

# Pinus Seeds

## Competition Among Insects, Birds and Mammals for Conifer Seeds

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**SYNOPSIS** Species of at least 5 orders of insects, 6 families of birds, and 2 orders of mammals, in various combinations, can exploit the cones and seeds of most species of conifers. Lodgepole pine is the exception to this pattern of broad taxonomic diversity of seed predators in that only pine squirrels and coreid bugs attack its serotinous cones. The contrast between lodgepole pine and other conifers demonstrates that large intrinsic variation in the abundance of a resource fosters the evolution of a broad range of taxonomic groups to exploit the resource. The diverse groups are limited by different predators and alternate resources when conifer seeds independently decrease in abundance.

### INTRODUCTION

Because conifers are such an important source of lumber, a great amount of effort has been put into the study of their biology (Fowells, 1965), their seeds (USDA, 1974), and the predators of their seeds (Keen, 1958). People concerned with the lumber industry are interested in how many seeds escape predation to allow reforestation of logged or burned areas. Questions of general biological interest that do not relate directly to reforestation may go unasked even though pertinent information is available. In this paper, we use the extensive literature on conifer seeds and their predators to outline the nature of these seeds as a food resource and the manner in which the various seed predators use this resource. The information can then be used as a basis for answering three questions: 1) Why are there many different distantly related taxa of animals exploiting a distinctive and easily delimited resource? 2) How do the various taxa interact in using the resource? 3) How do the different taxa avoid competitive ex-

clusion? Our personal experience is mainly limited to the conifers of western North America and our discussion will be concentrated on those, although some of the patterns probably apply generally to conifers in the Northern Hemisphere (Bock and Lepthien, 1976).

### THE RESOURCE

As a food resource, single viable conifer seeds are highly uniform as to size (weight of female gametophyte and embryo) and quality (caloric value of female gametophyte and embryo) within an individual cone, tree or species population (Table 1). The total number of viable seeds in single cones within a single annual crop for one tree or a species population is more variable than seed size or quality, especially in lodgepole pine (*Pinus contorta* Dougl.) (Table 1). The sizes of annual cone crops for single trees or species populations are by far the most variable feature of conifer seeds in all western North American species, except lodgepole pine (Table 1).

The variation in caloric value of seeds given in Table 1 is probably an underestimation because 5 to 10 seed kernels were burned to derive each value thus masking the variation between individual seeds. The similar variations between samples from the same cone, cones from the same tree,

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TABLE 1. The source of variation in conifer seeds as a food resource.

| Species                                                            | Source of units                                                        | Number | Range     | Mean | Coefficient of variation |
|--------------------------------------------------------------------|------------------------------------------------------------------------|--------|-----------|------|--------------------------|
| Caloric value of female gametophyte and embryo (Cal/g dry weight): |                                                                        |        |           |      |                          |
| Lodgepole pine                                                     | groups of 6 to 10 seeds from one cone                                  | 5      | 6.55-6.91 | 6.74 | 2.0%                     |
| Lodgepole pine                                                     | groups of 6 to 10 seeds from one tree                                  | 6      | 6.63-7.04 | 6.79 | 2.3%                     |
| Lodgepole pine                                                     | groups of 5 to 10 seeds from one population                            | 7      | 6.54-6.96 | 6.83 | 2.2%                     |
| Weight of female gametophyte and embryo (mg/seed):                 |                                                                        |        |           |      |                          |
| Engelmann spruce                                                   | seeds from one cone                                                    | 40     | 1.6-2.0   | 1.91 | 7.5%                     |
| Lodgepole pine                                                     | seeds from one cone                                                    | 25     | 1.7-2.3   | 1.88 | 9.5%                     |
| Lodgepole pine                                                     | 10 means of seeds from 10 cones from one tree                          | 10     | 2.01-3.27 | 2.49 | 14.8%                    |
| Lodgepole pine                                                     | 6 means of seeds from 6 cones from different trees                     | 6      | 1.86-3.03 | 2.53 | 24.0%                    |
| Filled seed content of cones (filled seeds/cone):                  |                                                                        |        |           |      |                          |
| Lodgepole pine                                                     | cones from one tree                                                    | 5      | 9-23      | 15.8 | 40.4%                    |
| Lodgepole pine                                                     | 10 means of cones from 10 trees                                        | 10     | 4.4-18.8  | 11.6 | 39.5%                    |
| Ponderosa pine                                                     | cones from one tree                                                    | 5      | 53-89     | 70.4 | 22.9%                    |
| Ponderosa pine                                                     | 7 means of cones from 7 trees                                          | 7      | 39.0-70.4 | 53.5 | 20.6%                    |
| Annual cone crops (cones/tree or cones/acre):                      |                                                                        |        |           |      |                          |
| Douglas-fir                                                        | 11 annual means for several trees (cones/tree)                         | 11     | 0-14,244  | 4219 | 124.6%                   |
| Ponderosa pine                                                     | 10 annual crops (cones/acre)                                           | 10     | 316-7521  | 2437 | 93.1%                    |
| Ratios of successive cone crops (%):                               |                                                                        |        |           |      |                          |
| Douglas-fir                                                        | smaller crop/larger crop $\times$ 100 for 10 pairs of successive years | 10     | 0.0-67.2  | 6.9  |                          |
| Ponderosa pine                                                     | smaller crop/larger crop $\times$ 100 for 9 pairs of successive years  | 9      | 4.2-94.4  | 40.2 |                          |
| Lodgepole pine                                                     | smaller crop/larger crop $\times$ 100 for 4 pairs of successive years  | 4      | 50.8-73.5 | 62.4 |                          |

|                                 |                                                       |                                                              |                                              |  |
|---------------------------------|-------------------------------------------------------|--------------------------------------------------------------|----------------------------------------------|--|
| Family: Sittidae                |                                                       |                                                              |                                              |  |
| ✓ White-breasted Nuthatch       | <i>Pinus</i>                                          | uses and makes cache of seeds and finds seeds on ground      | alternate foods                              |  |
| ✓ Red-breasted Nuthatch         | <i>Abies, Picea, Pinus, Pseudotsuga, Tsuga</i>        | seeds from open cones cached and eaten by adults             | alternate foods, emigration                  |  |
| ✓ Tyto Nyctalech                | <i>Abies, Picea, Pseudotsuga, Pinus</i>               | seeds from open cones cached and eaten by adults             | alternate foods                              |  |
| Family: Fringillidae            |                                                       |                                                              |                                              |  |
| ✓ Crossbills                    | <i>Abies, Larix, Picea, Pinus, Pseudotsuga, Tsuga</i> | seeds from closed and open cones fed to young and adults     | nomadic nesters, emigrate to alternate foods |  |
| ✓ Pine Siskins                  | <i>Abies, Larix, Picea, Pinus, Pseudotsuga, Tsuga</i> | seeds from open cones and the ground fed to young and adults | emigration, alternate foods                  |  |
| genus: <i>Carduelis</i>         |                                                       |                                                              |                                              |  |
| MAMMALS:                        |                                                       |                                                              |                                              |  |
| Order: Rodentia                 |                                                       |                                                              |                                              |  |
| pine squirrels                  | <i>Abies, Larix, Picea, Pinus, Pseudotsuga, Tsuga</i> | cache and feed from whole closed cones                       | territoriality, emigration, alternate foods  |  |
| genus: <i>Tamiasciurus</i>      | <i>Pinus</i>                                          | seeds from closed cones                                      | alternate foods                              |  |
| tree squirrels                  | <i>Abies, Larix, Picea, Pinus, Pseudotsuga, Tsuga</i> | cache and eat seeds from closed or open cones                | alternate foods                              |  |
| genus: <i>Sciurus</i>           | <i>Pinus</i>                                          | forage for single seeds                                      | alternate foods                              |  |
| chipmunks                       |                                                       |                                                              |                                              |  |
| genus: <i>Eutamias</i>          |                                                       |                                                              |                                              |  |
| golden-mantled ground squirrel  | <i>Larix, Picea, Pinus, Pseudotsuga, Tsuga</i>        | forage for single seeds and cache seeds                      | alternate foods                              |  |
| ✓ <i>Spermophilus lateralis</i> | <i>Larix, Picea, Pinus, Pseudotsuga, Tsuga</i>        | forage for single seeds and cache seeds                      | alternate foods                              |  |
| deer mice                       |                                                       |                                                              |                                              |  |
| genus: <i>Peromyscus</i>        | <i>Larix, Picea, Pinus, Pseudotsuga, Tsuga</i>        | forage for single seeds and cache seeds                      | alternate foods                              |  |
| red-backed voles                |                                                       |                                                              |                                              |  |
| genus: <i>Clethrionomys</i>     |                                                       |                                                              |                                              |  |
| Order: Insectivora              |                                                       |                                                              |                                              |  |
| shrews                          | <i>Larix, Picea, Pinus, Pseudotsuga, Tsuga</i>        | forage for single seeds                                      | alternate foods                              |  |
| genus: <i>Sorex</i>             |                                                       |                                                              |                                              |  |

TABLE 3. *continued*

| Taxonomic group<br>of seed predators | Genera of trees exploited               | Method of conifer exploitation                                                           | Method of escaping starvation<br>during cone crop failure |
|--------------------------------------|-----------------------------------------|------------------------------------------------------------------------------------------|-----------------------------------------------------------|
| <b>BIRDS:</b>                        |                                         |                                                                                          |                                                           |
| Family: <i>Psittacidae</i>           |                                         |                                                                                          |                                                           |
| Parrots                              | <i>Pinus</i>                            | extracted seeds from closed and<br>open cones                                            | emigration, nomadic                                       |
| Genus: <i>Rhynchophaga</i>           |                                         |                                                                                          |                                                           |
| Family: <i>Picidae</i>               |                                         |                                                                                          |                                                           |
| Hairy Woodpecker                     | <i>Pinus</i>                            | extracted seeds from closed and<br>open cones eaten by adults<br>and juveniles           | alternate foods                                           |
| White-headed Woodpecker              |                                         |                                                                                          |                                                           |
| Genus: <i>Picoides</i>               |                                         |                                                                                          |                                                           |
| Family: <i>Corvidae</i>              |                                         |                                                                                          |                                                           |
| Pinon Jay                            | <i>Pinus</i>                            | cache seeds extracted from closed<br>and open cones to feed young<br>and adults          | alternate foods, emigration                               |
| Genus: <i>Gymnorhinus</i>            |                                         |                                                                                          |                                                           |
| Clark's Nutcracker                   | <i>Pinus</i>                            | cache seeds extracted from open<br>and closed cones to feed young<br>and adults          | alternate foods, emigration                               |
| Genus: <i>Nucifraga</i>              |                                         |                                                                                          |                                                           |
| Gray Jay                             | <i>Abies, Picea</i>                     | may extract seeds from open cones<br>or retrieve from ground to eat<br>and store as boli | alternate foods, territorial                              |
| Genus: <i>Perisoreus</i>             |                                         |                                                                                          |                                                           |
| Steller's Jay                        | <i>Pinus</i>                            | cache seeds from open cones to<br>feed adults                                            | alternate foods, territorial, emigration                  |
| Genus: <i>Cyanocitta</i>             |                                         |                                                                                          |                                                           |
| Scrub Jay                            | <i>Pinus</i>                            | cache seeds from open cones and<br>ground to feed adults                                 | alternate foods, territorial                              |
| Mexican Jay                          |                                         |                                                                                          |                                                           |
| Genus: <i>Apeltes</i>                |                                         |                                                                                          |                                                           |
| Black-billed Magpie                  | <i>Pinus</i>                            | cache seeds from open cones and<br>ground to feed adults                                 | alternate foods, territorial                              |
| Genus: <i>Pica</i>                   |                                         |                                                                                          |                                                           |
| Family: <i>Falconidae</i>            |                                         |                                                                                          |                                                           |
| Mountain Chickadee                   | <i>Abies, Picea, Pseudotsuga, Pinus</i> | cache seeds from open cones and<br>ground to feed adults                                 | alternate foods                                           |
| Boreal Chickadee                     | <i>Abies, Picea, Pseudotsuga</i>        | cache seeds from open cones and<br>ground to feed adults                                 | alternate foods                                           |
| Plain Titmouse                       | <i>Pinus</i>                            | cache seeds from open cones and<br>ground to feed adults                                 | alternate foods, territorial                              |
| Genus: <i>Parus</i>                  |                                         |                                                                                          |                                                           |