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Double keystone bird in a keystone species complex

(sapsucker/community/extinction)

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ABSTRACT **Species in a Colorado subalpine ecosystem show subtle interdependences. Red-naped sapsuckers play two distinct keystone roles. They excavate nest cavities in fungus-infected aspens that are required as nest sites by two species of swallows, and they drill sap wells into willows that provide abundant nourishment for themselves, hummingbirds, orange-crowned warblers, chipmunks, and an array of other sap robbers. The swallows thus depend on, and the sap robbers benefit from, a keystone species complex comprised of sapsuckers, willows, aspens, and a heartwood fungus. Disappearance of any element of the complex could cause an unanticipated unraveling of the community.**

Early attempts to explain the distribution and numbers of species stressed two types of factors: (*i*) physical features of the environment (climate, topography, insolation, and habitat patch size and degree of isolation) and (*ii*) availability of other resources (especially food) (1, 2). More recently, a major effort to characterize evident species interactions, such as those between predators and prey or between competitors for common, limiting resources (3, 4) has also led to an appreciation of the complexity and ubiquity of subtle biological associations. Indirect interrelationships may have profound effects on the structure of ecological communities (5–7); understanding their prevalence and influence is crucial to guiding efforts to slow the loss of biodiversity (8).

Here we report the importance of a complex of keystone species to the distribution and abundance of other species. Keystone species are those whose removal from a community would precipitate a further reduction in species diversity or produce other significant changes in community structure and dynamics. Keystone species may act in a variety of ways (9–20): for example, by preying on dominant species, by causing disturbance, by providing resources in times of scarcity, by pollinating and thereby enhancing the persistence of highly dispersed and rare plants, and (as in this case) by providing key, limiting resources or by supporting other keystone species.

The red-naped sapsucker (*Sphyrapicus nuchalis*, a woodpecker; hereafter "sapsucker") appears to play two keystone roles that help to support different suites of species in a subalpine ecosystem in the Rocky Mountains. One role has already been described. The sapsucker drills sap wells into spruce (*Picea engelmannii*), aspen, and shrubby willow (*Salix* spp.). The willow sap constitutes a major portion of the sapsucker's diet during the summer breeding season and is stolen by over 40 species, including hummingbirds, warblers, chipmunks, squirrels, wasps, and butterflies (21, 22). The sapsuckers thus make available a rich resource to numerous species at times when they are reproducing and storing fat for the winter migration and hibernation. In fact, the breeding distribution of the closely related yellow-bellied sapsucker (*S. varius*) appears to determine the northern limits of the breeding ranges of the Rubythroat and Rufous hummingbirds (23).

The second keystone role is elucidated by the research reported here. The sapsucker provides nest cavities to secondary cavity-nesting species. Each breeding season, a sapsucker pair creates a new nest cavity in an aspen (*Populus tremuloides*) tree infected with the fungus *Fomes igniarius* (which causes heartwood decay and makes cavity excavation possible) (refs. 24 and 25; G.C.D., unpublished data). The old cavities are utilized by at least seven secondary cavity-nesting bird species in Colorado. In 4 years of monitoring nest cavity excavations in the study region (as part of another project), we have found that the sapsucker makes >1 order of magnitude more cavities than other primary cavity nesters (other woodpecker species) and is thus potentially important to secondary cavity nesting species.

We show the significance of this second keystone role to community structure as follows. First we determine that the sapsucker is restricted to habitat with both aspen and willow in close proximity. Since experimental removal of the sapsucker is not desirable, we use aspen groves without willow as treatments (i.e., sapsuckers "removed") and groves with willow as controls (i.e., sapsuckers present) to test for associated differences in bird-community composition. Breeding-bird censuses confirm that the only significant avifaunal difference between sites is that species of swallows that locally are obligate secondary cavity nesters are restricted to groves with sapsuckers; they are therefore dependent upon a keystone complex comprised of certain species of willow, *Fomes*-infected aspen, and sapsuckers.

MATERIALS AND METHODS

We conducted this investigation in the vicinity of the Rocky Mountain Biological Laboratory in Gunnison County, Colorado, during the 1991 breeding season. Study areas were distributed along the East and Taylor River drainages at elevations ranging between 2650 m and 3050 m.

We located suitable sapsucker habitat by looking for the unique and prominent signs of well excavation. This damage on aspen trees is easily recognizable for at least 10 years after creation, and thus provides an indication of habitat occupied by the sapsucker that is integrated over time.

To determine the relationship between the occurrence of the sapsucker and the proximity of willow and aspen, we surveyed the prevalence of sapsucker damage in aspen groves located at various distances from shrubby willow. Only willow species with sufficiently thick stems to be used by the sapsucker were considered (*S. subcoerulea*, *S. pseudocordata*, and *S. brachycarpa*). We examined a minimum of 400 randomly selected trees in each aspen grove; the numbers of trees with sapsucker wells and with nest cavities were recorded. Sapsucker wells are very distinctive; in contrast, we could not generally attribute a nest cavity to any particular primary cavity-nesting species.

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Breeding-bird surveys were conducted in six of these aspen groves to determine the relationship between the distribution of sapsuckers and that of other birds. Three of the sites (SMN, 2950 m; SMS, 2950 m; and WG, 3020 m) were located in close proximity (<50 m) to or included suitable shrubby willow. The other three sites (AS, 2985 m; LR, 2750 m; and DR, 2800 m) were situated at least 1 km from the nearest willow shrub. The surveys also provided a means of determining whether the principal difference between sites as habitat for insectivorous birds was the presence or absence of willow.

Grids measuring 350 m × 150 m (5.25 hectare) were established in each site. Two types of surveys were conducted, a "standard" survey employing variable-strip transect methods and an "intensive survey" using a modification of the territorial spot-mapping method (26–28). The standard survey, performed by two investigators, involved censusing birds (visually or aurally) along bands about two transects trisecting the study area. Nests discovered in the course of this routine were also recorded. Intensive surveys, conducted by the third investigator, involved censusing the entire study area thoroughly and making an intensive effort to locate nests. The mean durations of standard and intensive surveys were 1 hr 12 min and 3 hr 32 min, respectively.

A total of 25 standard and 17 intensive surveys were made. Each site was surveyed a minimum of five times during the peak of the breeding season. A total of 7 intensive and 3 standard surveys each were conducted in SMN and SMS to assess the accuracy of the standard-survey protocol relative to that of the intensive survey. Finally, some features of the vegetation were characterized at each site to assess habitat similarity.

The relative abundance of bird species in each site was calculated as follows. An adult pair was inferred from either (*i*) an active nest or (*ii*) the presence of an adult individual on at least 3 census days within a circle of a species-specific radius. The radius was greatest (25 m) for woodpeckers and flycatchers, which frequently left the nest unattended, and was smallest (10 m) for dark-eyed juncos, which usually left a vociferous sentry at the nest. Exact corrections for differential detectability are available from the authors.

RESULTS AND DISCUSSION

Our first result is that the distribution of sapsuckers (as measured by prevalence of damage) is significantly correlated with habitat where aspen and suitable willow cooccur (Fig. 1). The small amount of damage found in groves situated far from willow may have been created by birds in migration. The frequency of nest cavities was also significantly higher in aspen trees in close proximity (<50 m) to willow ($P < 0.001$; G test; $n = 13{,}162$ trees). Extensive sapsucker damage found on and in the vicinity of trees with nest holes suggests that many of those cavities were created by sapsuckers.

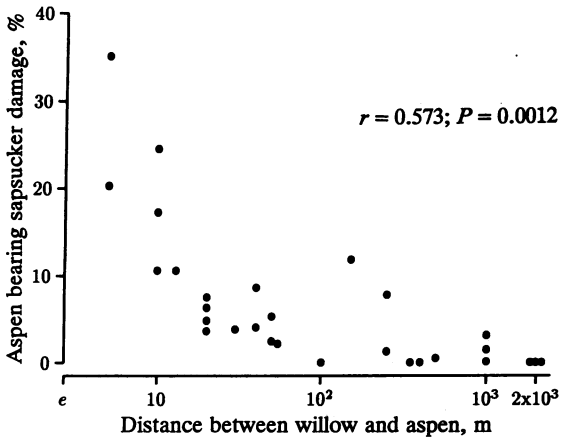

FIG. 1. Prevalence of sapsuckers versus the proximity of willow and aspen. Sapsucker damage on aspen was plotted as a function of the meter distance between willow and aspen. The percent damage was arcsine-transformed and regressed against (distance between willow and aspen)$^{-1}$.

The survey results are presented in Table 1. The standard surveys produced results highly correlated to those of the intensive surveys (SMN: $r = 0.829$, $P < 0.01$; SMS: $r = 0.724$, $P < 0.01$). Aside from the sapsuckers, only one obligate primary cavity nester was found in any of the sites (a hairy woodpecker, *Picoides villosus*, pair in sites WG and DR each).

Note first that the two obligate secondary cavity nesters (the tree and violet-green swallows) were found only in sites occupied by the sapsucker. The probability that the distributions of both of the swallows and the sapsucker coincided exactly by chance alone was calculated as the following multinomial:

$$\frac{6!}{3!3!}(1/4)^3(1/4)^3 = 0.0049.$$

An alternative calculation using Bayesian statistics yields a slightly stronger result of $P < 0.0002$. Both are conservative estimates, since the probabilities that the swallows occur in a site may not be independent of each other if the swallows compete for a limited resource (such as nest cavities).

Second, facultative secondary cavity nesters occurred in all sites. Their abundance was higher (on average) in sites occupied by the sapsucker. The probability that all of the facultative secondary cavity nesters occurred in higher abundance in sapsucker sites than in nonsapsucker sites by chance alone is $(1/2)^4 = 0.06$. At our study sites, Mountain Bluebirds might be better classified as obligate secondary cavity nesters, but they were too uncommon to ascertain the frequency with which they nest in other than abandoned woodpecker cavities.

The abundance of facultative secondary cavity nesters seemed to depend upon the availability of alternative locations for nests. For example, the abundance of house wrens is correlated with the abundance of rotting, fallen trees ($P = 0.05$). The distribution and abundance of facultative secondary cavity nesters is thus not entirely dependent upon, but may be broadened and enhanced by, the sapsucker (29).

Third, while the sites do not constitute perfectly identical replicates, there are no significant avifaunal differences in habitat as reflected in the distribution of open-nesting birds ($P > 0.05$; G-test). The presence in comparable numbers in each site of the western wood pewee—a bird that, like swallows, forages on flying insects—makes it unlikely that the absence of swallows from sites without willow was due to anything but absence of nest cavities. The sites were remarkably similar in vegetation type and cover, and there was no evidence of a direct swallow–willow association.

This work shows that the presence of two obligate secondary cavity nesters is dependent upon a cooccurrence of at least three elements of a keystone complex: certain shrubby willow species, aspens, and sapsuckers. The importance of the heartwood fungus (the fourth element) to facilitating sapsucker nest excavation is discussed extensively in the literature (e.g., refs. 24, 25). Disappearance of any element of the complex would presumably result in the local extinction of the swallows.

Biologists have typically considered the tropics as the locus of elaborate species interactions. Yet, even from the limited scope of this study, it appears that the complexities of temperate zone community structure may be considerably

Table 1. Results of the breeding bird censuses in the 5.25-hectare study sites

Species	Adults at census site, no.					
	SMN	SMS	WG	AS	LR	DR
Primary cavity nester						
Red-naped sapsucker (*Sphyrapicus nuchalis*)	4	2	2	0	0	0
Obligate secondary cavity nesters						
Tree swallow (*Tachycineta bicolor*)	2	4	2	0	0	0
Violet-green swallow (*Tachycineta thalassina*)	2	4	4	0	0	0
Facultative secondary cavity nesters						
Mountain bluebird (*Sialia currucoides*)	*	*	2	*	0	0
Chickadee (*Parus gambeli* and *P. atricapillus*)	2	2	4	2	*	2
Northern flicker (*Colaptes auratus*)	2	2	3	0	2	2
House wren (*Troglodytes aedon*)	18	10	11	*	14	12.5
Common noncavity nesters						
Dark-eyed junco (*Junco hyemalis*)	14.7	12	10	12	4	12
American robin (*Turdus migratorius*)	6	8	2.7	*	2	*
Hermit thrush (*Catharus guttatus*)	4	4	2	6	2.7	4
Warbling vireo (*Vireo gilvus*)	6	8	8	10	16	6
Yellow-rumped warbler (*Dendroica coronata*)	4	6	8	4	2	*
Western wood-pewee (*Contopus sordidulus*)	4.7	4	2	2	2	4.7

*Present but not detected a sufficient number of times to qualify as a breeding resident.

more intricate than previously thought. Indeed, the subtleties in the requirements of the sapsuckers and their dual keystone roles suggests that preserving some species depends upon the distributions of species with which they have no obvious interaction. The disappearance of a single species could precipitate a wholly unanticipated unraveling of community structure.

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1. Andrewartha, H. G. & Birch, L. C. (1954) *The Distribution and Abundance of Animals* (Univ. of Chicago, Chicago).
2. MacArthur, R. H. & Wilson, E. O. (1967) *The Theory of Island Biogeography* (Princeton Univ. Press, Princeton).
3. Tilman, D. (1987) *Am. Nat.* **129**, 769–774.
4. Roughgarden, J. (1989) in *Perspectives in Ecological Theory*, eds. Roughgarden, J., May, R. M. & Levin, S. A. (Princeton Univ. Press, Princeton), pp. 203–226.
5. Futuyma, D. (1973) *Am. Nat.* **107**, 443–446.
6. Vitousek, P. M. & Walker, L. R. (1989) *Ecol. Monog.* **59**, 247–265.
7. Polis, G. A. & Holt, R. D. (1992) *Trends Ecol. Evol.* **7**, 151–156.
8. Ehrlich, P. R. & Wilson, E. O. (1991) *Science* **253**, 758–762.
9. Paine, R. T. (1966) *Am. Nat.* **100**, 65–75.
10. Paine, R. T. (1969) *Am. Nat.* **103**, 91–93.
11. Janzen, D. H. (1971) *Science* **171**, 203–205.
12. Howe, H. F. (1977) *Ecology* **58**, 539–550.
13. Estes, J. A., Smith, N. S. & Palmisano, J. F. (1978) *Ecology* **59**, 822–833.
14. Duggins, D. O. (1980) *Ecology* **61**, 447–453.
15. Gilbert, L. E. (1980) in *Conservation Biology*, eds. Soule, M. E. & Wilcox, B. A. (Sinauer, Sunderland, MA), pp. 11–34.
16. Terborgh, J. (1983) *Five New World Primates* (Princeton Univ. Press, Princeton), p. 60.
17. Owen-Smith, N. (1987) *Paleobiology* **13**, 351–362.
18. Owen-Smith, N. (1989) *Conserv. Biol.* **3**, 405–412.
19. Brown, J. H. & Heske, E. J. (1990) *Science* **250**, 1705–1707.
20. Hunter, M. D. (1992) in *Effects of Resource Distribution on Animal-Plant Interactions*, eds. Hunter, M. D., Ohgushi, T. & Price, P. W. (Academic, San Diego), pp. 288–317.
21. Tate, J. (1973) *Auk* **90**, 840–856.
22. Ehrlich, P. R. & Daily, G. C. (1988) *Am. Birds* **42**, 357–365.
23. Miller, R. S. & Nero, R. W. (1983) *Can. J. Zool.* **61**, 1540–1546.
24. Basham, J. T. (1958) *Can. J. Bot.* **36**, 491–505.
25. Kilham, L. (1971) *Wilson Bull.* **83**, 159–171.
26. Williams, A. B. (1936) *Ecol. Monogr.* **6**, 317–408.
27. Kendeigh, S. C. (1944) *Ecol. Monogr.* **14**, 67–106.
28. Emlen, J. T. (1977) *Auk* **94**, 455–468.
29. Short, L. L. (1979) *Wilson Bull.* **91**, 16–28.