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INSIDE

"Science affects the way we think together."

Lewis Thomas

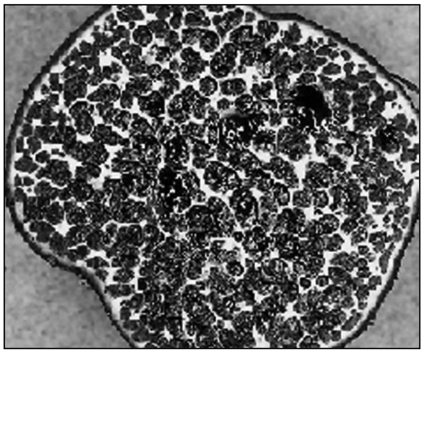
SQUIRRELS CANNOT LIVE BY TRUFFLES ALONE: A CLOSER LOOK AT A NORTHWEST KEYSTONE COMPLEX

"'Tis true; there's magic in the web of it."

—William Shakespeare (*Othello*)

Flying squirrels have a tough life in the Pacific Northwest. They face a variety of tradeoffs that would be daunting to the most aggressive survivor. They're nocturnal, which means they can hide from predators in the dark, but it's colder then. And because they are superbly built for gliding, their mass-to-surface area ratio makes them more susceptible to cold. Northern spotted owls love them, but not in a nice way; weasels and martens do, too. Their predator-avoidance program requires that they change dens frequently.

Goshawks like Douglas' squirrels, and weasels love chipmunks. The diurnal Douglas' squirrels and Townsend's chipmunks don't suffer as much from predation by nocturnal owls and cold nighttime temperature as flying squirrels do, yet they are wickedly competitive with flying squirrels in their shared habitat. But flying squirrels are pacifists. They're shy and retiring, and in general they're just looking for stability. They're also looking for truffles—practically all the time—and they're very good at it. They find them fast, and eat them fast. But truffles, in case we get confused about our own so-called gourmet foods, are not particularly nutritious.



A northern spotted owl (top) requires high densities of prey, especially northern flying squirrels; a northern flying squirrel (center) forages for its primary food, truffles. A microscopic cross section of a truffle (bottom) .

IN SUMMARY

Tree squirrels in the Pacific Northwest are part of a keystone complex that includes ectomycorrhizal fungi, Douglas-fir, and spotted owls. All three squirrel species—the northern flying squirrel, the Douglas' squirrel, and the Townsend's squirrel—consume truffles produced by fungal partners of important tree species. The squirrels then spread the spores of these fungi throughout the forest in their feces.

The fungi are important to the growth and health of many Northwest tree species. Squirrels, in their turn, are major prey for vertebrate predators in the forest, including threatened and sensitive species such as the northern spotted owl. Thus, as an essential link in the web of interdependence, squirrels are good indicators of forest function and can be used to evaluate management effectiveness in promoting biodiversity and sustainability.

Management for habitat elements that contribute to truffle production—coarse woody debris, a variety of tree species, and ericaceous shrubs—has been proposed to benefit squirrels and consequently their predators. But there has been little research on the nutritive value of truffles, the relationship between truffle biomass and squirrel biomass, the importance of other food for the squirrels, or effects of management on truffle production.

Several research projects out of the Pacific Northwest Research Station's Olympia, WA, laboratory are beginning to answer preliminary questions in these areas.

In the Pacific Northwest, there's not a whole lot else on the menu for flying squirrels. Conifer seeds are tiny and highly variable in supply. Second-growth forests don't offer a whole lot in the way of hardwood seeds or berries and nuts in the undergrowth. Nor do even-aged young conifer forests offer much in the way of tree rot for cavity dens.

Tough life, indeed. About the only thing flying squirrels seem to have going for them is they can drop their feces wherever they want in the forest. This turns out to be crucial.

The flying squirrel is a centerpiece in what's called a keystone complex, a web of animals and food, predators and prey, that is especially important in defining the ecosystem.

KEY FINDINGS

- Tree squirrels in the Pacific Northwest are part of a keystone complex: squirrels consume truffles—fungi that are important to the growth and health of trees such as Douglas-fir. The squirrels are themselves prey of northern spotted owls, which in turn prefer old-growth Douglas-fir forests as habitat.
- The flying and Douglas' squirrels and the Townsend's chipmunk consume truffles as a major part of their diet. They also consume a variety of mushrooms, lichens, maple seeds, poplar catkins, and salal fruit, many of which are more nutritious than truffles. Thus retention of diverse hardwoods is important for biodiversity.
- Truffles may be relatively indigestible and low in nutritive value; a single species or two may be insufficient for survival and reproduction of the squirrel. Thus, diversity of truffles and mushrooms is important to maintaining abundant prey bases.

"A keystone species such as the flying squirrel is easy to define: it's a species that has a disproportionate influence on the ecosystem relative to its abundance within that ecosystem," Andy Carey, a research biologist with the Pacific Northwest Research Station in Olympia, WA, explains. "A keystone complex is a more complicated idea that recognizes a number of essential components that are building blocks of an ecosystem and supporters of its processes."

A WEB OF MUTUAL SUPPORT

The flying squirrel hunts regularly for truffles, is very good at finding and eating them, then moves around the forest, randomly depositing its droppings. The spores, yeasts, and bacteria from the truffle pass unharmed through the squirrels' digestive tracts, to colonize anew the roots of nearby trees. The truffles are the spore-producing bodies of mycorrhizal fungi, which have a mutually beneficial, or symbiotic, relationship with the roots of many forest trees, including Douglas-fir.

"Mycorrhizal fungi enhance the ability of trees to absorb water and nutrients from soil and they move photosynthetic carbohydrates from trees into the soil," explains Carey. "In turn, this carbon supports a vast array of microbes, insects, nematodes, bacteria, and other organisms in the soil."

The northern spotted owl, which preys on the squirrel, is not the only squirrel-lover: weasels, martens, share its tastes in this respect. But the spotted owl has a well-known preference for old-growth Douglas-fir habitat, so these trees, surrounded by the nurturing fungi and their associates in the soil, complete the loop that in total forms the keystone complex.

NUTRITIONAL CHECKUP

Despite the symmetry of this mutually nourishing web, however, the nutritional value of truffles for squirrels is low. At best they differ in nutrient content among species, which means that to provide an adequate squirrel diet, truffle species diversity becomes important. According to Carey, it has been established that a diet of a single truffle species is rarely sufficient to maintain body weight.

"While truffles are most likely the caloric staple for the flying squirrel in the Pacific Northwest, the more highly digestible seeds, fruits, nuts, and insects could be occasional, but nutritionally significant additions to its diet," Carey explains.

In the Pacific Northwest, annual and seasonal truffle abundance varies widely, he says. Peak abundance typically occurs in the spring, and to some extent in the fall, although it varies further with forest type and age. Notably, fruiting of a variety of non-truffle foods coincides with periods of reduced truffle availability, thus stabilizing an otherwise fluctuating food supply.

So what do squirrels find when the truffle numbers drop, because of seasonal fluctuations, a recent timber harvest, or insect and disease infestation among their local trees?

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Sherri Richardson Dodge, Editor
srichardsondodge@fs.fed.us

Send new subscriptions and change of address information to pnw_pnwpubs@fs.fed.us

Keith Routman, layout
kroutman@fs.fed.us

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"Use of ancillary foods is not well documented due to difficulty identifying digested remains, possibly minor or sporadic consumption, and infrequent observations of foraging, which mostly happens at night," Carey explains. Nonetheless, it has been established that flying squirrels will go for catkin-, seed-, fruit-, and nut-bearing plants, and the fungal mutualists that prefer these plants.

"Although nontruffle food items are probably consumed in smaller quantities than truffles, they could be of more value to the flying squirrel than the relative frequency in the diet suggests," says Carey.

LAND MANAGEMENT IMPLICATIONS

- Management can have diverse effects on truffle diversity and abundance. In general, managing for biocomplexity—multiple tree species, understory diversity, decaying trees—at fine scales contributes to biodiversity and ecosystem resilience.
- Variable-density thinning can increase the diversity of both belowground (truffles) bodies and aboveground (mushroom) fungal fruiting bodies without impairing production in the mid to long term.
- A diverse deciduous understory of trees and shrubs that produce edible fruits, seeds, and nuts in conifer forests helps stabilize squirrel populations and those of the predators that depend upon them.
- Diverse overstories including some deciduous trees can reduce impacts on squirrels of variability in seed production by individual species of conifers, and by root rot infestations. Deciduous trees may also provide cavities in even young stands.

SQUIRRELS AND THE COMPLEX FOREST

Clearly, then, it is not a difficult logical leap to recognize that flying squirrels can be extremely useful indicators of forest ecosystem health. Abundant populations of these and also of Douglas' squirrel and Townsend's chipmunk are characteristic of old, natural forests in the Pacific Northwest and indicate a high carrying capacity for vertebrate predators. The densities of flying squirrels in particular seem to correlate jointly with truffle biomass and diversity, according to Carey.

Abundance of all three mammal populations is associated with high production of seeds and fruiting bodies by forest plants and fungi, along with complexity of ecosystem structure, function, and composition.

In second-growth forests, however, the broad mixture and variation of vegetation species and ages of an older, natural forest are uncommon.

"In such settings, availability of den sites and truffle abundance have been suggested as limiting factors for the flying squirrel," Carey says. "Other food availability is likely also a limiting factor. In closed-canopy, competitive-exclusion forests such as second-growth Douglas-fir, nontruffle foods such as seeds, nuts, and fruits, are infrequent, so those vital alternatives for squirrels are less available."

A northern flying squirrel feeds on a mushroom.

He notes that by consuming a variety of nontruffle foods along with truffles, the flying squirrel could forage in areas with more brush and hardwood species and in young forest stands. "In the process, the flying squirrel would ensure dispersal of a diversity of fungal taxa, help maintain genetic diversity for mycorrizhal fungal species and other soil microbes, and contribute to the increase in truffle diversity that is associated with forest development."

The implications for forest management begin to take shape.

CAN WE MANAGE FOR TRUFFLES?

The ecology of truffle production is poorly understood. Truffle abundance varies greatly through space and time; some truffles are available year-round, but there have been no definitive studies of truffle abundance in summer and winter, when normally they are less abundant.

"Most studies of truffle growth and habits have lasted less than 1 year, and do not explain how the functional relationship between squirrels and truffles is maintained in winter and summer," Carey says. "Nor do these few studies explain how the flying squirrel can compete for truffles with the more aggressive Douglas' squirrel and Townsend's chipmunk, especially in winter, when food—except stored food—is scarce, and truffles still make up the principal and crucial food source of flying squirrels."

As a result of this lack of understanding, we still don't know in what ways management may affect truffle production; all we know is it seems to affect different truffle species differently.

Because active management of second-growth forests on long rotations in the Pacific Northwest is a relatively recent phenomenon, and because early clearcutting left behind highly variable stand conditions, few studies have attempted empirical evaluations of management strategies.

In forests managed for late seral attributes, rotation lengths generally exceeds 70 years and has fallen into one of two typical categories of management in the Pacific Northwest, Carey says. The first, referred to as legacy retention, retains biological legacies at harvest with no further intervention. Such legacies include old live, dead, and fallen trees and their associated biota, and no thinnings are performed. The understory is poorly developed. This so-called extensive approach is believed to be a suitable pathway for maintaining or restoring natural biodiversity in second-growth forests.

"The second category is termed 'intensive management,' and involves multiple commercial thinnings and long rotations to produce forests with developed understories that are hypothesized to function as late-seral, natural forests," he says. "This approach, emphasizing growing large trees through long rotations, has been called 'high-quality forestry,' but is more appropriately labeled management for high-quality timber." He calls this strategy management with thinnings.

To determine the effects of forest management on production of truffles and on diets of northern flying squirrels and Townsend's chipmunks in second-growth Douglas-fir forests, Carey designed an experiment in the Puget Trough of Washington to compare effects of the two alternative strategies for managing second-growth forests on long rotations.

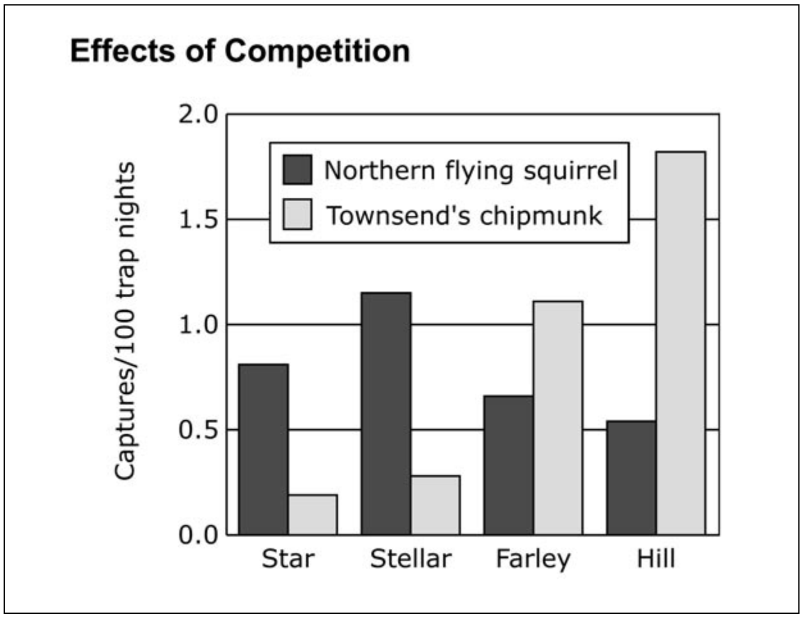
CONSIDERING ALTERNATIVE MANAGEMENT STRATEGIES

"Ideally, such an examination would be in the form of the response of a key species or species group," he explains. "The three types of forest squirrels have been found particularly responsive to forest environmental conditions, so management strategies claiming to accelerate development of late-seral forest conditions should be able to tell us a great deal about how effectively the forests are moving toward the conditions favored by these small mammal species."

Many second-growth forests on both private and public lands in the region are currently reaching merchantable age, and decisions are being made about their harvest and future management amidst a wide array of assumptions about late-seral forest species and their conservation, Carey notes.

"These decisions are often made in an adversarial context within which inferences drawn from retrospective comparisons of natural and variously managed forests—the only kind of comparisons available—are discounted, either because the studies are too broad scale, or because current management practices have changed." Hence Carey's recognition of the urgent need for retrospective examination of second-growth stands representing commonly recommended forest strategies and determination of the potential of alternative strategies that might promote late-seral forest conditions.

Retrospective studies cannot demonstrate cause and effect, which are difficult to establish in most biological and social field studies, he notes. Instead, he has used his results to pose several hypotheses explaining differences in abundance of flying and other squirrels under differing forest conditions.



The abundance of northern flying squirrels trapped in fall 1991 and in spring and fall 1992, and the abundance of Townsend's chipmunks trapped in spring and fall 1992, in four blocks of forest on Fort Lewis Military Reservation. Note the opposing relationship, possibly demonstrating competition between the two species.

First, the activity, abundance, and carrying capacities of flying squirrels in dry Douglas-fir forests in the western hemlock zone seem tied to coarse woody debris through its influence on production of truffles. The thinned forests almost entirely lacked coarse woody debris, and even legacy-retention forests did not carry as much of the debris as commonly found in old-growth Douglas-fir.

Second, closed canopies of legacy-retention forests provided the right microclimates in the canopy to support stick nest use by flying squirrels. Thinned forests had virtually none, and neither forest supported many cavities suitable for dens. Third, closed canopies and relatively open forest floors allowed efficient movement of flying squirrels through the canopies and quick location of truffles in the forest floors of the legacy-retention stands.

Diversity of truffles was similar in both forests, but species composition changed after thinning, potentially to the detriment of squirrels.

WRITER'S PROFILE

Sally Duncan is a science communications specialist and writer focusing on forest resource issues. She is also a candidate for a Ph.D. in Environmental Sciences at Oregon State University in Corvallis, Oregon, where she lives.

CHOOSING OTHER PATHWAYS

"It appears that neither forest management strategy was adequate to develop or maintain the complex trophic pathways that support the diverse vertebrate communities associated with old-growth forests within a 50- to 70-year time frame," Carey says.

Instead, he proposes the third alternative of variable-density thinning, as a solution to the need for complex forests with mixed development stages. Under such management, he explains, "legacies are retained at specific, empirically documented levels for specific purposes. Thinnings are done in the novel manner of variable density based on empirical studies of forest communities formed through self-thinning and gap formation. Decadence is managed actively to alleviate the loss of decadence resulting from reduced tree density."

In the resulting very mixed and complex forest mosaic, it is difficult to locate a forest's specific successional stage according to the textbooks. "We've been taught in classical forestry that forests move through 'successional stages' which 'replace' each other through time," he says. "But ecologists talk about development, wherein each stage envelops the preceding stage and builds upon it. This makes infinitely more sense than the many management models that begin with simplifying assumptions, and thus are additive and simplistic."

One of Carey's hypotheses was that silvicultural manipulations of second-growth forests such as variable-density thinning offers could result in the messy complexity (which scientists call spatial heterogeneity) that would reproduce the biocomplexity and plant-fungal productivity associated with high squirrel populations.

The point of management, then, is to design for multiple opportunities for squirrels and other small mammals to find and forage for food, to evade predators just enough to survive and yet continue feeding them, to compete with each other at a sustainable level, and to continue their given job of completing the keystone complex loop.

"Our results in general support the hypothesis that simultaneously high populations of northern flying squirrels, Townsend's chipmunks, and Douglas' squirrels in the Douglas-fir keystone complex result from ecological processes wherein habitat breadth and niches are able to develop," he explains. "They do not, in other words, result from a single limiting factor."

A northern flying squirrel peeps out from a natural tree cavity, possibly created by a woodpecker.

In other words, the physical character of a stand has more bearing on squirrel abundance than its supposed seral stage, and no single management strategy will adequately address the future health of the keystone complex.

What this approach to management offers is not just good for the truffles and therefore for the squirrels and therefore for the owls and so on, Carey insists.

"This research demonstrates the potential for reconciliation of interest in wood production, sustainable human communities, recovery of threatened species, maintenance of forest health, and promotion of general sustainability when compared to narrow-focus approaches of maximizing net present value of wood, setting aside reserves for threatened species and maintenance of biodiversity, and concerns over ecosystem health that arise from past management practices."

The thing is, the flying squirrel's life is supposed to be tough, although it may not be aware of this. The real question is, can we figure out how to learn from its ability to adapt?

> *The reasonable man*
> *adapts himself to the world:*
> *the unreasonable one*
> *persists in trying to adapt*
> *the world to himself.*
>
> — George Bernard Shaw (1856–1950)

FOR FURTHER READING

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SCIENTIST PROFILE

Andrew Carey is a research biologist and leader of the Ecological Foundations of Biodiversity Research Team in Olympia, Washington. He has spent his career comparing old-growth forests to managed forests in an effort to devise management systems appropriate to diverse land ownerships (large to small federal or private) and to providing people with the diverse products and values they want and need from forests.

Carey can be reached at:

Pacific Northwest Research Station/USDA Forest Service
Forestry Sciences Laboratory
3625 93rd Ave. SW
Olympia, WA 98512
Phone: (360) 753-7688
E-mail: acarey@fs.fed.us