One of the most intriguing mysteries about the system was whether or not other species really depend upon the sapsuckers.

As READERS OF THIS column will remember, Paul Ehrlich watches Red-naped Sapsuckers for fun more than any other bird. His collaborator in this activity (and in writing this column) is Gretchen Daily, whose Stanford doctoral dissertation included work on sapsucker biology.

At first it seemed nothing could be more fascinating about Rednaped Sapsuckers than the feeding and social activity of the birds, mammals, and insects that crowd into willow shrubs to gorge on the sugary sap flowing from sapsucker wells. Curiosity drove us to spend months in sapsucker habitat, crawling through and examining the willow thickets for miles around, enduring persistent clouds of mosquitoes and biting flies to film and take data on visitors of the wells, plotting endlessly to outsmart and capture

wiley sapsuckers and chipmunk visitors, and generally driving our friends crazy with daily "sapsucker stories" (*American Birds* 42(3): 357–365 [1988] and 44(5): 1067–1070 [1990]). Instead of satisfying our curiosity, this work further intensified our interest in the sapsucker system.

One of the most intriguing mysteries about the system was whether or not other species really depend upon the sapsuckers. The visitors to sapsucker wells may benefit substantially from exploiting the rich sap resource, supplied when many are breeding and then storing fat for the winter's migration or hibernation.



Sapsuckers, Swallows, Willow, Aspen, and Rot

Illustration by Darryl Wheye Most of those species are highly omnivorous, however, making it difficult to determine exactly how much their populations would suffer were the sapsucker, and hence the sap resource, to disappear.

This led us to delve into another feature of the sapsucker's lifestyle that appeared to benefit a second suite of species-the excavating of nest holes. In the vicinity of the Rocky Mountain Biological Laboratory in Gunnison County, Colorado, a sapsucker pair drills a new nest hole each year in an aspen infected with heartwood fungus. Of 36 active sapsucker nests in the area, only one was situated in an old hole (one that had been excavated the previous year). We tracked the occupancy of old holes and found seven different bird species raising their young in them: Tree Swallows, Violet-Green Swallows. House Wrens, Moun-

tain Bluebirds, Mountain Chickadees, Northern Flickers, and a Williamson's Sapsucker pair.

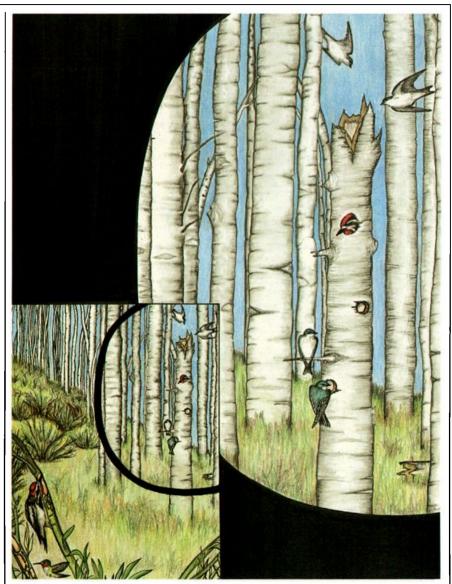
We found that Red-naped Sapsuckers create at least ten times as many nest holes as any of the less common woodpeckers near the Rocky Mountain Biological Laboratory. Since a shortage of nest holes may limit the population sizes of species incapable of creating their own cavities, we suspected that the presence of sapsuckers might be vital to these secondary cavity nesters. How could we find out whether the sapsuckers were indeed crucial to the others?

Back in the 1950s, biologists would have simply shot all the sapsuckers near the Biological Laboratory to see whether the populations of other bird species would change as a consequence. Fortunately, the times have changed, and such brute-force approaches are now rightly condemned. We sought an indirect method that, with luck, would give us the answer. Our strategy involved first identifying a critical feature of habitat required by the sapsuckers themselves. Then, we planned to compare the bird communities in habitat patches with and without that one feature, and thus with and without sapsuckers. This would allow us to infer the effect of removing the sapsucker.

Sensing that all of this would require a lot of work, we enlisted the enthusiastic help of Nick Haddad, a Stanford honors student with experience in censusing birds. The three of us embarked on this project together during the summer of 1991 at the Rocky Mountain Biological Laboratory.

The most obvious candidate for a critical habitat feature for supporting sapsuckers seemed to be the proximity of suitable willow shrubs (for drilling sap wells) and aspen (for nesting). Our working hypothesis was that the sapsucker would not occur in areas near the Biological Laboratory lacking in either willow or aspen. To test this, we surveyed over 13,000 aspen trees located at varying distances from willow shrubs for signs of sapsucker wells. Sapsuckers drill wells into aspen early in the breeding season, before the willows leaf out; the damage they cause remains distinctive for at least 10 years, providing an indication of habitat occupied by sapsuckers.

Indeed, we found that as many as 35 percent of the aspens in very close proximity (fewer than 15 meters) to willows bore sapsucker damage, whereas fewer than 5 percent that were far (more than 1000 meters) from willow did. Not only was there much more damage on trees close to



Sapsucker systems may contain subtle interrelationships between species.

willow, there were also more nest cavities. In general, we couldn't attribute a nest cavity to any particular primary cavity nester. However, the high prevalence of wells drilled around the nest trees suggested that many were created by sapsuckers.

We also surveyed willow clumps situated close to and far from aspen for signs of damage. Here again, we only found sapsucker damage in willows close to aspen. Willows near large spruce stands or in open, treeless mountain meadows bore no damage at all. These surveys showed us that sapsuckers were only present in areas with both willow and aspen.

This provided an ideal way to test the importance of the sapsucker to other birds. We established census plots of 5.25 hectares (about 13 acres) in six aspen groves, three near (fewer than 20 meters) willow and three over one kilometer away from the nearest willow shrub. Then, for the next six weeks, the three of us spent each early morning censusing the breeding birds in the plots.

Other than the proximity of the willow, the aspen groves were selected to be as similar as possible. We found out, for example, that it was possible to be bitten and sucked dry by voracious mosquitoes in a matter of minutes at all sites. It was certainly encouraging that insect populations seemed able to support a rich community of avian insectivores at each site.

As we predicted, sapsuckers were only present in the three sites close to

willow. Interestingly, we found both Violet-green and Tree swallows *only* in the three sites which had sapsuckers. A statistical test showed that the chance of the association of swallows and sapsuckers being purely coincidental was vanishingly small. Tree Swallows virtually always nest in cavities, and while Violet-green Swallows are known to nest in cliffs, no such opportunity was available at any of our sites.

All of the other secondary cavity nesters were present in each of the six sites. We discovered that they were generally more common in the sapsucker sites, however. Their abundance in the non-sapsucker sites (far from willow) seemed to depend upon the availability of alternative nesting locations. So, for example, we found many House Wrens in sites littered with fallen, rotting logs, a favorite non-cavity nesting location, and no House Wrens at all in a nonsapsucker site without fallen logs.

It thus seemed that the sapsuckers could be quite important in the persistence of secondary cavity nesting birds. But how could we be sure that the absence of swallows and lower abundances of other secondary cavity nesters in non-sapsucker sites was not due to some other factor? Perhaps there happened to be less food in the non-sapsucker sites. The swarms of insects present at all sites made that possibility seem unlikely, but such anecdotal evidence is not very admissible in science. That's why we also censused species of insectivorous birds that were not secondary hole-nesters, to see whether they too would be much more abundant in the plots with sapsuckers.

We found that open-nesting insectivorous birds occurred in roughly equal abundances on all sites. Most sites had 5–6 pairs of Dark-eyed Juncos, 2–4 pairs of American Robins, 1–2 pairs of Hermit Thrushes, 3–6 pairs of Warbling Vireos, and a couple of pairs of Yellow-rumped Warblers and Western Wood-Pewees. The Western Wood-Pewee forages aerially upon insects, like swallows do, further making it unlikely that the absence of swallows could be attributed to anything but the absence of nest holes.

This project led to three discoveries about the biological communities around Rocky Mountain Biological Laboratory. First, we found that swallows, and to a lesser extent the other secondary cavity nesters, depend upon the co-occurrence of at least four elements of what we have called a keystone species complex: the Rednaped Sapsucker, aspen trees, certain willow species (in which the sapsuckers can drill wells), and the heartwood fungus. The disappearance of any one element could result in the local extinction of the swallows and declines in the populations of the other secondary cavity nesters.

Second, the sapsucker has the unusual characteristic of playing two distinct keystone roles: enhancing the persistence of both sap-robbers and cavity nesters. Finally, while the tropics have classically been thought of as supporting species with complex, indirect, and subtle interrelationships, this work suggests that such interdependencies may be common in the temperate zone as well. Saving a species may therefore depend upon the persistence of another species with which it has no obvious interaction. Or, put another way, the already blinding rate of extinctions may accelerate even more because of the domino effect, in which seemingly independent species all disappear at once from disturbed habitat.

Despite the somewhat disturbing conclusions, this work has inspired us to delve deeper into sapsucker biology. We hope to expose you to solutions to more sapsucker mysteries soon!

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