Red-naped Sapsuckers feeding at willows: possible keystone herbivores

Paul R. Ehrlich and Gretchen C. Daily

KEYSTONE MUTUALISTS ARE PLANT species that are critical to the support of pollinators and seed dispersers and thus to the persistence of other plant species (Gilbert 1980). Animal species may play similar roles by making food resources accessible to other species. For example, grazing zebras and wildebeests on the Serengeti Plain of East Africa mow the drying grasses at the end of the wet season, thereby exposing protein-rich non-grass herbs to the small Thomson's gazelles, whose slender muzzles permit them to eat selectively (Sinclair and Norton-Griffiths 1979). Lorikeets in New Guinea also prepare the way for other herbivores; they use their strong, short bills to bite holes in tough fruits, allowing honeyeaters, which are important pollinators, to feed in them with their longer, more delicate bills (Terborgh and Diamond 1970).

Sapsuckers, which create "wells" in the bark of trees and shrubs from which sap flows (Tate 1973), similarly provide other herbivores with access to a resource. The sap is an important component of the diet of sapsuckers, and the use of the wells as a source of nourishment by insects, mammals, and other birds is well known (*e.g.*, Bolles 1891; Batts 1953; Kilham 1953; Kilham 1958; Foster and Tate 1966; Miller and Nero 1983). Much of the literature on sapsucker foraging behavior and interactions with guests has been based on Yellow-bellied Sapsuckers (*Sphyrapicus varius*) and on the use of trees as a sap source. Here we describe the behavior of Red-naped Sapsuckers (*S. nuchalis*) drilling wells in shrubby willows, their impact on the willows, and their rela-

***Figure 1.** Well 3 on August 6. The bark between the active well (major excavation) and the adjacent excavation has been pulled loose (see unfused excavations in Figures 3–5). Note also the exploratory drillings below the main excavation and on the adjacent branch.*

tionships with the other organisms that feed at the wells. Our observations indicate, among other things, that visitors to those wells compete with the sapsuckers for sap, rather than being commensals as is often suggested, and that the sapsuckers do major damage to local willow populations.

Materials and methods

On July 18, 1987, we discovered a Red-naped Sapsucker excavating one of a series of flowing wells in a willow (*Salix subcoerulea*) clump. The clump was located in a moist meadow roughly six hectares in extent, at an elevation of 3000 meters, 0.7 kilometers north of the Rocky Mountain Biological Laboratory (RMBL) at Gothic, Gunnison County, Colorado. The meadow was largely surrounded by groves of Quaking Aspen (*Populus tremuloides*) and scattered Engelmann Spruce (*Picea engelmannii*), and approximately one-half of its surface was occupied by dense patches of shrubby willows, *Salix subcoerulea, S. pseudocordata,* and *S. brachycarpa,* from two to three meters in height.

Our primary study site (Clump A) consisted of a single willow bush (*S. subcoerulea*), roughly five meters × six meters and about three meters high, situated near the center of the meadow. Approximately 90 percent of its branches bore sapsucker wells. Most of the flowing wells were visible at a distance of three meters from the willow, permitting detailed observations of foraging behavior without any apparent disturbance of visitors.

A secondary study site (Clump B), similar in many respects to Clump A, consisted also of a single *S. subcoerulea* bush containing numerous active sapsucker wells. Clumps A and B were located 27 meters apart. A third *S. subcoerulea* bush (Clump E), situated about 20 meters from both Clumps A and B, was excavated late in the study period. Each of these sites was exploited by the same family of four sapsuckers.

A total of 54 hours between July 18 and August 8 was spent watching activity at Clump A, mostly with two observers (101 person-hours). Since this entire study started on the basis of a serendipitous observation, our techniques evolved as we became more familiar with the system. For each session which ranged between 30 minutes and

Figure 2. Close-up of top of Well 3 showing "bearding" of inner bark and phloem caused by the sapsuckers' efforts to keep sap flowing, and the vespid wasp Dolichovespula arenaria *feeding.*

4 hours 20 minutes (average 95 minutes), general records were kept of all activities in the clump—presence or absence of feeding birds, mammals, or insects, feeding behavior, interactions, etc. Times of arrival and departure of all visitors were recorded. Notes were also made on general weather conditions.

In addition, four stems bearing active wells (hereafter, Wells 1–4) were tagged and records were kept of the identity and number of visitors at those wells per five minute interval for a total of 39 of the 54 hours of observation. Many (542) individual visits were timed, a visit being defined as the period of time beginning when an individual first arrived at a well and began to feed and ending when it departed. We also kept record of the number of visits individuals made to all wells during a single visit to the clump. While the four sapsuckers observed could be identified individually, it was not possible to keep track of individuals of other species except during a single foraging bout in the clump.

Most observations were made between 0515 hrs. and 2100 hrs. Some night observations were made with the use of a flashlight, but no visitors were detected in the clump during the hours of darkness.

In order to get a measure of the quality of the resource available to the visitors, the percent sugar content of the sap present in the four tagged wells in Clump A and of three tagged wells in Clump B was monitored. Measurements were made with a Kyowa temperature-compensated hand refractometer which could detect sugar concentrations from 0 to 92 percent (weight/weight, expressed as sucrose). The sap measurements were made weekly at 0600 hrs., before any feeding occurred at the wells, and more frequently at other times of day. The sap, presumably sieve tube exudate, was transferred on a finger tip from the area of the well where it was most abundant (usually the top) to the refractometer. In some cases this procedure probably led to overestimates of the sugar concentration in the phloem sieve tubes, since some concentration by evaporation doubtless occurred over the course of a day. The amount of sap available at each well was recorded qualitatively.

Artificial wells were cut in willows with a penknife in an attempt to simulate sapsucker activity. Both small and shallow cuts resembling exploratory wells, and large, rectangular, deeper cuts resembling major wells were made.

While the only active sapsucker wells we found in the meadow initially were in Clumps A and B, damage from past sapsucker activity was visible in many other clumps. This damage was assayed along three 50 meter transects running parallel across the meadow. The percentage of willow limbs showing characteristic sapsucker damage within a quadrat one meter square, located one meter into the bush, was estimated at 20 places (determined from a table of random numbers) along each transect. The percentage of the damaged limbs which were dead was also recorded.

Willows in the vicinity of RMBL and in other areas of Gunnison County were surveyed for signs of sapsucker activity. In clumps currently being exploited by sapsuckers, a count of the number of active wells was made.

All appropriate statistical tests have been done; the details are available from the authors.

Figure 3. *Top: Adult male Red-naped Sapsucker visiting Well 3 on July 29. Bottom: Same individual enlarging top of well.*

Results

Wells in willows

The creation of wells in willows by the Red-naped Sapsucker is apparently an old but previously uninvestigated practice in the vicinity of RMBL. While we and many others were conscious of the extensive scarring of aspen caused by sapsucker drilling early in the season, the extensive use of shrubby willows had not attracted the attention of biologists working at the lab. In the meadow where most observations were made, 72 percent of the willow bushes assayed bore severely damaged stems. Within a bush, 28 percent of the stems were damaged on average and 98 percent of the damaged stems were dead. All of the recent damage was clearly the result of sapsucker excavation—the well cavities were still sharply defined. However, some dead stems, estimated to be at least five years old, had decayed to a point where the agent of the damage could not be determined for certain.

It appears that sapsucker exploitation of a willow bush involves the following sequence. First, the birds drill small exploratory wells (about 2 mm $\times$ 5 mm $\times$ 1 mm deep), which just penetrate the bark, and in off-set rows completely girdle the branch (Fig. 1). Some of the exploratory wells, drilled into stems of all sizes, exude sap that runs down the branch. Sapsuckers remove the outer, corky bark and the inner bark (phloem) as far in as the cambium or the outer surface of the xylem, enlarging a number of exploratory wells until they form a single major well (Fig. 1, 3–5). A fully excavated stem typically bears numerous (20 to 80) exploratory wells and several (two to 15) major wells. Foraging was observed only at major wells.

As the season progresses, the major wells are enlarged from the top by hammering at the bark and peeling it back. Eventually these wells may achieve considerable size (up to about 100 mm $\times$ 15 mm $\times$ 3 mm). While remaining apparently healthy during the season in which damage is inflicted, in the following spring the buds on the damaged branches do not expand, presumably because destruction of the cambium prevents formation of necessary new transport systems (xylem and phloem), and these branches die. It thus appears that new wells are drilled into healthy, previously unused branches, each season.

Clump A had apparently been exploited by sapsuckers and possibly by the same adult pair, for several consecutive years. The wells in the bush became progressively older from the exposed side (consisting of 32 stems bearing active wells) which was under current excavation to the opposite side (consisting of at least 50 well-bearing stems) where the scars from sapsucker activity appeared to be several years old. Virtually all of the stems (over 100) of another active clump used by a different sapsucker family, however, were completely girdled by recently drilled wells. It seems unlikely that this clump will recover sufficiently to be used in the next few years.

Active sapsucker wells were eventually located in six willow clumps in the immediate vicinity of RMBL. Both old sapsucker damage and active wells in willows were also found near Peanut Lake, nine kilometers south of RMBL, at an elevation of 2680 meters, at the end of the Virginia Mine Road (about two kilometers north of RMBL) at 3230 meters elevation, and at the second crossing of Copper Creek, about four kilometers northeast of RMBL, at 3200 meters elevation. In each case the surrounding habitat included aspen trees and a source of water. No signs of sapsucker activity were noted in extensive willow stands in the vicinity of Blue Mesa reservoir, 60 kilometers south of RMBL, at 2380 meters elevation. Where we assayed, only two willow species, *Salix subcoerulea* and *S. pseudocordata,* were used by sapsuckers.

Sap

We made 97 successful sap measurements (there was not enough sap to get a reading in 22 attempts). The sugar content of the sap, expressed as sucrose, ranged from 7.0 (diluted by rain) to 48.5 percent (weight/weight) with a mean of 29.0 percent. The sugar concentration of the sap was consistently about 20 percent at each well in the early morning (before 0900 hrs.), as is typical of sieve tube exudate (Crafts and Crisp 1971). The concentration increased throughout the day as evaporation took place. Wells 1, 2, and 4 were highly correlated ($P < 0.05$ in each case) in sap concentration. Well 3 did not correlate significantly with any other well. We found no significant difference between the mean sap concentration at the wells on mostly sunny versus mostly cloudy days. We also found that the amount of sap varied independently of cloud cover (mostly sunny versus mostly cloudy).

Figure 4. *Juvenile male Red-naped Sapsucker visiting Well 3 about August 6. Note enlargement of the well from its size roughly a week before shown in Figure 5.*

Continuous sap flow seemed to require daily maintenance and excavation at the top of the wells by sapsuckers, where the cambium is shredded to a bearded state (Fig. 2). Our artificial wells, which were not continuously worked, never yielded any sap. Natural wells unattended by sapsuckers rapidly dried up.

Figure 5. *Juvenile female Red-naped Sapsucker visiting Well 3 on July 29. Adult male at bottom right.*

Sapsucker foraging activity

The sapsucker family that worked Clump A consisted of an adult male (Fig. 3) and female and a juvenile male (Fig. 4) and female (Fig. 5). Only the adult sapsuckers created, maintained, and enlarged the wells. The juveniles foraged upon the sap thus provided and were also fed adult stoneflies, crane flies, and sap-soaked willow fibers procured by their parents. The average duration of the 80 timed visits to monitored wells by the adult male sapsucker was 49 seconds, while the adult female, timed on 43 occasions, spent an average of 51 seconds at monitored wells. The adults divided this time between feeding and hammering at the tops of the wells. The juvenile female, which spent most of its visit time feeding, averaged 52 seconds on 42 timed visits. No times were obtained for the juvenile male.

Use of the wells in Clump A by the sapsucker family declined over the study period. Initially (through July 27), sapsuckers were present during 57 percent of the observation time, but in the latter part of the study period they were seen there only 13 percent of the time. This decline coincided both with an increase in activity at Clump B and with the initial excavation of a nearby bush, Clump E. In addition, the sapsuckers were frequently seen flying toward and from one direction, suggesting that they may have been developing other wells which we did not locate.

On six occasions we observed an adult sapsucker arrive at Clump A with a stonefly or crane fly, at least one of which was then soaked in sap from the wells. We never saw the adult eat the insect. Twice we observed it fed to a juvenile, and four times the adult flew with it toward the presumed location of a juvenile (we heard the juvenile give the usual begging call on two of these latter occasions).

Throughout the study period the sapsuckers were rarely unaccompanied in Clump A (22 percent of the time alone); in fact, during 84 percent of the total observation time, other species were feeding on sap from the wells (this includes substantial periods when the sapsuckers were absent).

Figure 6. *Orange-crowned Warbler visiting Well 2 on August 5.*

Avian visitors

Orange-crowned Warblers (*Vermivora celata*) were the most frequent visitors to the sapsucker wells (Fig. 6). The individuals were either first-fall immatures or molting adults (or a mix of the two). It was not possible to determine which without having the birds in hand. On two occasions we caught a glimpse of a female or immature Wilson's Warbler (*Wilsonia pusilla*) in the clump, but not feeding.

Warblers were observed in the clump during 94 percent of our observation sessions. At least one individual was present 42 percent of the total observation time. The average visit length of 284 timed warbler visits to monitored wells was 18 seconds. Virtually all of this time was spent feeding where sap was most abundant—either from the top or from accumulations at the bottom of major wells. Warblers were found at the wells at virtually all times of day between 0545 hrs. and 2020 hrs. The warblers did not enlarge or maintain the sapsucker wells.

The visiting warblers were thoroughly familiar with the location and productivity of wells in Clump A. They typically arrived directly at an active well and proceeded to forage at the most productive wells in a stereotyped sequence, spending no time searching for wells and avoiding those which were dry.

Very rarely were two warblers observed feeding from the same well simultaneously, though frequently up to four foraged in the clump together. Dominance clearly existed, allowing one warbler to consistently displace another from a well. Often the displacements involved chasing and fighting (the clashing of wings).

Female and juvenile male hummingbirds were the next most common visitors to the wells in Clump A and were present 19 percent of the time, although often resting, rather than foraging. Their visits occurred during 22 of our 32 observation periods at all times of day between 0545 hrs. and 2020 hrs. Both Rufous Hummingbirds (*Selasphorus rufus*, Fig. 7) and Broad-tailed Hummingbirds (*S. platycercus*) were positively identified on several occasions. The data for all species of hummingbird are lumped, since in most cases positive determinations of the species could not be made.

The average length of 74 timed hummingbird visits to monitored wells was 8 seconds. Usually the hummingbirds hovered beside the well to feed and then perched nearby for several minutes before feeding again or flying off. The hummingbirds also moved only among the most productive wells. Considerable chasing occurred among foraging female and juvenile male hummingbirds. No adult males ever visited the wells though they commonly flew to within a meter of them and displayed to foraging females.

Mammalian visitors

Chipmunks, identified without trapping as *Eutamius minimus*, were observed in Clump A on 16 occasions, at various times of day between 0645 hrs. and 1830 hrs. They quickly and furtively licked the sap only from the active wells, sometimes feeding along a length of stem below wells where sap had dried and was not exploited by the birds. They clearly knew the positions of flowing wells precisely. On one occasion two chipmunks fed simultaneously in the clump without interacting.

The average length of 19 timed chipmunk visits to a well was 26 seconds. Their visits to the clump were often cut short by sapsuckers, which sometimes chased the chipmunks out even before feeding had taken place.

A Red Squirrel (*Tamiasciurus hudsonicus*, Fig. 8) was observed feeding at the sapsucker wells on four occasions. Foraging bouts which involved visiting several productive wells lasted on av-

Figure 7. Juvenile male Rufous Hummingbird visiting Well 2 about July 28.

erage 20 minutes. The squirrel licked sap from the wells and stems in a manner similar to that of the chipmunks.

Insect visitors

Yellow-and-black (hereafter, "yellow") vespid wasps (*Dolichovespula arenaria* Fabricius, Fig. 2) frequented the wells in Clump A with increasing regularity as sapsucker activity declined toward the end of the season. Both the numbers of these vespids and the amount of time they were present increased dramatically at the end of the study period. Initially the wasps were present only 16 percent of the observation time, and at most a few were in the clump simultaneously. In the last days of the study (August 1 to 8), yellow wasps foraged at the wells 81 percent of the observation time and one or two dozen were usually present.

The yellow vespids fed almost exclusively from the small area at the top of wells. The wasps fought with each other a great deal, and the turnover of individuals on a well was very high. On August 7, over a two-minute period, we observed 58 battles in which pairs of wasps fell together in combat from a single well. During about 95 percent of that period, there was more than one wasp at the well, and an additional one or more arriving and trying to displace the occupant.

Largely black vespids (*Vespula*? sp.) and sarcophagid flies were also seen at the wells a few times, usually individually. Only occasionally were other insect species seen visiting. Ants were never seen at the wells during the day, and night observations revealed neither ants nor moths taking sap. On two occasions an adult sapsucker made halfhearted, unsuccessful attempts to catch bumblebees (*Bombus* sp.), and once one ate an insect gleaned from a willow branch. A warbler was once observed catching and eating an insect from a well. No other predation by any of the birds on insects feeding at the wells was observed.

Interspecific interactions

The foraging behavior of each visitor to the sapsucker wells was determined to a large degree by which other visitors were present at the same time. The sapsuckers aggressively chased hummingbirds, warblers, and chipmunks from the wells, with only momentary success. Usually the uninvited guest would move to the next nearest well and continue feeding there until chased again. Sometimes a sapsucker pursued warblers along a circuit of many wells and then gave up and tolerated their presence. By the end of the observation period, the juvenile sapsuckers were as aggressive and effective as the adults. After a chase, the sapsucker resumed working or feeding at the nearest active well, not at the one it had originally occupied.

Although the visiting squirrel appeared to cause great distress to the sapsuckers, it was never chased. On one occasion it fed continuously for 33 minutes; all the while, the adult male sapsucker called loudly and followed the squirrel from well to well, but never got within striking distance. Twice the squirrel chased a juvenile sapsucker to gain access to another well.

The warblers assumed dominance over the hummingbirds and chipmunks in the absence of sapsuckers and squirrels. They did not lunge after them as the sapsuckers did in an attempt to guard the wells, but when a warbler landed on an occupied well, the original resident quickly and quietly departed. The chipmunks were the most nervous of the vertebrates and usually left the clump at the slightest disturbance.

The yellow-and-black vespid wasps were very attuned to the presence of birds and mammals at the wells and rarely fed when they were there. Virtually all of the wasps vanished immediately when a vertebrate entered the clump, only to return just as quickly upon its departure.

Discussion

Although our observations cover only a segment of a season in one locality, we suspect that many of our conclusions about the biology of Red-naped Sapsuckers and associated species in Gunnison County will apply in a much broader geographic area, and to other species of sapsuckers as well. For example, the classic work of McAtee (1911) on the impact of woodpeckers on trees suggests that the Red-naped Sapsucker also depends heavily on shrubby willows in other areas. Use of numerous species of willows is recorded, and damage very similar to that we observed is pictured (Plate V, Figs. 4,5). The almost completely debarked branch shown on McAtee's Plate V, Fig. 5, was collected in the Black Hills of South Dakota, where Red-naped Sapsuckers apparently damage willows heavily just as they do in Colorado.

Figure 8. Red squirrel feeding at Well 4.

Similar use of shrubby willow appears to occur in populations of the Red-breasted Sapsucker (*S. ruber*), which has (under the name *S. varius*) been reported to feed extensively on willows in the Grizzly Creek drainage of northwestern California (Sutherland *et al.* 1982). The Red-breasted Sapsuckers there maintained wells in dense thickets of alders and willows at about 1900 meters in late July and early August in a manner that appears to be entirely analogous to the behavior of the Gunnison County Red-naped Sapsuckers. "Flocks of immature warblers" (mostly Nashville, *Vermivora ruficapilla,* Orange-crowned, and Wilson's), visit these wells, which also form the resource base of feeding territories of Rufous Hummingbirds. Sutherland and his colleagues were, however, studying the system from the point of view of the hummingbirds, so a detailed comparison of the behavior of the two sapsucker species is not possible. Damage by Red-breasted Sapsuckers (McAtee 1911) on a rather large willow in California looks (Plate VI, labeled *S. varius daggetti*) and is described (p. 28) as similar to that figured and described here for the Red-naped Sapsucker.

The degree to which Yellow-bellied Sapsuckers and Williamson's Sapsuckers (*S. thyroideus*) may use shrubby willows is not clear. Damage to willows is listed by McAtee within the range of both, but no details are given. Crocket (1975) reported Williamson's Sapsuckers taking sap and sapwood exclusively from conifers on the breeding grounds.

The impact of the Red-naped Sapsuckers on willow populations in the vicinity of Gothic is severe, probably greater than that of any other herbivore that feeds on the willows in the summer, but we have not been able to evaluate mammalian browsing in other seasons. Indeed, damage is so extensive that it might influence the longevity and dimensions of individual willow clumps. The willows do not appear to have evolved any chemical defenses against the sapsuckers, in spite of what appears to be a potentially strong selective pressure to do so. Perhaps the sapsuckers are able simply to avoid eating the portion of the bark that contains unpalatable or potentially toxic compounds, the best known of which is salicylic acid. Typical plant defensive compounds remain in place in structures such as leaves, flowers, fruits, and bark. To defend the phloem sap with toxins, however, the plant would have to add poisons continuously at the leaves and then detoxify the sap at its destinations. Evolution of such a defensive strategy would involve high metabolic costs, but these might be compensated by reduced sapsucker activity.

The sapsucker-willow association may, however, be too recent evolutionarily for the willows to have been able to respond to the sapsucker attack. The willows probably exist as large clones, are slow-growing at high altitude, and only suffer from sapsucker attack when quite large. Therefore, the time required for the sapsuckers to cause significant differential reproduction among the clones might be very long. Nonetheless, detailed investigations of the chemical defenses of willow stems such as those done on toxic phenolglucosides of willow leaves (*e.g.*, Rowell-Rahier *et al.* 1987) would be desirable.

One of the more interesting findings was the necessity for the sapsuckers to work assiduously at the upper end of the wells to keep the sap flowing, presumably by repeatedly injuring the phloem sieve tubes, circumventing their sieve plate plugging mechanisms. Although in many plants sieve tube exudation ceases within minutes after an injury, the sieve tubes in certain plants will continue to exude sap for up to several hours (Crafts and Crisp 1971). The sieve-plate plugging time for the willows appeared to be in the latter range, since we often saw warblers feeding hours after the most recently recorded sapsucker visit and, as noted above, warblers did not work to maintain sap flow or enlarge the wells. We could not, of course, determine the extent to which the warblers were just taking residual sap that had been exuded earlier. The girdling or near-girdling of the stems by the sapsuckers probably caused nutrients to accumulate just above the wells (Kilham 1964), where they could be tapped by further drilling. The "beard" of phloem fibers at the well's upper edge, created by the sapsuckers' drilling activities, appeared to act as a wick, making the flow more accessible to the birds.

The sap of *Salix subcoerulea* was a rich resource in comparison with that of *Salix commutata* at the California site (Sutherland *et al.* 1982), which averaged only 15.3 percent sugar. Also, in contrast, there was no significant variation in sap flow during the day in *S. commutata,* although detailed studies of the sugar content of the sieve tube exudate of oak (Huber *et al.* 1937) and white ash (Zimmermann, 1958) both showed peak concentrations at night and lower concentrations in the morning. Our measurements of sugar concentration in the sap are also higher than those reported by Southwick and Southwick (1980) for the yield from Yellow-bellied Sapsucker wells in Paper Birch (*Betula papyrifera*) in Michigan (16 percent) but well within the "normal" range of 15–25 percent for angiosperms (Huber 1958) if we consider our higher readings to be a result of concentration by evaporation on the stem. Baker (1975) found the nectar of average hummingbird flowers to average somewhat over 20 percent sugar. That is generally less concentrated than the nectar of bee flowers (30–50 percent), possibly because higher concentrations would involve higher viscosity and increase the hover time required to "fill up", and possibly because of the need of hummingbirds for water as well as sugar. In any case, willow phloem sap may be most suitable for hummingbirds when it has not been concentrated by evaporation.

The persistently aggressive behavior of the sapsuckers toward the smaller vertebrate visitors certainly suggests that the other birds and mammals are serious competitors for the resource. The sapsuckers were more than "dominant" to the visitors; sapsuckers did not simply displace "commensals" from wells, but often actively pursued the visitors in obvious attempts to chase them out of the clump. The Yellow-bellied Sapsucker shows similar behavior, chasing all visitors except for Red Squirrels that, as at RMBL, would feed for almost 30 minutes while the birds "appeared to be annoyed" at being driven from their wells (Kilham 1958). It seems safe to conclude, since the wells are defended against all smaller vertebrate visitors, that for both species the visitors are not "commensal" feeders (Freer and Murray 1935; Kilham 1958; Kilham 1964; Foster and Tate 1966; Miller and Nero 1983). By definition commensals do not cause harm to their partners, and there would be no reason for the aggressive behavior of the sapsuckers if the resource were superabundant. The original description of Bolles (1891) of "numerous parasitical Hummingbirds" visiting the wells appears to be more accurate. In addition, both warblers and wasps showed evidence of competing for the sap resource. Much of their aggressive activity was at periods when flow in the wells was far from copious and many wells were dry, suggesting that the supply of sap was then severely limited.

It was not clear why the sapsuckers partly shifted their activities from Clump A to Clumps B and E (and possibly others) toward the end of the season. It may have become more difficult to keep the large wells in clump A flowing, although the leaves above them showed no signs of wilting. Or it is possible that the vertebrate competitors for the sap were becoming too efficient at robbing the wells? Shifting to a new clump may reduce competition from chipmunks and squirrels, which could have difficulty locating the new site.

Our results confirm the results of others (*e.g.*, Bolles 1891; Kilham 1964) that any taking of insects near the wells is coincidental, and that the sap from the wells does not function primarily as an attractant for insect prey. Indeed, in contrast to reports for Yellow-bellied Sapsucker wells (*e.g.* Nickell 1956; Nickell 1965; Foster and Tate 1966), the scarcity of insects other than the wasps was striking at all times. Furthermore, on the few occasions when stoneflies were brought by adults to the clump, the insects were not always worked into the sap. The frequency of this behavior may be lower in the Red-naped than in the Yellow-bellied Sapsucker (Foster and Tate 1966). Further observations on parental feeding earlier in the season, when the juveniles are younger, are needed.

It appears that the sapsuckers are making a key resource available to other species. Evidence is building, for example, that the dates of spring arrival and the northern breeding range of Ruby-throated Hummingbirds and, possibly, of Rufous Hummingbirds, are determined by the availability of sap from the wells of Yellow-bellied Sapsuckers (Bertin 1982; Miller and Nero 1983). The heavy warbler-hummingbird use of the RMBL area wells suggests that the wells could provide a vital late-season dietary supplement at a time when both insects and floral nectar are becoming less available.

That only juvenile and female hummingbirds visited the wells is especially intriguing—and follows the pattern reported by Sutherland *et al.* (1982) at the Red-breasted Sapsucker wells in California. Is the sap resource in some way inferior, so that male hummingbirds do not use it? If adults need higher protein to rebound from the rigors of reproduction it is difficult to explain the use of sap by female hummingbirds.

Many other questions need answering. For instance, do the warblers also visit flowers for nectar? Do individual warblers or hummingbirds trapline among wells and other points of resource concentration as do some tropical bees and butterflies (*cf.* Janzen, 1971)? What proportion of the sapsuckers' and visitors' diets is actually supplied by the willow wells? Does a decline in bird feeding activity permit the late-season build-up of wasp visitors? Why are there no nocturnal visits from ants or moths?

Much, of course, could be learned by investigating the foraging of sapsuckers and their associates during the rest of the season in the RMBL area. For instance, do any of the visitors to the willow wells also use sap from sapsucker wells drilled into aspen earlier in the season? Does the carbohydrate content of different plants change seasonally and influence sapsucker and visitor feeding patterns? What limited the array of avian visitors during our observations? Based on visitors to Yellow-bellied and Williamson's sapsucker wells reported by Foster and Tate (1966), Batts (1953), and Crockett (1975), at least Downy and Hairy woodpeckers (*Picoides pubescens* and *P. villosus*), White-breasted Nuthatches (*Sitta carolinensis*), House Wrens (*Troglodytes aedon*), Mountain Chickadees (*Parus gambeli*), Ruby-crowned Kinglets (*Regulus calendula*), Yellow-rumped Warblers (*Dendroica coronata*), and Pine Siskins (*Carduelis pinus*), a mix of residents and migrants, would seem to be potential users.

Answers to several of the questions posed above will help to test our preliminary hypothesis that the sapsuckers serve as keystone species by providing access to food. They could, of course, also play a keystone role by excavating tree holes that are later used by secondary cavity-nesters. If we are correct, however, they would not be "keystone mutualists" in the strict sense of Gilbert (1980). First of all, although some of the animals the sapsuckers help to support are involved in pollination or seed dispersal, the visitors to the wells do not constitute a "large complex of mobile links"—that is, of animals that are significant to the support of several plant species. Playing a central role in the maintenance of such a complex is the defining characteristic of a keystone mutualist (Gilbert 1980). In addition, the sapsuckers are not mutualists. They are probably harmed by the species that take sap from the wells, are not benefited by species that may subsequently nest in their cavities, and do considerable damage to willows. It would thus seem best to describe them simply as "keystone herbivores."

ACKNOWLEDGMENTS

We thank Susan Allen, Jack Baughman, Paul Buck, William Calder, Jared Diamond, Karen Holl, John McLaughlin, Stuart Pimm, Peter Ray, Van Remsen, Thomas Sisk, Philip Ward, Nickolas Waser, and David Wilcove for help with various aspects of this work.

LITERATURE CITED

BAKER, H. G. 1975. Sugar concentrations in nectars from hummingbird flowers. *Biotropica* 7:37–41.

BATTS, H. L. 1953. Siskin and goldfinch feeding at sapsucker tree. *Wilson Bull.* 65:198.

BERTIN, R. I. 1982. The Ruby-throated Hummingbird and its major food plants: ranges, flowering phenology, and migration. *Can. J. Zool.* 60:210–219.

BOLLES, F. 1891. Yellow-bellied Woodpeckers and their uninvited guests. *Auk* 8:256–270.

CRAFTS, A. S., and C. E. CRISP. 1971. Phloem transport in plants. Freeman, San Francisco.

CROCKETT, A. B. 1975. Ecology and behavior of the Williamson's Sapsucker in Colorado. Unpublished Ph.D. diss., University of Colorado, Boulder.

FOSTER, W. L., and J. TATE, Jr. 1966. The activities and coactions of animals at sapsucker trees. *Living Bird* 5:87–113.

FREER, R. S., and J. J. MURRAY. 1935. The Yellow-bellied Sapsucker and the Ruby-throated Hummingbird—commensals? *Auk* 52:187–188.

GILBERT, L. E. 1980. Food web organization and the conservation of neotropical diversity. Pp. 11–33 *in* Soulé, M. E. and B. A. Wilcox (Eds.). Conservation Biology: An evolutionary-ecological perspective, Sinauer, Sunderland, Mass.

HUBER, B. 1958. Anatomical and physiological investigations of food translocation in trees. Pp. 367–379 *in* Thiman, K (Ed.). The Physiology of Forest Trees Ronald Press, New York.

——, E. SCHMIDT, and H. JAHNEL 1937. Untersuchungen über den Assimilatstrom I. *Tharandt. forstl. Jahrb.* 88 1017–1050.

JANZEN, D. H. 1971. Euglossine bees as long-distance pollinators of tropical plants. *Science* 171:203–205.

KILHAM, L. 1953. Warblers, hummingbird, and sapsucker feeding on sap of yellow birch. *Wilson Bull.* 65:198.

——. 1958. Red squirrels feeding at sapsucker holes. *J. Mammal.* 39:4–5.

——. 1964. The relations of breeding Yellow-bellied Sapsuckers to wounded birches and other trees. *Auk* 81:520–527

McATEE, W. L. 1911. Woodpeckers in relation to trees and wood products. U.S Department of Agriculture, Biological Survey, Bulletin No. 39.

MILLER, R. S., and R. W. NERO. 1983 Hummingbird-sapsucker associations in northern climates. *Can. J. Zool.* 61:1540–1546.

NICKELL, W. P. 1956. Bird and insect guests at a sapsucker tree. *Jack-Pine Warbler* 34:117.

—— 1965. Birds and insects feed at sapsucker trees. *Bird-Banding* 36:192.

ROWELL-RAHIER, M., P. SOETENS, and J. M. PASTEELS. 1987. Influence of phenolglucosides on the distribution of herbivores on willows. Pp. 91–95 *in* Labeyrie V., G. Fabres, and D. Lachaise (Eds.). Insects—Plants. Junk, Dordrecht.

SINCLAIR, A. R. E., and M. NORTON-GRIFFITHS. (Eds.) 1979. Serengeti: Dynamics of an ecosystem. Univ. of Chicago Press, Chicago.

SOUTHWICK, E. E. and A. K. SOUTHWICK. 1980. Energetics of feeding on tree sap by Ruby-throated Hummingbirds in Michigan. *Amer. Midl. Nat.* 104. 328–334.

SUTHERLAND, G. D., C. L. GASS, P. A. THOMPSON, and K. P. LERTZMAN 1982. Feeding territoriality in migrant rufous hummingbirds: defense of yellow-bellied sapsucker (*Sphyrapicus varius*) feeding sites. *Can. J. Zool.* 60:2046–2050.

TATE, J. Jr. 1973. Methods and annual sequence of foraging by the sapsucker. *Auk* 90:840–856.

TERBORGH, J., and J. M. DIAMOND. 1970. Niche overlap in feeding assemblages of New Guinea birds. *Wilson Bull* 82:29–52.

ZIMMERMANN, M. H. 1958. Translocation of organic substances in the phloem of trees. Pp. 381–400 *in* Thiman, K. (Ed.). The Physiology of Forest Trees. Ronald Press, New York.

—*Department of Biological Sciences, Stanford University, Stanford, CA 94305 and Rocky Mountain Biological Laboratory, Crested Butte, CO 81224*
(Ehrlich and Daily)