow shift in relative site fidelity over time. The measures of movement patterns are also confounded by the fact that adults increased their nest attendance as young grew (*i.e.* parents make more frequent feeding trips as the nestlings grow to meet the energetic demands of the young). This increased demand on parents means that they must forage more often and travel greater distances (Orians and Pearson, 1977).

Samples were taken at 10-minute intervals to maintain independence between sample points. Successive locations are said to be independent if the sampling interval is greater than the time it would take for the organism being sampled to travel the length of its home range (White and Garrott, 1990). Based on an estimated flight speed of 22-42 km/hr (Tobalske, 1996) a sapsucker could travel at least 3.67 km in 10 minutes, assuming constant flight. Given that Howell (1952) found that sapsuckers have an overall range of approximately 24 ha (assuming a circular range with radius of 274 m), it would take a bird 90 s to traverse that range and thus, my sampling interval of 10 min would satisfy the requisite. However, organisms do not necessarily travel at theoretical flight speeds. Despite my efforts to ensure independence of successive 10-min interval locations, the data points were serially correlated. Many studies ignore the serial correlation of data and merely enter values into home range statistical packages to obtain erroneous (*i.e.* they have violated assumptions inherent in the statistical technique) range estimates. For

example, in a review of 93 papers in 18 scientific journals, Harris *et al.* (1990) found that most were flawed with respect to analysis techniques (*e.g.* not assessing accuracy of location signal, ignoring autocorrelation effects, and not testing for adequate sample size).

Few estimates of home range exist for sapsuckers. My derived estimate (calculated from radius measurement) of 24 ha was based on the work of Howell (1952) in a hybrid zone between *S. ruber*, and *S. nuchalis* in California. Lawrence (1966) estimated 2.1-2.2 ha for *S. varius*. Further, Thomas *et al.* (1979) provided “territory” estimates of 2.1-4.9 ha for *S. nuchalis* but do not indicate their source for this data. My estimate of home range is higher than those previously published for *S. nuchalis* but my study is also the first to use telemetric techniques (and probably provides the best estimate to date).

Given that greater than 95% of sapsucker locations were within 500 m of their nests, one might hypothesize that home range would be approximately 78 ha (based on 500 m radius). However, as evidenced by the ECC values, sapsuckers have non-circular home ranges. As mentioned above, nesting birds do not utilize open areas such as lakes or agricultural fields. Thus, pairs nesting beside such habitat will tend to have asymmetric home ranges because birds, on average, are flying towards preferred habitat. Nesting sapsuckers may also be avoiding open habitat because of the risk of predation. For example, one of the radiotagged birds in my study (bird 8) that nested near a beaver pond was killed by a Cooper’s Hawk (*Accipiter cooperii*; unpub. data). Similarly, birds that are nesting near another conspecific pair will usually avoid entering that pair’s territory (presumably to avoid territorial conflict). If habitat were less patchy in my study site, one

might expect more symmetrical use of habitat and different home range size estimates as a result. Sapsucker nests in the Hat Creek valley are in aspen, that forms thin ribbons along the valley bottom, found within disturbed (*e.g.* road construction, beaver ponds, cleared land for agricultural purposes) habitat. Many parts of the valley contain agricultural fields or bodies of water and one typically finds nests on the perimeters of such non-utilized habitat.

The minimum convex polygon is the oldest and most common method of estimating home range (White and Garrott, 1990). The advantages of the method are its simplicity, flexibility of shape, and ease of calculation but the method has been criticized because of its inherent biases. For example, the size of the home range estimate increases indefinitely as the number of locations increases (Jennrich and Turner, 1969). *Sequitur*, studies that use different sample sizes (*i.e.* numbers of points) cannot be compared (White and Garrott, 1990). Further problems include the fact that outliers are given greater weight than they should be (*i.e.* area utilized in normal activity is overshadowed by total area utilized) and habitat that is not utilized is included within the polygon (*e.g.* water bodies; White and Garrott, 1990). Caution should, thus, be exercised when comparing my estimates of home range with other studies.

I have shown that sapsuckers possess a home range during the breeding season. Home range size is considered an important predictable aspect of an animal's feeding strategy (Schoener, 1981), but will vary with habitat structure. This chapter, thus, sets the stage

for chapters 2 and 3 where I examine habitat use in terms of foraging and nesting, respectively.

CHAPTER 2

Habitat use during the nesting season by Red-naped Sapsuckers in the Hat Creek valley,
British Columbia

Introduction

Chapter 1 examined the use of space by Red-naped Sapsuckers in the Hat Creek valley, British Columbia. Following on the findings in that chapter, this chapter examines habitat use. Documenting sapsuckers' use of habitat is important with respect to both management issues and ecological theory. By knowing what habitat is used, we can manage forests for important habitat requirements. If sapsuckers are truly keystone species, as has been discussed previously, then habitat needs of sapsuckers are important to the entire community in which they are found. In order to determine the magnitude of keystone species' effects on communities (*i.e.* interaction strength), a basic understanding of their habitat needs seem imperative.

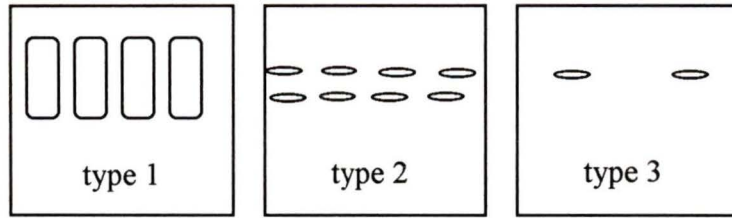
This chapter discusses habitat use of adult sapsuckers during the nesting season. Overall habitat use is compared with availability, both within and across nest sites. Types of foraging and habitat associated with foraging are examined.

Methods

Red-naped Sapsuckers were studied during the 1993 and 1994 nesting seasons (April-July). Observations were made by following individual birds, both opportunistically and during radiotelemetric studies (see Chapter 1). For birds foraging on trees (dbh > 120 mm), I recorded species of tree and type of foraging activity. Foraging was classified into four types (after Tate, 1973): sap feeding at wells (including drilling), feeding on aspen buds, gleaning insects (including bark removal), and flycatching. Size of tree used for foraging was compared between years with a t-test (assuming unequal variances). Similarly, trees used for foraging were compared with randomly sampled trees (see below) with a t-test (assuming unequal variances).

I used the term “deciduous scrub thickets” (DSTs) to collectively describe willow, swamp birch, water birch, choke cherry, and mountain alder because they were all found together in riparian areas. If any of these thicket species had a dbh > 120 mm, they were not considered as part of the DST but instead were categorized as trees. Because all plants within these thickets were used exclusively for wells (as opposed to some other foraging type), I took detailed measurements of the plants being used. Wells were classified according to how elaborate they were (*type 1* = rectangular wells, *type 2* = continuous groups of slits, or *type 3* = a few small slits; figure 2-A). I also recorded sap flow as active (wells were wet from sap) or not active (wells dry). Well size and location were recorded as width (width of stem), length (measured from bottom of lowest well to top of highest well along stem), height to bottom of well (vertical distance from the ground to

Figure 2-A. Illustration of the three types of sap wells made by sapsuckers.



the bottom of the lowest well), and height to top of wells (vertical distance from the ground to the top of the uppermost well).

To compare use with availability I categorized habitats where birds were located at each 10-minute interval. Because of the extreme patchiness of habitat and use by sapsuckers of particular species for sap well construction, I chose to classify habitat based on tree species. Habitat was classified as mountain alder (MA), trembling aspen (A), black cottonwood (C), Douglas-fir (DF), Rocky Mountain juniper (J), lodgepole pine (LP), ponderosa pine (PP), hybrid white spruce (S), and deciduous scrub thicket (DST). Habitat that I deemed “unavailable” to birds was not included (*i.e.* open water and agricultural fields). No birds in my study were ever recorded using open water or agricultural fields, they merely flew over these areas (pers. obs.).

To assess availability of habitat types, I sampled points randomly within 500 m of the nests (*i.e.* those nests for which telemetry data were available), following the methods of Marcum and Loftsgaarden (1980). This 500 m radius was chosen based on an inspection of the telemetry data (*i.e.* >95% of telemetry locations were within 500 m of the nest). Using a standard radius from the nest in order to delineate the area to which habitat availability will be determined reduces the variability that is inherent in other methods such as using MCPs (like those generated in Chapter 1) or arbitrarily assigning study site boundaries (Porter and Church, 1987). Sampling locations (*i.e.* a cartesian coordinate) were determined using a table of random numbers and then located by pacing off the distance, using a compass to maintain direction. If the sampling location occurred within

non-utilized habitat (*e.g.* middle of field or beaver pond) I used the closest available habitat. Sample sizes necessary to estimate true proportions of habitat were determined following Zar (1984:380). My estimate of true availability will increase with sample size. However, time and cost associated with this greater accuracy eventually reach a prohibitive level. Given this trade-off, I used $n=30$ which results in a detectable difference (δ) equal to 0.179. Indeed, δ exceeds the Type I error rate (0.05) but use of a non-parametric ranking (*i.e.* Friedman) test (see below) should reduce probability of type II errors (Johnson, 1980; Alldredge and Ratti, 1992) and avoids experimentwise error rates associated with a parametric alternative (Thomas and Taylor, 1990). I pooled available habitat within 500 m radii across all birds to approximate overall availability within the overall area used for nesting.

In order to test the hypothesis that habitats have identical effects on the difference between selection and availability I used Friedman's (1937) randomized complete block design. My application of the Friedman test involved computing the difference between percent usage and percent availability of each habitat by each bird, within and across nest sites. The differences were ranked for each bird, and the ranks were used to compute Friedman's test statistic where habitats represented "treatments" and vector of ranks for a bird was a "block" (after Alldredge and Ratti, 1986). The hypothesis being tested was whether the ranks of the differences between usage and availability for sapsuckers in the breeding season were the same for all 9 habitats. If this hypothesis was rejected then a second hypothesis was to be tested: the rank of the difference in selection and availability was the same for habitat i and habitat j . The latter hypothesis was tested using Fisher's

least significant difference procedure based on ranks (Sokal and Rohlf, 1981; Alldredge and Ratti, 1986).

Aebischer *et al.* (1993) suggest that the Friedman test is not appropriate due to unit-sum constraint (*i.e.* the proportions of habitats sum to 1 and are thus not independent) but simulations performed by Alldredge and Ratti (1986, 1992) show that the test is robust enough even if the unit-sum constraint is present.

Non-parametric tests based on ranks were used to test the above hypotheses because measurements of habitat availability were estimated and thus preclude the use of parametric tests (Alldredge and Ratti, 1992). Several assumptions were made with respect to the individuals being tracked: the results for one animal did not influence results for other animals; the number of individuals sampled was large enough for the approximation to the F-distribution to be close (Iman and Davenport, 1980); and that for my *post hoc* test of differences between pairs of habitats, ranks for each habitat were normally distributed and had homogenous variances (Alldredge and Ratti, 1986). The Friedman test seemed appropriate because it is robust with respect to analyses when number of habitats is large (as in my case) and inclusion or exclusion of habitats does not seem to alter results (Alldredge and Ratti, 1986).

Results

Within nest sites:

The ranks of the differences between selection and availability for sapsuckers were not the same for all 9 habitats ($T_2=5.575$, $df_{num}=8$, $df_{den}=72$, $P<0.001$). The ordering of habitat types from most to least preferred (left to right; sum of ranks in brackets) and significant differences from the LSD procedure ($LSD = 1.745$, $\alpha=0.05$, $df=81$) were:

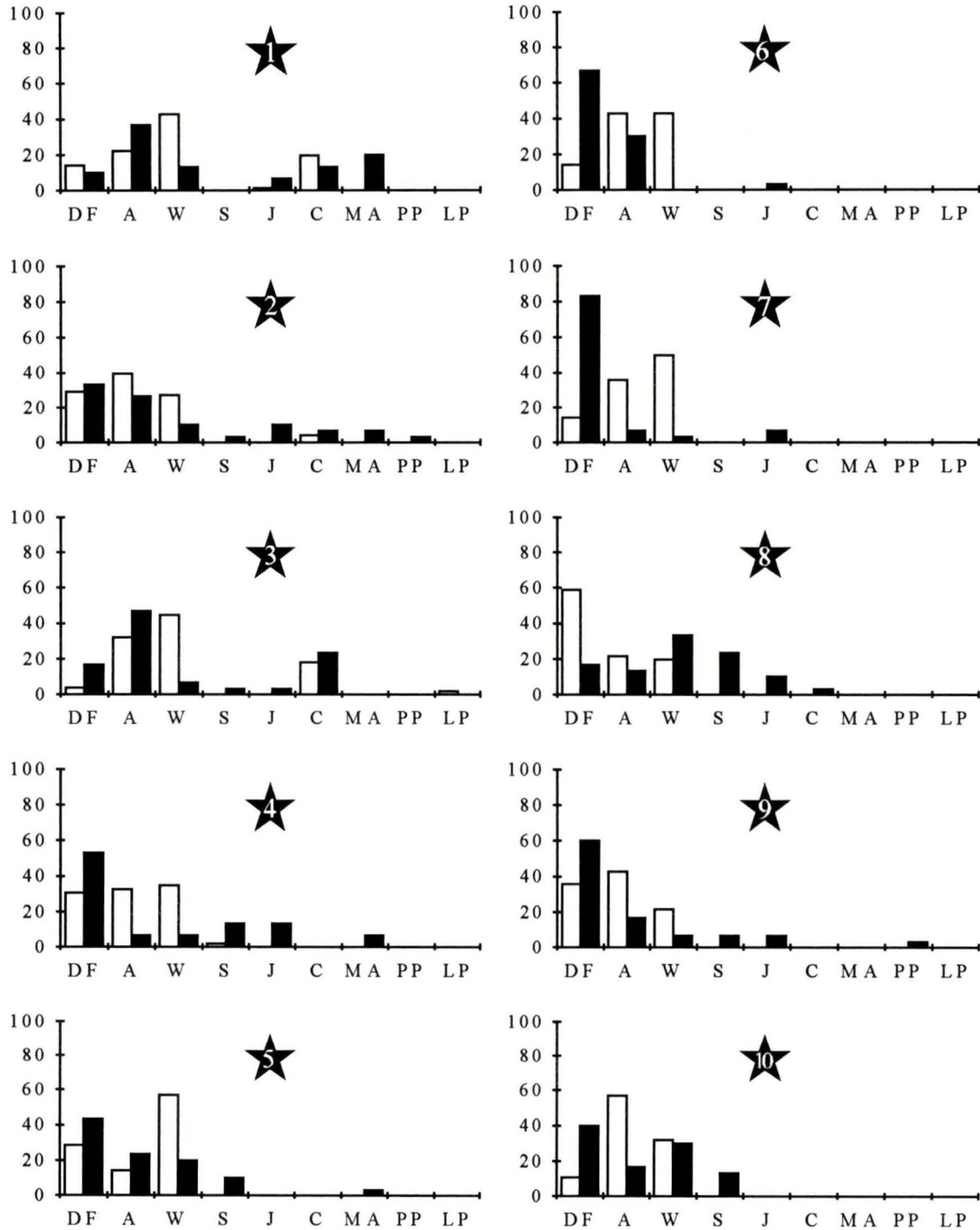
DST (81) A (64) LP (58.5) C (54.5) PP (53) MA (45) S (34.5) J (31.5) DF (27)

Cottonwood and ponderosa pine habitat types (those underscored) were not significantly different from each other. Deciduous scrub thicket was selected more than expected by 9 of the 10 birds, aspen was selected more than expected by 7, spruce by 3, Douglas-fir by 2, and both lodgepole pine and cottonwood by 1 (Figure 2-B).

Across nest sites:

Similar to what I found within nest sites, ranks of the differences between selection and availability were not the same for all 9 habitats ($T_2=27.290$, $df_{num}=8$, $df_{den}=72$, $P<0.001$). The ordering of habitat types from most to least preferred (left to right; sum of ranks in

Figure 2-B. Observed and expected (within nest sites) percent usage of 9 habitat types by 10 radiotagged sapsuckers (numbers within stars refer to nest site in Figure 1-B).



□ observed value; ■ expected value; DF = Douglas-fir; A = trembling aspen; W = deciduous scrub thicket; S = hybrid white spruce; J = Rocky Mountain juniper; C = black cottonwood; MA = mountain alder; PP = ponderosa pine and LP = lodgepole pine

brackets) and significant differences from the LSD procedure ($LSD = 1.208$, $\alpha=0.05$, $df=81$) yielded the following ordering:

DST (86) A (71) LP (70) PP (58) C (50) MA (47) J (29) S (20) DF (19)

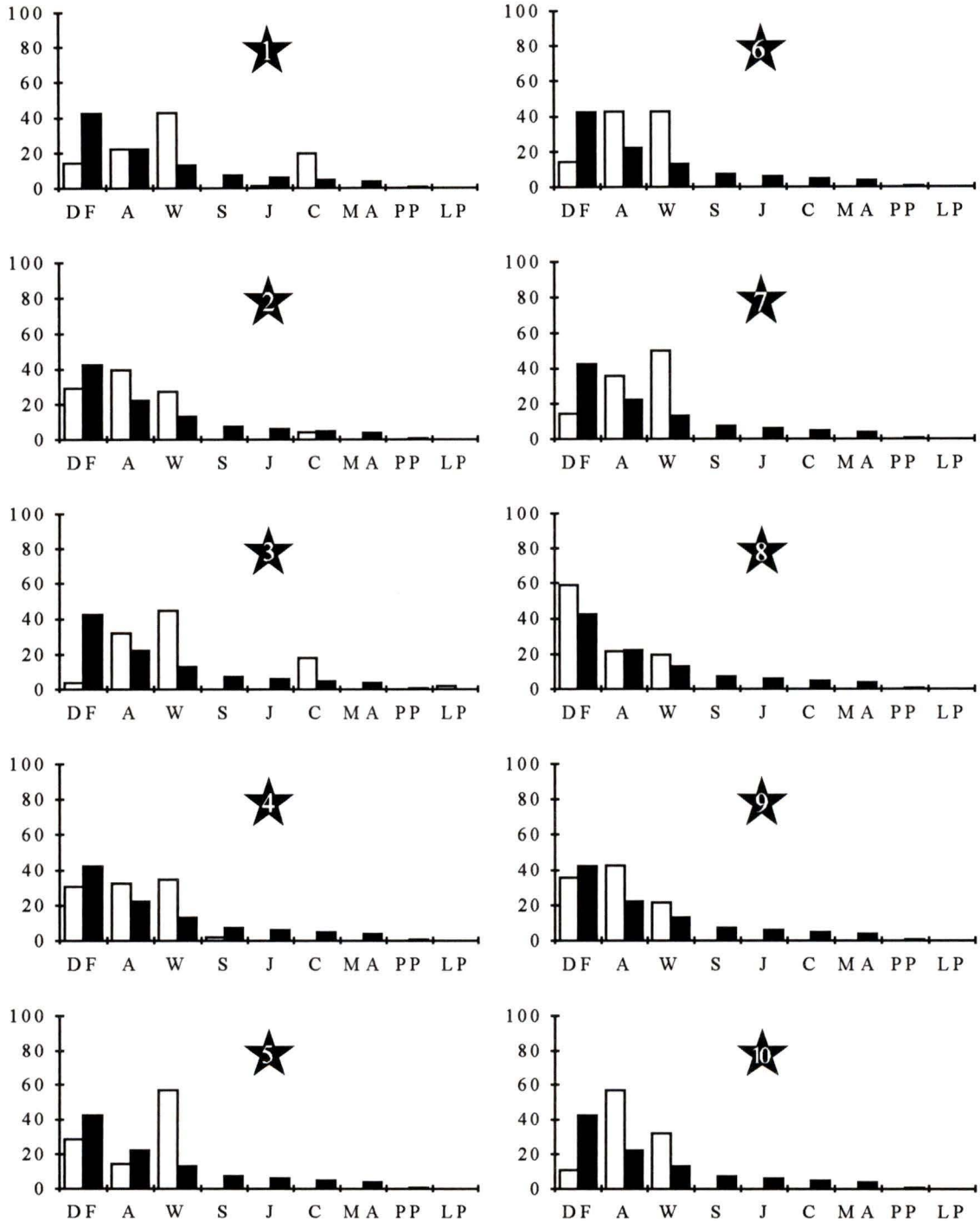
The relative ordering was similar to that observed within nest sites except that cottonwood / ponderosa pine and spruce / juniper were transposed, respectively. There was no significant difference between aspen and lodgepole pine nor between spruce and Douglas-fir. In this analysis there was a significant difference between cottonwood and ponderosa pine, whereas there was not in the within-nest sites case.

Deciduous scrub thicket was selected more than expected by all 10 birds, aspen by 7 of 10, cottonwood by 2, lodgepole pine by 1, and Douglas-fir by 1 (Figure 2-C).

Foraging

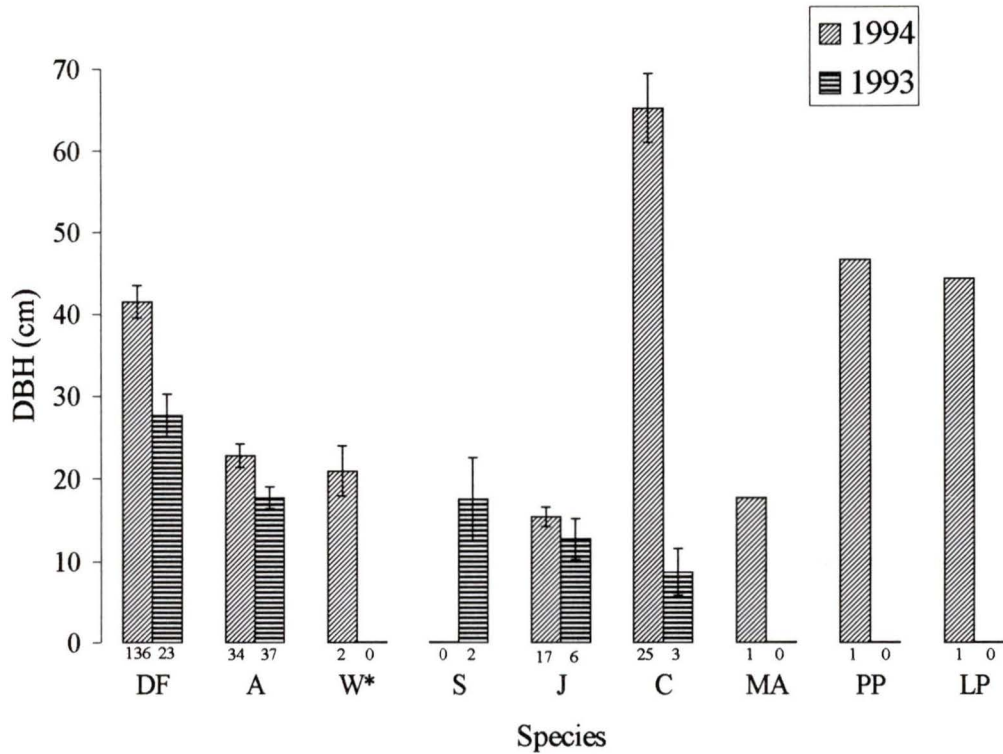
Sapsuckers foraged on a variety of plant species of varying sizes (Figure 2-D). Of the nine most common tree species found within my study site, aspen, cottonwood, Douglas-fir and juniper were the ones most foraged upon. On average, cottonwood used while foraging were the largest ($\bar{x} = 59.0 \pm 5.04$ SE cm, $n=28$), followed by Douglas-fir ($\bar{x} = 39.5 \pm 1.77$, $n=159$), aspen ($\bar{x} = 20.1 \pm 1.01$, $n=71$) and juniper ($\bar{x} = 14.7 \pm 1.10$, $n=23$).

Figure 2-C. Observed and expected (across nest sites) percent usage of 9 habitat types by 10 radiotagged sapsuckers (numbers within stars refer to nest site in Figure 1-B).



□ observed value; ■ expected value; DF = Douglas-fir; A = trembling aspen; W = deciduous scrub thicket; S = hybrid white spruce; J = Rocky Mountain juniper; C = black cottonwood; MA = mountain alder; PP = ponderosa pine and LP = lodgepole pine

Figure 2-D. Mean diameter (cm) at breast height (\pm SE) of tree species used for foraging by Red-naped Sapsuckers in 1993 and 1994 (sample size is indicated at base of columns).



DF = Douglas-fir; A = trembling aspen; W = willow; S = hybrid white spruce; J = Rocky Mountain juniper; C = cottonwood; MA = mountain alder; PP = ponderosa pine; LP = lodgepole pine.
 * only willow > 12 cm is included, smaller willow was treated as a shrub and use is reported under "deciduous scrub thicket".

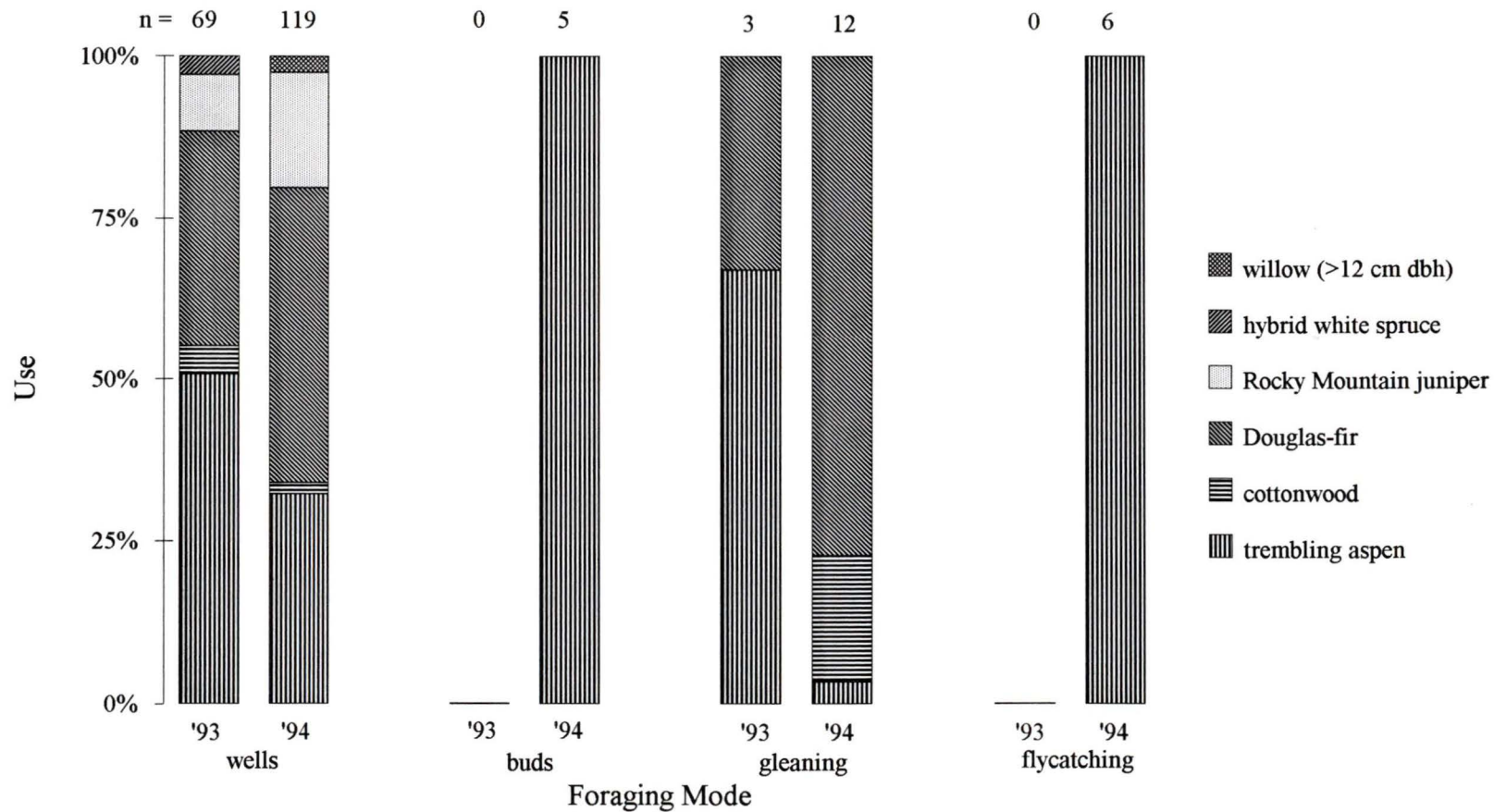
Other trees used included lodgepole pine, mountain alder, ponderosa pine, spruce, and willow. Of the tree species foraged upon in both 1993 and 1994; cottonwood ($t=11.10$, $p<0.001$, $df=14.5$), Douglas-fir ($t=4.18$, $p<0.001$, $df=50.7$), and aspen ($t=2.62$, $p=0.01$, $df=67.7$) were significantly larger in 1994. Juniper was not significantly different between years ($t=0.98$, $p=0.36$, $df=7.6$). When I compared the dbh of trees used for foraging with those randomly sampled; I found that cottonwood ($t=2.17$, $p=0.04$, $df=26.3$), Douglas-fir ($t=3.98$, $p<0.001$), and juniper ($t=3.18$, $p<0.01$, $df=40.4$) were all significantly larger than those randomly sampled. Only aspen ($t=0.96$, $p=0.33$, $df=105.9$) did not differ significantly from the random sample of trees.

The method of foraging (presumably a reflection of nutritional need) varied according to the foraging substrate (Figure 2-E). Bud feeding and flycatching were done exclusively in aspen. Of trees used for wells; aspen, Douglas-fir, and juniper were the most important species. Insect gleaning took place mainly in Douglas-fir and aspen and to a lesser extent in cottonwood. As mentioned above, lodgepole pine, mountain alder, ponderosa pine, spruce and willow (>12 cm dbh) were rarely used.

Deciduous scrub thickets

In 1993, I found wells in DSTs being used by 17 of 25 known breeding pairs. Of the thickets associated with these 17 pairs, I took detailed measurements from 13. One thicket was measured for a bird whose nest was not found. In 1994, I found DSTs

Figure 2-E. Percent use of tree species by sapsuckers in 1993 and 1994 in terms of foraging mode. The sample size, n, is indicated at the top of the columns and tree species used < 1% have been excluded.



associated with 21 of 27 nests. All radiotagged birds had willow patches associated with them. Of the 14 nests for which I quantified the wells found within the DST, approximately 23% of the total wells found per nest were active. In terms of well types, 46% were type 1, 33% were type 2, and 21% were type 3. Stem widths were similar among the three types of wells ranging from 26.5 - 29.4 mm (Table 2-A). Length, as expected, differed: type 1 wells were the greatest in length, followed by types 2 and 3, respectively. Mean heights for bottom and top of all wells pooled ranged from 1.851 - 1.960 (n=1,198), respectively.

Discussion

Sapsuckers were clearly selecting DST habitat more often than would be expected, based on availability. This was found for both levels (*i.e.* within and across nests) of selection. Of all habitats available, sapsuckers preferred DST. Most sapsuckers were found to have a system of wells in DST associated with their nest. In fact, evidence from the individuals that were radiotracked would suggest that all pairs maintain a system of wells. The sap from these wells forms a large part of the diet of sapsuckers (Tate, 1973; pers. obs).

My finding that sapsuckers are frequenting DST more than expected lends support to the suggestion by Daily *et al.* (1993) that willow (*i.e.* a source of sap) is an important component in the life-history of sapsuckers. It is the reliance on this willow, and hence the opportunity for other organisms to capitalize on this available resource, which is key to the hypothesis that Red-naped Sapsuckers play a keystone role within the communities in

Table 2-A. Summary of sap well measurements in “deciduous scrub thickets” showing mean \pm SE and range in brackets.

TYPE	WIDTH (mm)	LENGTH (mm)	HEIGHT-B (m)	HEIGHT-T (m)	N
1	29.4 \pm 1.02 (9-297)	177.4 \pm 4.33 (23-698)	1.899 \pm 0.0367 (0.39-5.78)	2.070 \pm 0.0367 (0.57-6.17)	516
2	26.5 \pm 0.63 (11-152)	89.2 \pm 2.76 (22-515)	1.864 \pm 0.0358 (0.52-3.85)	1.952 \pm 0.0361 (0.56-3.96)	403
3	26.6 \pm 0.98 (10-187)	27.3 \pm 1.29 (2-168)	1.743 \pm 0.0428 (0.23-4.17)	1.771 \pm 0.0429 (0.23-4.18)	279
ALL	27.8 \pm 0.54 (9-297)	112.7 \pm 2.74 (2-698)	1.851 \pm 0.0223 (0.23-5.78)	1.960 \pm 0.0225 (0.23-6.17)	1198

which they are found. In fact, Daily *et al.* (1993) have suggested that if a source of sap (*e.g.* willow) were removed, one would expect local extinction of Tree and Violet-green swallows (obligate secondary cavity nesters) at their Colorado study site. Willow seems to form an integral part of this complex within much of the range of the Red-naped Sapsucker.

Aspen was the second most preferred habitat when comparing use with availability. Aspen was used for nesting (see Chapter 3) and thus relative use was high. As central-place foragers (*i.e.* an organism that returns with prey to some fixed central location; Orians and Pearson, 1977), sapsuckers use the nest site as the centre of activity through most of the breeding season. During cavity excavation they actively defend (*i.e.* aggressively chase any other bird other than the mate) the nest site (Lawrence, 1966). Once eggs hatch and young are present in the nest cavity, adults will make frequent foraging forays in an effort to minimize the time the young are left unattended. As a result, adults spend much of their time in the vicinity of the nest and, hence, use of aspen habitat increases.

Like DST, aspen appears to be another important habitat type. Not only is aspen used for nesting but results from this study indicate that aspen is also used for flycatching, bud eating, and sap wells. Aspen thus forms an integral part of the habitat needs of this species, both within my study site (south-central British Columbia) and that of Daily *et al.* (1993; Colorado). These findings lend support to Daily *et al.*'s (1993) assertion that aspen forms part of the 4-factor keystone complex (as mentioned previously).

Lodgepole pine scored very high on the relative ranking of preferred habitat but this appears to be an artifact of the statistical test used. This particular habitat was used by only one bird and the relative abundance of this habitat type was not high enough to be detected in my measure of expected abundance. Thus, 9 of 10 birds did not use lodgepole pine habitat (as expected based on my prediction of relative abundance) and 1 bird used it more than expected. This non-use of a rare habitat type caused lodgepole pine to rank third within nest sites and across nest sites.

Similarly, ponderosa pine was not used by any radiotagged birds and was recorded in only two nest ranges. Thus, its level of relative use appears high because most of the points compared expected use of 0 with observed use of 0 (as above). In reality, ponderosa pine was rarely used (*cf.* Oliver, 1968, 1970). This may have been related to its low abundance in the study area. For example, in central Arizona, where ponderosa pine is abundant, Red-naped Sapsuckers readily use the tree species for sap wells (*pers. obs.*).

Cottonwood was not distributed evenly throughout the study site. At the west end of the study area, there was a large stand of cottonwood trees. Three of the birds randomly chosen for radiotracking (birds 1, 2 and 3; figure 1-B) had nests near this stand. Thus, these three birds were found using cottonwood whereas birds in other areas did not have the opportunity because there was none available. It appears that cottonwood is used to a large degree when available, based on my observations of both radiotagged individuals and those birds that were found opportunistically.

Juniper scored fairly low in the relative preference analysis but this is a bias of the stage of the breeding season when birds were fitted with radiotags. Telemetry studies were implemented well after sapsuckers had switched from using juniper to DST, as a source of sap. From observations on foraging birds, it is clear that juniper, when used by sapsuckers, is used almost exclusively for sap wells. As mentioned previous, sapsuckers were not fitted with radiotags until the clutch was complete, so as to avoid nest desertion. As a result, observations of radiotagged individuals were limited to post-egg-laying and, thus, the results of this study are biased toward this stage of nesting.

Douglas-fir ranked lowest among the available habitats in terms of relative use. However, to conclude that Douglas-fir is “avoided” would be a mistake. By far, this tree species exceeded all others in terms of absolute use for both insect gleaning and conifer wells. The reason for the low ranking is that Douglas-fir habitat dominates all other available habitat. Thus, its availability is high and use is often less than what one would expect based on its availability. One should bear in mind that the habitat preferences presented here are merely relative measurements (*i.e.* the ranks of the differences between selection and availability). I would not, for example, want to say that Douglas-fir was avoided because it was used less than expected based on its availability. One must remember that in terms of across-nest site selection, the bird has already chosen the site before one measures habitat preference. To illustrate this point, let us assume that an imaginary bird nests only in tree species A. Suppose now that this bird selects a nest patch that contains 50% tree species A and 50% tree species B. Let us also assume that this imaginary bird does not use tree species A for anything but nesting and tree species B only for foraging.

Our habitat analysis of use would show that this bird never forages on tree species A, only on B. Thus, we would most likely conclude that tree species A is used less in proportion to its availability and tree species B is used more. If we were then to erroneously conclude that tree species A was avoided, we would be making a mistake (remembering that this bird only nests in tree species A). Thus, one should exercise caution when using terms like “preference” and “avoidance” in these types of studies.

Questions remain, however: for example, in the southern portion of the range of Red-naped Sapsuckers (*e.g.* central Arizona), willow is not found (Martin, 1988a; pers. obs.). Thus, it may be that a source of sap is the keystone component, not specifically willow, but this remains to be studied further in areas where willow does not occur within the range of Red-naped Sapsuckers. Evidence to support this also comes from the fact that sapsuckers use conifers (*e.g.* Douglas-fir, juniper and spruce) for wells in late April, before deciduous trees and shrubs have leafed out (pers. obs.; Tate, 1973; Eberhardt, 1994). In early May there appears to be a shift from these conifers to deciduous plants (*e.g.* aspen, willow) and these deciduous plants are used until at least mid August (well after birds have fledged; pers. obs.; Ehrlich and Daily, 1988).

This study examined use versus availability of habitat. Other forms of analysis may address factors such as interspersed and juxtaposition of habitats (Porter and Church, 1987). This type of investigation was beyond the scope of this study.

CHAPTER 3

Nest site characteristics of the Red-naped Sapsucker in the Hat Creek valley, British Columbia.

Introduction

As mentioned previously, effective conservation of species requires identification of specific habitat features that directly influence reproduction. Presence of suitable nesting habitat is obviously necessary for successful breeding. Within British Columbia, forest managers now protect “wildlife trees” during harvesting (B.C. Wildlife Tree Committee, 1993). However, management for presence of wildlife trees is not sufficient; size, species, and age of trees, plus distribution of nest trees and vegetation in surrounding patches can affect presence and even reproductive success of birds (Conway and Martin, 1993). Thus, it follows that we must first identify important habitat features that are associated with nesting in order to properly manage for sapsuckers.

This chapter focuses on the habitat associated with nesting. I characterize trees used for nesting and then compare these trees with those found within the nest plot, the area immediately surrounding a nest tree.

Methods

Red-naped Sapsuckers were found during the nesting season (April-July) from 1992 through 1994. Nests were located by observing birds excavating or entering cavities. These were later confirmed by observing parents that were incubating eggs or feeding young. I visually checked the inside of the cavity each day (with mirror and flashlight) to note stage of nesting, where possible. Ladders were kept at most nests and wooden blocks were nailed to trees that had nests higher than 7 m, to facilitate climbing. Nests were defined as those cavities in which at least two eggs were laid or in which there was evidence that eggs had been laid (*e.g.* feeding young). If two eggs had been laid but all young did not survive long enough to fledge, the nesting attempt was considered a failure.

The following parameters were recorded, where possible, for nest trees: species, height, diameter at breast height (dbh), age of cavity (new / old), whether other cavities were present besides the nest, orientation of cavity, direction of lean of tree, presence/absence of heart rot conks (*Phellinus igniarius*), presence/absence of heart rot in centre of pith (determined by inspection of increment core) and condition of nest tree (dead/live). All directions were recorded using a compass and are reported relative to magnetic north. Declination in 1994 at this site was 21°15' and all orientations were taken in 1994 to maintain consistency.

To determine whether sapsuckers were choosing nest trees that differed from available trees (*i.e.* trees within the 1 ha nest plot), I recorded dbh, species, condition, and

presence/absence of cavities and fungal conks on all trees greater than 12 cm dbh in the 1 ha plot surrounding 17/31 nest trees found in 1994. I considered available trees to be those greater than 12 cm, based on the minimum dbh ever recorded for a sapsucker nest tree (Kilham, 1971). The plot size (1 ha) was chosen by extrapolating an area based on the minimum distance (*i.e.* 100 m) I observed between adjacent nest trees. This size seemed to be a reasonable estimate based on Howell's (1952) finding that territory size (equivalent to nest plot) varied from 46-137 meters radius and Gibbon (1970), who found territories of 0.8-1.2 ha. The nest plots were further demarcated into an inner (0.25 ha) plot and an outer (0.75 ha) plot. I also wanted to determine if trees in the inner plot differed from those in the outer, with respect to the variables previously mentioned.

Roost trees were documented by following birds fitted with radiotags (see Chapter 1) at night. Males are known to roost in nesting cavities (Howell, 1952), so only females were tracked.

Ordinal data (*i.e.* dbh and height) were tested for normality using Shapiro-Wilks' W-statistic and normality plots. Proportions of new versus old cavities were compared between years using chi-squared goodness-of-fit with Yates' correction for continuity (Zar, 1984, p. 64).

Circular data (*i.e.* nest orientation and direction of lean) were tested for uniformity using Rayleigh's test of uniformity (Batschelet, 1981). If the data differed significantly ($p < 0.05$) from a uniform distribution, then the data were plotted to see if the points were unimodal.

If they were non-uniform and unimodal then a mean vector was calculated, assuming the data fit a von Mises distribution. Orientation of cavity was compared with direction of tree lean using a non-parametric Moore test for paired angles (Zar, 1984, p. 464).

Nest trees were compared with available trees using a Chi-square goodness-of-fit test (Zar, 1984) for nominal variables (*i.e.* species, state, presence/absence of conks and cavities) and a t-test for independent samples for dbh. Samples were tested for equal variance using Levene's test. Differences between nest tree dbh and mean dbh of available trees in the 1 ha nest plot subareas were tested using paired sample t-tests. Differences in tree density between the inner plot (0.25 ha) and outer plot (0.75 ha) were compared with paired t-tests.

All analyses were carried out using the SPSS® statistical package except for the circular data, which were analyzed using the circular statistics package, Oriana for Windows™.

Results

Approximately 81% (25/31) of nests in 1994 and 64% (16/25) in 1993 were in new cavities (*i.e.* the cavity was constructed in the year the nest was found). Proportions of nests in new cavities did not differ significantly between years ($\chi^2=1.199$, $df=1$, $0.25 < p < 0.50$).

Nest orientations were examined for uniformity with respect to year (1992-94) of nesting and success of nest. When all nests were pooled over all years ($p < 0.01$, $n = 71$) and all successful nests pooled over all years ($p < 0.01$, $n = 57$), they were found to differ significantly from a uniform distribution (Table 3-A). Similarly, in 1993, all nests pooled ($p < 0.01$, $n = 25$) and successful nests ($p < 0.01$, $n = 21$) differed significantly from a uniform distribution: all other nest-year combinations did not.

Mean vector of nest orientations for all nests pooled over all years was $222.6^\circ \pm 13.53$ SE, with those that were successful having a mean of $211.6^\circ \pm 14.2$ SE (Figure 3-A).

Similarly, the mean vector for all nests in 1993 was $213.2^\circ \pm 13.3$ SE and $206.4^\circ \pm 12.1$ SE for those nests that were successful. All other subsets did not meet the assumption of a von Mises distribution (Table 3-A) so no mean was calculated, and multiple comparisons were not carried out. Failed nests, thus, did not differ from a uniform distribution.

To determine whether orientations were related to tree lean, I measured trees which exhibited a noticeable lean. Data fit a uniform distribution ($p = 0.53$, $n = 14$ for cavity orientation; $p = 0.12$ for tree lean), indicating that a specific direction was not associated with the lean of the tree nor the nests within the leaning trees. Of 14 trees measured in 1994, the direction of the lean did not differ significantly from the cavity orientation ($r^2 = 0.74$, $df = 14$, $p > 0.20$).

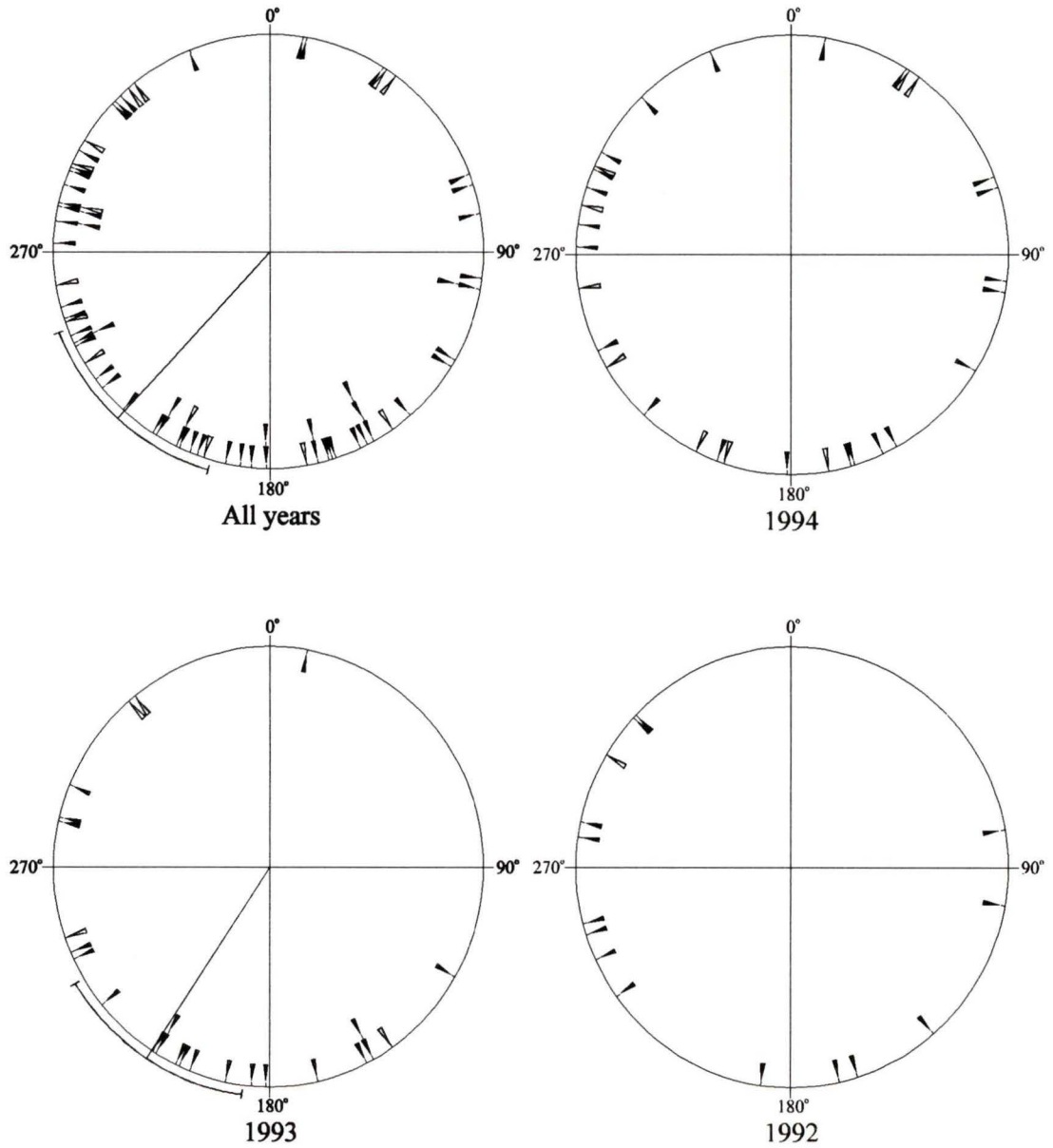
Table 3-A. Statistical summary ($\bar{x} \pm SE$) of nest orientations. Sample sizes are in parentheses.

Nest Year	Successful	Failed	Totals
All years	211.6 \pm 14.23 ^{o*} (57)	p=0.10 (14)	222.6 \pm 13.53 ^{o*} (71)
1994	p=0.79 (22)	p=0.28 (9)	p=0.41 (31)
1993	206.4 \pm 12.09 ^{o*} (21)	p=0.52 (4)	213.2 \pm 13.28 ^{o*} (25)
1992	p=0.13 (14)	p=0.51 (1)	p=0.11 (15)

* p<0.01

Raleigh's test of uniformity; p-values are indicated for nests where distribution of directions did not differ significantly (*i.e.* p>0.05) from a random distribution.

Figure 3-A. Circular plots of nest orientations showing mean and 95% confidence intervals (where applicable) for both successful (solid) and failed nests (hollow).



Fifty-five of fifty-six (98%) nest trees for which data were available were in aspens, the other tree being a live cottonwood. Of the aspens used, most (82%) were live but of the 4155 available trees measured within the 1 ha plots around nests, only 47% were live aspens. Thus, live aspens were used more than expected ($\chi^2=24.98$, 1 df, $p<0.001$). When treated separately, aspens were selected more than expected ($\chi^2=32.76$, 1 df, $p<0.001$) but live trees were not ($\chi^2=0.02$, 1 df, $0.75<p<0.90$). Aspens used for nesting were found within riparian areas at the bottom of the valleys (figure 1-B).

Virtually all (98%) of the aspen nest trees used for nesting in 1993 and 1994 were infected with heart rot but only 18% of the nest trees had conks on their trunks. Conversely, of the 2528 aspen available within the 1 ha plots, less than 1% had conks. Trees with conks were, thus, used for nesting significantly more than expected based on their availability ($\chi^2=556.64$, 1 df, $p<0.001$).

Diameter at breast height of nest trees ($\bar{x} = 288.0$ cm \pm 9.43 SE, $n=56$) was significantly larger than dbh of available aspen trees ($\bar{x} = 226.1$ cm \pm 1.56 SE, $n=2528$) within the 1 ha nest plot ($t=-5.85$; equal variances $F=0.419$, $p=0.518$; $df=2582$; $p<0.001$). Mean height of nest trees was 17.2 m \pm 0.79 SE ($n=56$) and this height was significantly correlated with dbh ($r=0.3898$, $n=56$, $p=0.003$).

Of the 55 trees used for nesting in 1993 and 1994, nearly 91% had other cavities besides the nest cavity in the tree. Conversely, only 2% (57/2528) of available trees in the 1 ha

plot harboured cavities. Significantly more nest trees contained cavities than would be expected based on availability within the 1 ha nest plot ($\chi^2=11.66$, $df=1$, $p<0.001$).

Given that aspen was preferred for nesting, I examined within-nest plot differences. I compared the density of trees (>12 cm) per hectare between the inner and outer tree plots. The inner plot contained significantly more live and dead aspen, dead trees, and total trees than the outer nest plot (Table 3-B). The only subset of trees measured that did not differ significantly between the two plots was overall live trees (of any species).

Live aspens were significantly ($p<0.001$, $t=4.26$, $df=16$) larger (in terms of dbh) within the inner plot ($\bar{x} = 244.7 \pm 11.01$ SE) compared with the outer plot ($\bar{x} = 223.7 \pm 11.2$ SE) but dead aspen were not significantly different ($p=0.051$, $t=2.11$, $df=16$) between the inner ($\bar{x} = 219.1 \pm 9.28$ SE) and outer ($\bar{x} = 207.4 \pm 7.73$ SE) plots. Finally, mean dbh of live trees ($\bar{x} = 231.4 \pm 11.04$ SE) was significantly larger ($p=0.034$, $t=2.32$, $df=16$) than dead trees ($\bar{x} = 213.6 \pm 8.00$ SE) within the 1 ha plot.

Nest success differed among years. In 1992, 17/19 (89.5%) were successful, 21/25 (84.0%) in 1993, and 20/27 (74.1%) in 1994. Nests failed due to predation in 3 cases, eviction by House Wrens in 2 cases, and were unknown in 8 other cases. Three pairs were ultimately successful after having their first nesting attempt fail (two of the incidents resulted from one parent being depredated, the other involved a nest that was usurped by House Wrens).

Table 3-B. Comparison of tree density (trees/ha) between inner (in; 0.25 ha) and outer (out; 0.75 ha) nest plots using paired t-test.

Variable	Aspen			All Trees		
	Live	Dead	Total	Live	Dead	Total
$\bar{x}_{in} \pm SE^*$	164.0 \pm 24.27	57.6 \pm 7.75	221.6 \pm 28.87	223.7 \pm 29.06	63.1 \pm 7.60	286.8 \pm 33.25
$\bar{x}_{out} \pm SE^*$	98.6 \pm 18.41	25.8 \pm 4.89	124.4 \pm 22.09	195.5 \pm 28.2	34.8 \pm 5.70	230.3 \pm 32.88
t	4.06	3.90	4.37	1.90	3.72	3.05
p	<0.001	0.001	<0.001	0.075	0.002	0.008

* n=17

Adult males roosted in nest cavities until the young were large (*ca.* 25 days). For five females observed, seven roost trees were documented; six were in live Douglas-fir and one in a dead aspen (dbh: $\bar{x} = 276.6 \pm 25.49$ SE, $n=7$; height: $\bar{x} = 16.9$ m ± 1.51 SE, $n=6$). In all cases, birds were clinging to the trunk of the tree below a branch. None were observed to roost within cavities. Of the two females that were checked twice, both had used different trees from their previous roost.

Discussion

Sapsuckers tend to excavate new cavities in trees for each nesting attempt. My findings agree with those of others (*e.g.* Daily, 1993, 97%) in that most cavities are excavated in the year of nesting. In all likelihood, my numbers are likely underestimates of the true number of new cavities: in some cases, the external appearance of a cavity may suggest that it is old but the inner area may have been freshly excavated (or reworked).

Sapsuckers often abandon excavations when only part way completed and these “false starts” may be re-excavated in subsequent years (*pers. obs.*). Thus, my estimates of the proportion of newly excavated cavities is probably conservative and the true proportion is most likely even higher. Several hypotheses have been advanced to explain why cavity-nesting birds excavate new cavities, as opposed to using existing ones. For example, Kilham (1983) believes it may be a method of avoiding higher parasite loads (*i.e.* old nests will contain parasites from the previous nesting season). Others have suggested (*e.g.* Sonerud, 1985, 1989; Nilsson *et al.*, 1991) that excavating new cavities is an anti-

predation tactic (*i.e.* old cavities are more susceptible to predation). Evidence to support these theories comes from Eberhardt (1994) who found sapsuckers that used old holes fledged fewer young than did birds in new cavities.

The orientation of cavities has been examined in many studies of cavity-nesting (primary and secondary) birds but no conclusive trend (*i.e.* whether or not a particular direction is favoured) has been found. Secondary cavity-nesting birds are those that cannot excavate their own cavity but rely on other species (*i.e.* primary cavity-nesting birds) to excavate a cavity for them. For a review of cavity orientation in secondary cavity-nesting birds, a topic that is beyond the scope of this thesis, refer to Rendell and Robertson (1994). Non-excavating species are limited by the availability of cavities whereas primary cavity-nesting birds usually are not limited because they can excavate their own cavity, provided that the appropriate habitat is available. In a sense, one could say that these excavators “choose” the direction of the cavity. The situation is confounded because some excavating species will reuse old cavities (*i.e.* facultative cavity-nesting species).

There is conflicting evidence among studies that have examined cavity orientation in birds that excavate: some authors found no preference for cavity orientation (*e.g.* Keisker, 1987; Conway and Martin, 1993); some found that cavities are oriented to maximize thermal irradiance from the sun (*e.g.* Lawrence, 1966; Dennis, 1969; Baker, 1971; Reller, 1972; Crockett and Hadow, 1975; Inouye, 1976); some (*e.g.* Inouye *et al.*, 1981; Korol and Hutto, 1984) have found the opposite, that cavities may be oriented to counter thermal irradiance to minimize water loss in very hot environments; and even others that

found birds excavate cavities near the open end of a stand of trees rather than toward its centre (Crockett and Hadow, 1975), possibly to facilitate arrival at and departure from the nest tree. Many theories have been advanced to explain cavity orientation but no study has provided conclusive evidence that only one factor is responsible for the trends that have been shown.

Conner (1975) found that most cavities in his study were oriented northeasterly and offered the explanation that tree lean was the most important factor. This was supported by Bull (1975) during studies of Pileated Woodpeckers in which all nest openings were on the underside of the leaning tree, and by Stauffer and Best (1982) who found that 94% of primary cavity-nesting birds' nests were located on the underside of sloping limbs / trunks. By excavating a cavity on the underside of a leaning tree, the chance of rain entering the cavity would be reduced (Conner, 1975). Another reason for locating cavities on the underside of a tree may be as a result of fungal growth. Undersides of trees tend to have a higher moisture content and thus are more conducive to fungal growth. This fungal-infected wood is easier for woodpeckers to excavate (Blume, 1961; Dennis, 1969). Evidence in favour of this hypothesis comes from Kilham (1971) who states that Yellow-bellied Sapsuckers prefer *Phellinus igniarius*-infected nest trees. Also, a thinner layer of firm lignified wood is produced on the underside of trees than on the upper areas (Conner, 1975). Cavities on the underside of trees may also be better protected against predators that will have more difficulty gaining access than if the cavity was situated on the upper side of the tree (Conner, 1975).

My results support the direction-of-lean hypothesis for the trees that were noticeably leaning. When I tested the direction of the cavity against tree lean I found no significant difference. Nests overall seemed to favour a southwest orientation (*cf.* Li and Martin, 1991) but leaning trees did not all lean southwest. If there was a thermal advantage to a southwest direction one would expect nests in all years to show this trend. However, it was only during 1993 that a preferred direction was detected statistically. Both 1992 and 1994 samples had random orientations. What this suggests is that if a bird chooses a tree which is leaning, it will place its cavity on the underside of the tree. If the tree is not leaning then cavity orientation will be variable.

Failed nests did not face the same direction as successful nests (*i.e.* failed nests did not show any trend in orientation but successful nests did show the trend towards the southwest). Thus, one could postulate that nests that faced southwest increased breeding success, at least in 1993. Perhaps a southwest direction offered a selective advantage during 1993, a year that was very wet (*pers. obs.*). Because there was no directional trend among leaning trees, one might suggest that the thermal benefits of a southwest direction were more important in a wet year. Derby and Gates (1966) showed that temperatures are significantly higher in the part of the tree facing the sun during daylight hours. They found that the temperature gradient can be as large as 12°C. Soule (1964, cited in Inouye, *et al.*, 1981) and Krizman (1964, cited in Inouye *et al.*, 1981) both found that temperature within a nest hole is influenced by orientation for Gila Woodpeckers (*Melanerpes uropygialis*) in saguaro cacti in Arizona. The preference for a southwestern cavity orientation may have been a response to suboptimal nest site quality and reduced

insulative capacity of smaller diameter trees (*i.e.* trying to nest in warmer microsites; Conway and Martin, 1993). However, this hypothesis seems unlikely, given the fact that nesting success was high (84%) in 1993 and no preference for direction was shown in other years. McClelland (1977) felt that the sapsuckers in his study did not exhibit orientation preference because thermal factors were deemed to be unimportant when nesting activities were at a peak. Alternatively, my finding that failed nests did not show the same mean vector as successful nests may have been an artifact of low sample size (*e.g.* there was only 1 failed nest in 1992, of those for which orientation data were available). It does not, however, explain the non-preference for orientation in 1992 and 1994.

Sapsuckers are known to prefer aspens for nesting, where available (Erskine and McLaren, 1972; Keisker, 1987). Likewise, my study found almost exclusive use of aspen for nesting. Aspens chosen are typically live trees that have been infected with heart rot (*Phellinus igniarius*; Shigo and Kilham, 1968). Because of the nature of *P. igniarius* and its propensity to infect live aspens (Basham, 1958), most sapsucker nests are in live trees (Daily, 1993). Thus, live aspens were used for nesting significantly more than expected based on their availability. In areas where aspens are replaced by other species such as birch (*Betula papyrifera*) sapsuckers tend to nest in dead trees (Gibbon, 1970; Kilham, 1971). Harestad and Keisker (1989) attribute this to the fact that the heart rot that infects birch is *Fomes fomentarius* and typically attacks only dead trees, or dead portions of live trees. Similarly, Cannings *et al.* (1987) report that of *S. nuchalis* nests found in conifers in British Columbia, all were either dead or dying trees. These findings are probably related

to tree hardness and sap flow. Live coniferous trees are probably not used by Red-naped Sapsuckers to any extent because of their hardness and propensity to exude sticky resin when excavated (pers. obs.) whereas dead conifers are most likely softer and do not contain as much sticky sap. Interestingly, *Sphyrapicus thyroideus*, a congener of *S. muchalis*, prefers dead aspens over live ones in areas where both are available (Conway and Martin, 1993) and readily nests in live conifers in other areas (Cannings *et al.*, 1987).

The *thyroideus* taxon is believed to be the oldest of the four species within the *Sphyrapicus* genus. The *varius* superspecies is thought to have split from *thyroideus* about 5 million years ago and *muchalis* is believed to have split from the *varius* superspecies (*varius-ruber-muchalis*) about 1 million years ago (Cicero and Johnson, 1995). Thus, one might suggest that *muchalis* has recently evolved the ability to excavate nests within live deciduous trees. The nature of the evolutionary history of the genus *Sphyrapicus* has been debated (*e.g.* Short and Morony, 1970; Johnson and Zink, 1983). The current evidence would suggest that the species within the genus were derived through allopatric speciation and that the current zones of sympatry between *thyroideus* and *muchalis* is a recent event reflecting secondary contact after the last glaciation (Howell, 1952; Cicero and Johnson, 1995). Thus, morphologically it would appear that *muchalis* has the ability to nest within dead aspen or live conifers (based on its phylogeny) but behaviourally tends not to.

Decayed heartwood is required by virtually all primary cavity-nesting birds in British Columbia (Harestad and Keisker, 1989). In my study, practically every sapsucker nest

was infected, although only a small proportion of nest trees exhibited any external indication of disease (*i.e.* the presence of conks). In contrast to my finding of only 18.2%, Harestad and Keisker (1989) found that 70% of nest trees (aspens) had conks. Similarly they found that 10% of available trees had conks, whereas I only found 0.3% among the available trees sampled. Caution should be exercised when using conks to estimate heart-rot infection despite the fact that Basham (1958) states that the most reliable external indication of decay in aspen is the appearance of fruiting bodies (*i.e.* conks). Given the relationship that I found between external conks and internal rot, the findings of Harestad and Keisker are probably conservative estimates of true heart rot infection. This difference in prevalence of rot may be due to site-specific differences even though Harestad and Keisker's study site is only about 90 km away from Hat Creek. A better method of estimating heart rot infection is to use increment cores (*e.g.* Daily, 1993), although this presents its own problems. For example, increment coring can transfer pathogens between trees, bore holes make trees more susceptible to decay and disease, and staining associated with the bore hole can lower the value of commercial timber (Maeglin, 1979).

Nonetheless, nest trees with conks were selected more than their availability would suggest and this finding supports that of Harestad and Keisker (1989) who found that cavity-nesting birds in their study preferred trees bearing conks. Whether it is the presence of conks (Crockett and Hadow, 1975), or some other means (*e.g.* resonance of wood) that woodpeckers use to determine suitability of trees, remains to be determined. Evidence to suggest that woodpeckers can detect slight differences in tree resonance

comes from Miller and Miller (1980) who found that a Three-toed Woodpecker (*Picoides tridactylus*) excavated a cavity in a 20 m lodgepole pine precisely where a vertical section of rot was found, less than a metre in length. The assumption being that the rot changes the resonating characteristics of the wood.

Live trees were used for nesting in equal relation to their availability yet live aspens and pooled aspens (both live and dead) were used more than expected, suggesting that sapsuckers are choosing patches which are high in proportions of live trees, regardless of species (*cf.* Smith, 1982). Trees used for nesting were larger than other available trees and trees within the plot were larger in the 0.25 ha area surrounding the nest site than the outer 0.75 ha. Whether sapsuckers were choosing patches with large trees or simply choosing large trees (that happen to be in patches of large trees) remains to be determined.

The minimum size of aspen used in my study (17.2 cm dbh) agreed with the findings of Crockett and Hadow (1975) who suggested that this size was probably the minimum diameter that could provide adequate space for a nesting sapsucker. The average nesting tree dbh (23.3 cm) in Crockett and Hadow's Colorado study was less than that found in my study (28.8 cm) but, unfortunately, they do not indicate the sizes of available trees within their study site. Another study in Colorado (Winternitz and Cahn, 1983) found an average dbh of 26.2 cm in aspens that were used by a number of cavity-nesting species, a size which is closer to my findings. Oddly enough, Harestad and Keisker (1989) found that sapsuckers in their study avoided trees in the 25-29 cm range, preferred trees in the 30-34 cm range, and showed no further preference for trees larger than 34 cm. Their

explanation is that there is no further advantage to nesting in trees larger than 34 cm. Advantages associated with larger trees are the inherently thicker wall of the cavity, which should provide better insulation (see above) and protection from predators, and less chance of the tree breaking off at the cavity (Truslow, 1967; Miller and Miller, 1980; Raphael and White, 1984). As mentioned previous, sapsuckers in my study were using aspen of relatively small dbh, suggesting that this may have caused them to excavate cavities oriented in a southwest direction in some years. Li and Martin (1991) report a mean dbh of 37.1 cm (*i.e.* larger than my finding) but report that large trees were abundant and young trees scarce, suggesting that availability of trees dictates the size which is used. The results of my within-plot comparisons show that larger live aspens are being used, relative to the size of those available. Size of dead aspens did not significantly differ within plots, adding further evidence to suggest that live aspens are important for nesting.

Sapsuckers tend to re-use nest trees; nearly 91% of nest trees in my study had previous excavations within them. In contrast, Daily (1993) found that only 67% of nest trees contained previous cavities. What this may suggest is that fewer trees were infected with heart rot in my study area (see conk discussion above), assuming that heart rot was necessary for nesting, than in Daily's Colorado site. Evidence for this comes from the fact that only 2.3% of available aspen within my study site showed evidence of cavity construction. Thus, trees with heart rot would tend to be used in successive years and these nest trees may be used for 6 or 7 years in a row (Kilham, 1971).

Besides the hypothesis that there is a limited availability of trees infected with heart rot, several other explanations seem plausible. For example, Gibbon (1970) found that old cavities were frequently used by adults for shelter during wet and windy weather, prior to the completion of nesting cavities. What this suggests is that sapsuckers select nest site territories that contain trees with cavities. Thus, they would have potential roost sites available during inclement weather but, in my study, birds were never found roosting in cavities other than their nest cavity. And, of those birds that roosted in the nest cavity, all were males. Females were observed perched against the trunk of both deciduous and coniferous trees when roosting for the night.

In a study by Rosenberg (1985), it was found that neither adult males nor juveniles roosted in cavities. In his study, birds were found to roost on both live and dead trees on the trunk (including canker crevices < 8 cm deep) and at the fork of major limbs. His study took place after the young had fledged and, thus, males would not be expected to still be roosting in the nest cavity (as mentioned above). Some authors (*e.g.* Evans and Conner, 1979; Thomas *et al.*, 1979) have indicated that sapsuckers use roosting cavities but fail to cite the source of their information. Audubon (1842, referenced in Bent, 1964) made a curious observation of migrating sapsuckers settling in cavities at night during migration. As far as I am aware, no other observations are known to support this claim. Some may argue that this roosting behaviour (*i.e.* not using cavities) by females is a facultative response to cavity availability. However, many cavities were available within the immediate vicinity of the nest site (unpub. data) and were never observed being used. Thus, reasons underlying this roosting behaviour remain unclear.

Characteristics of the nest tree itself are not the only factors that influence nesting use and success. Several studies (*e.g.* Martin, 1988b; Martin and Roper, 1988; Sedgwick and Knopf, 1990; Li and Martin, 1991; Conway and Martin, 1993) have shown that habitat in the area surrounding a potential nest tree also influenced both use and nesting success. In this study, analysis of the patch surrounding the nest suggested that several habitat features were being selected. Tree densities were higher near the nest for live and dead aspens, all dead tree species pooled, and all (both live and dead) tree species pooled. This tendency to choose nest sites with more aspen may reflect choice of patches with more potential nest sites (*i.e.* aspen). Work by others (*e.g.* Martin and Roper, 1988) has shown that predation risk decreases as potential nest sites increase, within the patch. The predator is forced to search more sites to find nests. Alternatively, sites with abundant aspen may be selected to ensure that alternative nesting trees are available within the nest patch, should re-nesting be required.

The results of this study have important management implications. Red-naped Sapsuckers prefer live aspens of larger diameter as nest trees. In addition, nest trees tend to occur in local areas that have high densities of aspen. If trees of a given condition and size are to be left for sapsuckers, particular attention should be paid to clumping levels (*i.e.* trees should be in concentrated patches as opposed to being spread evenly over a given landscape). These trees should be in densities high enough to support successful nesting, the specific densities will depend on particular site characteristics. Some authors believe that tree diameters should be equal to or greater than the minimum dbh recorded for a nest (*e.g.* Bull, 1978; Thomas *et al.*, 1979); others recommend managing for mean diameter

(*e.g.* Conner, 1979). Land managers should bear in mind that many studies report minimum and average sizes of nest trees but fail to indicate the availability of other size ranges. Careful consideration should be given when interpreting the results of other studies.

Habitat that is conducive to aspen regeneration is often created through natural disturbances. Li and Martin (1991) documented declining aspen populations, and suggested that possible nest trees be managed to maintain populations of cavity-nesting birds. They point out that without wood-harvesting or fires (disturbance factors), conifers will eventually succeed aspen. Another factor determining available nesting habitat in riparian woodlands is intensive livestock grazing (Dobkin *et al.*, 1995). As Fahrig (1992) points out, it is the duration of patches as useable habitat that is important and patches should be maintained. If aspens are overtaken, then populations of cavity-nesting birds will most likely decline (Li and Martin, 1991). Thus, it should seem evident that we need to both maintain densities of aspens but also manage for the recruitment of younger trees. This can be achieved through disturbance (*e.g.* fire, forestry activities).

CONCLUSION / MANAGEMENT CONSIDERATIONS

Sapsuckers nesting within British Columbia have been shown to exhibit site fidelity, and hence a home range. Space use can be looked at upon several levels. Within the vicinity of the nest, nest patches (*i.e.* the defendable territory) are approximately 3 ha (*i.e.* 100 m radius). The home range varies but is at least 6 ha based on my measurements. Most activity takes place within 500 m of the nest (a total area of 78 ha assuming a circular range centred at the nest). However, my data show that home range shape is not circular but is dictated by proximity to nearby pairs and habitat availability. Open water and large fields are not utilized *per se* but nests are frequently located beside such open areas. This may be a response to availability of the nesting substrate (*i.e.* aspen grows in disturbed areas) or some inherent need to be near open areas. These questions still remain to be answered.

In Hat Creek, sapsuckers are choosing large diameter (>20 cm) live aspens for nesting. These aspens are infected with heart rot and many exhibit fungal conks on the trunk of the tree. However, reliability of the presence of conks to determine probability of heart rot infection is poor. Coring trees appears to be the only definitive way of confirming infection. Sapsuckers usually excavate new cavities each year. Many holes may be initiated but only one will be used for eventual nesting in that year. Trees used for nesting tend to be re-used and many trees will show numerous cavities within their trunk, as a result. If the nest tree is leaning then cavities are usually placed on the underside of the tree but if there is no significant lean, cavities will vary with respect to orientation.

Typically pairs choose aspens within a large patch of available aspen. Within these aspen patches, sapsuckers are selecting nest sites that are characterized by large diameter live aspens and higher tree densities than other areas within the patch.

Sapsuckers require a source of sap. Within the nesting season, sapsuckers will initially use coniferous trees (*e.g.* Douglas-fir, spruce or juniper) before the deciduous trees have leafed out. Once phloem sap is flowing within deciduous trees/shrubs (*e.g.* aspen, willow), sapsuckers will switch to these richer sources of sap. These plants will be used for the rest of the breeding season as a main source of nutrition. Because aspen and willow are found within riparian areas, this type of habitat (*i.e.* riparian) is crucial to sapsucker foraging activities.

Sapsuckers forage upon large diameter (>30 cm) trees (both coniferous and deciduous) for insects. In my study site, Douglas-fir are heavily utilized in this respect. Typically, birds forage in areas of little understorey and on parts of trees where few branches occur, gleaning insects from the trunks of trees. To a lesser extent, aspens are used for flycatching and bud-eating.

Males are known to roost in nest cavities at night (Howell, 1952) but females roost by clinging to the trunks (>20 cm) of both coniferous and deciduous trees. Reasons why females roost in this manner is unclear and begs further investigation.

Telemetry was an invaluable tool to obtain relatively unbiased estimates of individual's habitat and space use. Many birds travelled well out of visual contact with the nest. One bird travelled at least 1.4 km from its nest. To have relied only on incidental sightings would have biased against true habitat use. The most evident example of this comes from the insect gleaning observations. Very little use of conifers was detected with respect to insect gleaning in 1993 (no telemetry) compared with 1994 (telemetry). Also, observations of birds foraging while being radiotracked (*i.e.* 1994) resulted in larger trees being documented than when birds were merely observed through chance encounters (*i.e.* 1993). Thus, one should consider telemetry as an option when investigating habitat use, where applicable. Telemetry can be an important tool when clear objectives have been drafted *a priori* (Sargeant, 1980). This study was the first to use telemetry as a tool to measure movement and habitat use for any sapsucker species.

This study provides evidence to support the finding that aspen, willow, and heart rot are important components to the life-history of breeding sapsuckers (3 of the 4 factors forming what Daily *et al.* [1993] term the 4-factor keystone complex). Similarly, this study also provides data on the importance of wildlife trees to sapsuckers and hence, the importance of wildlife trees to species that are associated with sapsucker nesting and foraging. If we are to manage communities using keystone species, research must be directed at determining their relative importance within communities. The next step is to quantify the interaction effects that sapsuckers have within the communities they are found. For example, what effect would removal of sapsuckers have on organisms

associated with sapsucker wells? Our overall knowledge of keystone species is limited at this point: we have yet to determine how common they are or even whether all communities are structured by keystone species. As Power *et al.* (1996, p. 618) state with respect to such questions, “we hope that natural ecosystems remain intact long enough for such questions to be addressed, but this outcome depends critically on accelerating the feedback between science and management”.

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