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Cone opening phenology, seed dispersal, and seed predation in southwestern white pine (*Pinus strobiformis*) in southern Colorado[1]

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Abstract: Southwestern white pine (*Pinus strobiformis*), a little-studied pine of the southwestern United States and northern Mexico, is closely related to and often confused with limber pine (*Pinus flexilis*). Like limber pine, southwestern white pine has large, wingless seeds, which are considered an adaptation for avian seed dispersal. We studied southwestern white pine in the San Juan Mountains of southern Colorado, an area of sympatry with Clark's nutcracker (*Nucifraga columbiana*). First, we present morphological evidence confirming that the pines in our study area are southwestern white pine. Second, we present evidence that nutcrackers are important seed dispersers for the pine in this region and show that the cone opening phenology of southwestern white pine is asynchronous both among and within trees, a pattern adapted to avian seed dispersal. Red squirrels (*Tamiasciurus hudsonicus*) proved to be the major predator of southwestern white pine seeds, removing 93% of the cones in two of our study stands. Southwestern white pine cones show a combination of traits that facilitate avian seed dispersal and discourage squirrel predation. However, anti-squirrel defences fall short of those in limber pine; this may be due, in part, to gene flow from more southern populations without squirrels.

Keywords: Clark's nutcracker, *Nucifraga columbiana*, *Pinus strobiformis*, red squirrel, San Juan Mountains, seed dispersal, southwestern white pine, *Tamiasciurus hudsonicus*, tree clusters.

Résumé : Le *Pinus strobiformis*, une espèce de pin peu étudiée du sud-ouest des États-Unis et du nord du Mexique, ressemble au pin flexible (*Pinus flexilis*) avec lequel on le confond souvent. Tout comme le pin flexible, le *Pinus strobiformis* possède de grosses graines sans aile, une adaptation associée à la dissémination par les oiseaux. Nous avons étudié le *Pinus strobiformis* dans les montagnes San Juan, dans le sud du Colorado, une région où il est en sympatrie avec le casse-noix d'Amérique (*Nucifraga columbiana*). Nous présentons d'abord des caractéristiques morphologiques qui permettent de confirmer que les pins de cette zone d'étude sont bel et bien des *Pinus strobiformis*. Nous expliquons ensuite l'importance des casse-noix en tant que disséminateurs de graines de pin dans cette région. Nous montrons également que la phénologie de l'ouverture des cônes du *Pinus strobiformis* n'est pas synchronisée ni entre les arbres, ni chez un même individu, une caractéristique d'adaptation à la dissémination par les oiseaux. Les écureuils roux (*Tamiasciurus hudsonicus*) sont les principaux consommateurs des graines du *Pinus strobiformis*. Ils ont prélevé pour leur alimentation 93 % des cônes dans deux des peuplements étudiés. Les cônes du *Pinus strobiformis* présentent une combinaison de caractéristiques qui facilitent la dissémination des graines par les oiseaux et qui découragent la consommation de leurs graines par les écureuils. Malgré tout, les défenses contre les écureuils sont moindres que celles que l'on trouve chez le pin flexible, ce qui serait dû, en partie, au flux génique issu de populations de pins plus méridionales où il n'y a pas d'écureuil.

Mots-clés : casse-noix d'Amérique, dissémination des graines, écureuil roux, groupes d'arbres, montagnes San Juan, *Nucifraga columbiana*, *Pinus strobiformis*, *Tamiasciurus hudsonicus*.

Nomenclature: Flora of North America Editorial Committee, 1993; Fitzgerald, Meaney & Armstrong, 1994; American Ornithologists' Union, 2000.

Introduction

In pines (*Pinus*, Pinaceae), dispersal by wind and dispersal by animals, especially birds, are the two major alternative modes for primary seed dissemination, the initial movement of seeds out of cones and away from the parent tree (van der Pijl, 1972). For each dispersal mode, there are associated seed and cone traits that facilitate initial seed movement (Vander Wall & Balda, 1977; Tomback & Linhart, 1990; Lanner, 1998).

The bird-dispersed pines (subgenus *Strobus*, the soft or white pines) have large seeds that are not easily carried by wind. The dispersers for these pines are primarily specialized members of the family Corvidae (jays and nutcrackers) that have annual cycles dependent on fresh and stored pine seeds (Vander Wall & Balda, 1977; Ligon, 1978; Tomback, 1978; Vander Wall & Balda, 1981; Tomback, 1982). Seed dispersal by birds is associated with the following pine characteristics (the enticer pine syndrome, Smith & Balda, 1979): seeds larger than those of wind-dispersed pines, seeds with absent or rudimentary seed wings, seed retention in cones either by cone indehiscence or restraining flanges, cones that lack scale spines, and horizontally directed cones on tips of vertically oriented branches (Lanner, 1980; Tomback & Linhart, 1990). Winglessness and seed retention in cones reduce the probability of seed dispersal by wind or gravity and also reduce the probability of secondary seed dispersal by other birds and small mammals. Seed retention occurs

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only in the *Strobus* pine subsections *Cembrae* (the stone pines, *e.g., P. albicaulis*) and *Cembroides* (the piñon pines, *e.g., P. edulis* and *P. monophylla*) (see Critchfield & Little, 1966; Price, Liston & Strauss, 1998, for classification). These cone and seed features are attractive to birds, because they increase harvesting efficiency (Tomback, 1978; Lanner, 1980; Tomback & Linhart, 1990). Dropped or fallen seeds from the canopies of enticer pines may end up secondarily dispersed by birds and/or small mammals (Vander Wall, 1992; 1993).

Clark's nutcrackers (*Nucifraga columbiana*) are important dispersers of limber (*P. flexilis*) (Tomback & Kramer, 1980; Lanner & Vander Wall, 1980; Vander Wall, 1988), whitebark (*P. albicaulis*) (Tomback, 1978; 1982; Hutchins & Lanner, 1982), and both Colorado piñon (*P. edulis*) and single-leaf piñon pines (*P. monophylla*) (Vander Wall & Balda, 1977; Tomback, 1978; Ligon, 1978; Vander Wall, 1988). In late summer and fall when cones are produced, each nutcracker harvests tens of thousands of pine seeds, buries them in small clusters called caches, and retrieves seeds from stores during winter, spring, and the following summer months until fresh seeds are available again (Vander Wall & Balda, 1977; Tomback, 1978; 1982; Vander Wall & Hutchins, 1983; Tomback & Linhart, 1990; see review in Tomback, 1998). After snowmelt or rain, seeds not recovered by nutcrackers may germinate, leading to tree recruitment (Tomback, 1982).

Southwestern white pine (*P. strobiformis*) in its northernmost range may also be nutcracker-dispersed (Benkman, Balda & Smith, 1984; Tomback, 1998). This enigmatic pine is little studied. To date, there has been no published information on whether the seeds of southwestern white pine are actually cached by nutcrackers, jays, or rodents and whether tree recruitment occurs by this means. Southwestern white pine is closely related and similar in appearance to limber pine, but the two species differ in cone, seed, and needle characteristics (Steinhoff & Andresen, 1971). Like limber pine, southwestern white pine has large, wingless seeds, and cones that open after seeds ripen (Steinhoff & Andresen, 1971).

Southwestern white pine is found from northern Arizona and southern Colorado south through northern Mexico (Critchfield & Little, 1966; Farjon & Styles, 1997). Anecdotal evidence and Benkman, Balda, and Smith (1984) suggest that Clark's nutcracker disperses southwestern white pine seeds where it is sympatric with the pine. In this paper, we examine southwestern white pine in the San Juan Mountains of southwestern Colorado to determine whether its seeds are primarily dispersed by nutcrackers and to determine its interactions with other vertebrate seed dispersers and predators.

Previously, Benkman, Balda, and Smith (1984) studied the cone and seed morphology and cone ripening phenology of southwestern white pine in relation to seed harvest by red squirrels (*Tamiasciurus hudsonicus*) and Clark's nutcrackers in north-central Arizona, but they did not document seed caching. In addition, no data were presented to substantiate the identification of southwestern white pine. However, they concluded that southwestern white pine cones ripened synchronously among and within individual trees, a pattern that is associated with wind-dispersed conifers (Benkman, Balda & Smith, 1984) but appears nonadaptive for southwestern white pine (Benkman, 1995a).

Thus, additional goals of this study were to re-evaluate the cone ripening phenology of southwestern white pine, as well as to examine needle, cone, and seed morphology of the pine population in our study area with respect to the characteristics of southwestern white pine.

Methods

We studied seed use in southwestern white pine daily from 25 August through 30 September 1999 in the San Juan Mountains, Colorado. Southwestern white pine is a masting species; good cone production is an intermittent event, occurring every three to four years (Krugman & Jenkinson, 1974). We chose 1999 for study because there was good to moderate cone production in the San Juan Mountains. The study was conducted along the Williams Creek Trail in the San Juan National Forest and adjacent Weminuche Wilderness area (37° 32′.761 N, 107° 11′.546 W; elevation about 2,650 m). Southwestern white pine is a forest dominant for the first 1.5 km of the Williams Creek Trail. We partitioned the study area into three subareas (Study Area A, B, and C) to track animal use of cones in individual trees.

The other forest species in the study area were white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), and ponderosa pine (*Pinus ponderosa*). Ponderosa pine was mainly limited to the lower elevations of Study Area A, where the southwestern white pines were old-growth trees.

Limber pine and southwestern white pine differ in a number of needle, cone, and seed characteristics (Steinhoff & Andresen, 1971; Farjon & Styles, 1997). To confirm the identity of the trees in our study area as southwestern white pine, we measured morphological characteristics of our study population for comparison with data in Steinhoff and Andresen (1971).

We marked 10 southwestern white pine trees at Study area A to determine cone opening phenology at this site. Three additional trees were monitored at Study Area C to observe any differences in opening phenology based on elevation or site characteristics. All cones visible on each tree from a designated viewpoint were counted and mapped.

During cone opening, scales separated from the cone core in sequence from the basal to distal end. The stages of cone opening were sorted into four distinct categories: closed, scales separating, partly open, and open. Closed cones had completely closed cone scales along the entire cone. Scales-separating cones showed scales pulling away from the cone core, but seed beds were not visible. Partly-open cones had visible seeds on the basal and central portions of each cone. Seeds were visible on the basal, central, and distal portions of each open cone.

In order to determine whether Clark's nutcrackers or other avian dispersers preferred to harvest seeds from cones with a certain orientation relative to the horizontal, thus limiting seed-dispersal services, we surveyed cone orientation for southwestern white pine trees. On 11 September, 100 trees along the Williams Creek trail were surveyed, and all cones visible on each tree from a designated viewpoint were categorized. Frequencies of each cone position relative to the horizontal were estimated throughout the population as follows: upright, perpendicular to the horizontal, pointing vertically upwards; above horizontal, angled about 45° or 135° above the horizontal; horizontal; below horizontal, angled at about 45° or 135° below the horizontal; and pendulous, perpendicular to the horizontal, but pointing downwards. Any damage to cones from seed harvest by Clark's nutcrackers prior to this date (*e.g.*, frayed scales) was also noted.

Multi-genet tree clusters are one signature of seed dispersal by animals, with each trunk deriving from a single seed in a cache (Tomback & Linhart, 1990). On 26 September, we conducted a survey of these growth forms by following the Williams Creek trail for 1.5 km through the study area and noting the number of stems for all southwestern white pine trees, seedlings, and saplings within 3 m of the trail.

Daily, we observed diurnal vertebrates foraging on seeds from southwestern white pine cones for about 8 hours, beginning 1 hour after sunrise (0800) and ending in late afternoon when decreasing light conditions hindered observations. For each observation, the following data were recorded: species, length of foraging bout, number of seeds obtained, orientation of cone on tree, presence or absence of basal reflexed cone scales, and stage of openness of each cone. We also noted whether seeds were eaten or transported from the area.

STATISTICAL ANALYSES

We used Multifactor Analysis of Variance (ANOVA) tests (Statgraphics Plus, Version 2, Manugistics, Inc., Rockville, Maryland, U.S.A.) to compare seed extraction rates (seconds seed^{-1}) by Clark's nutcrackers for all cone orientations at various stages of openness. Log values of extraction rates were used to normalize data. Next, we performed Mann-Whitney (Wilcoxon) tests to compare median seed extraction times between paired openness categories for the same cone position (*e.g.*, closed horizontal-cones versus scales-separating horizontal cones; partly open pendulous cones versus open pendulous cones, etc.) to determine if extraction times varied significantly among successive stages of openness. Because we performed multiple comparisons for the same data, alpha values for the above analyses were set at $\alpha=0.01$. We determined means and standard errors (SE) for morphological characteristics of southwestern white pine in our study area for comparison with similar data from the literature. Chi-square (χ^2) tests were used to determine any foraging preferences by nutcrackers for specific cone orientations and to determine any preference by red squirrels for cones lacking reflexed cone scales.

Results

SOUTHWESTERN WHITE PINE MORPHOLOGY

Morphological measurements for the pine in our study area confirm its identity as southwestern white pine (Table I). Cone length, seed wing length (if wing was present), and seed weight for the collected cones were consistent with mean measurements reported by Steinhoff and Andresen (1971) for southwestern white pine. However, needle length was intermediate between limber pine and southwestern white pine.

Of 95 tree sites surveyed, 79 sites had a single stem, 15 had two stems, and one had three stems. Of 85 seedlings and saplings surveyed, 71 were single stemmed, six double stemmed, and five triple stemmed. In addition, three seedling sites had 5, 6, and 7 stems, respectively. Stem clusters at our study areas provided strong evidence of seed germination as a result of animal caches (Linhart & Tomback, 1985; Furnier *et al.*, 1987; Tomback & Linhart, 1990; Carsey & Tomback, 1994).

CONE OPENING PHENOLOGY AND ORIENTATION, AND SEED HARVEST BY CLARK'S NUTCRACKERS

The timing of cone opening varied among the three study sub-areas, and cones opened latest at Study Area A (see Figures 1a,b). Red squirrels were observed daily removing cones from trees throughout the study until cones were at the open stage (Figure 2). Apparently, in southwestern white pine, cone-opening phenology varies greatly from cone to cone and tree to tree and is not completed until early to mid-October.

Cone orientation on branches is more variable for southwestern white pine than for other bird-dispersed pines and, therefore, may impact disperser services. Below horizontal cones comprised the largest percentage of cones, with horizontal cones having the second-highest frequency in the population (Table II). Upright and above horizontal were the least frequent cone positions in the

TABLE I. Comparison of morphological measurements for southwestern white and limber pines from Steinhoff and Andresen (1971) with putative southwestern white pine from the study area in the San Juan Mountains of southern Colorado, San Juan National Forest and the Weminuche Wilderness Area. Values reported are mean ± SE.

Character	*P. flexilis*	*P. strobiformis*	Pine in the study area (*n*)
Needle length (mm)*	< 55 ± 2.6	> 70 ± 3.2	65.1 ± 1.08 (89)
Cone length (mm)	< 100 ± 3.4	> 110 ± 4.3	129.1 ± 4.86 (23)
Wing length (mm)**	2-6	2-6	4.3 ± 0.20 (17)
Total seed weight (mg)	< 140 ± 10.8	> 140 ± 20.9	150.0 ± 3.88 (73)
ADDITIONAL DATA			
Endosperm weight (mg)			60.0 ± 1.68 (73)
Seed coat thickness (mm)			0.4 ± 0.009 (75)
Number of seeds per cone			65.0 ± 7.0 (23)

* A total of 89 needle lengths was measured for 19 trees in the study area.

** Measured only on seeds with wing.

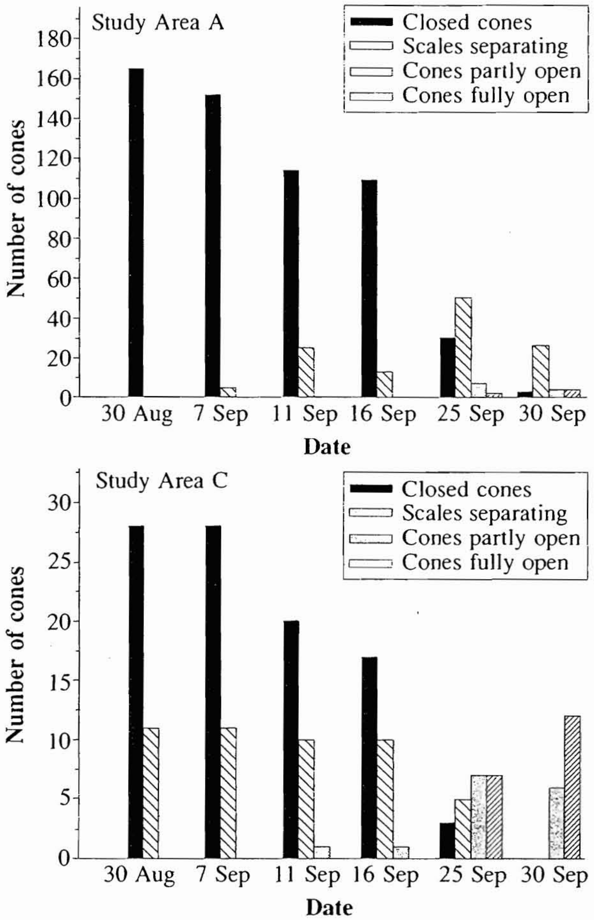

FIGURE 1. Cone opening phenology based on a) 10 marked southwestern white pines in Study Area A and b) three additional pines in Study Area C.

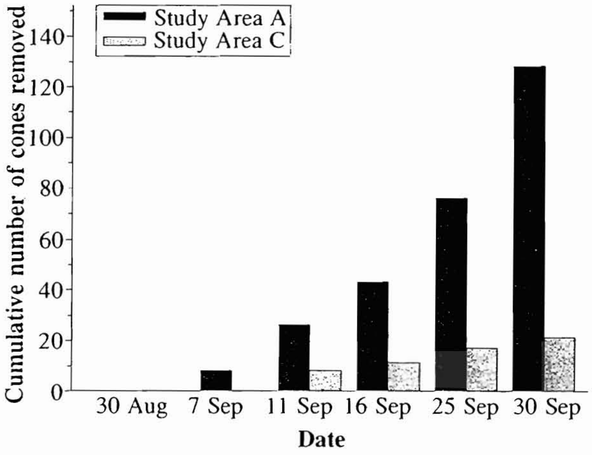

FIGURE 2. Cumulative numbers of southwestern white pine cones removed from marked trees throughout the study by red squirrels in Study Area A and C.

population. On the 11 September survey date, frayed-cone scales were counted as evidence of foraging by Clark's nutcrackers (Tomback, 1994). Horizontal cones were preferred for foraging by nutcrackers before cones opened (Table II), and closed, pendulous cones were usually avoided by nutcrackers.

Clark's nutcracker was the most frequently observed vertebrate species foraging in southwestern white pine trees, typically most active in mid-morning and late afternoon. By 25 August, nutcrackers had frayed the scales of many closed cones. We recorded up to 20 individuals at one time foraging within study sub-areas in loose groups of three to eight birds. Nutcrackers usually foraged in trees singly, but with as many as three birds per tree. Throughout the study, we recorded more than 11 hours of foraging data for Clark's nutcrackers on southwestern white pine cones. During these observations, nutcrackers ate 169 seeds and placed a total of 957 seeds in their sublingual pouches, presumably for transport to caching sites (Vander Wall & Balda, 1977; Tomback, 1978; 1982). We never saw nutcrackers take seeds with remnant wing, even though winged seeds represented about 12% of the total available seeds based on our own sampling (see Table I).

Seed extraction times differed significantly among the four stages of cone openness (Table III, Multifactor ANOVA, *F*-ratio=61.62, df=3, 120, $P=0.000$), but overall extraction times did not differ significantly among the various cone positions (Table III, Multifactor ANOVA, *F*-ratio=0.80, df=4, 120, $P=0.531$). Average extraction times were slowest for closed, pendulous cones (123 second seed^{-1}) and fastest for partly open, pendulous cones (6.7 seconds seed^{-1}). Paired comparisons between successive stages of openness at the same cone position were not significant for all positions; we report only the significantly different comparisons. Extraction times for below-horizontal cones decreased significantly between the closed and scales-separating stages (Mann-Whitney, W=3.0, $P=0.01$, $n_1=9$, $n_2=5$) and between horizontal cones at the scales-separating and partly-open stages (Mann-Whitney, W=5.0, $P=0.000$ (see above) $n_1=31$, $n_2=8$). Slower extraction times for open cones can be attributed to seed depletion, resulting in decreased harvesting efficiency.

During this study, nutcrackers preferentially foraged on horizontal cones (Table II, $\chi^2=67.6$, df=4, $P < 0.005$). Nutcrackers spent more than 15% of the observed time foraging on pendulous cones, but only two seeds were obtained from pendulous cones before the partly open stage.

Nutcrackers sometimes dropped seeds while foraging on open cones. Seeds also fell from open cones, dislodged by the movement of branches, while nutcrackers were foraging on cones nearby. Dropped seeds became available for secondary dispersers.

Nutcrackers placed most harvested seeds in sublingual pouches for seed caching, beginning on 27 August. Nutcrackers usually transported seeds to west-facing communal caching slopes across Williams Creek, about 0.25 to 0.5 km away from our study area. Throughout the day, single birds and flocks flew back and forth from our study area to these caching slopes. On several occasions, nutcrackers cached their pouchloads across the canyon and then returned to the same tree to forage. Nutcrackers were observed making seven seed caches in the study areas, and cache size ranged from one to five seeds. Southwestern white pine seedlings grew near the cache sites.

TABLE II. Cone orientation within a southwestern white pine population as determined on 11 September 1999 with evidence of foraging activity by Clark's nutcrackers in the San Juan Mountains of southern Colorado. Horizontal cones were preferred by nutcrackers for foraging before cone scale separation ($\chi^2=67.61$, df=4, $P=0.005$), and 9.7% of surveyed cones were damaged on this date.

Cone position	Total number of cones	Percentage of population	Number of cones with nutcracker damage at each cone position	Percentage of total damaged cones at each position
Upright	4	0.6	2	3.2
Above horizontal	19	3.0	7	11.3
Horizontal	230	36.1	46	74.2
Below horizontal	248	38.9	7	11.3
Pendulous	136	21.4	0	0
Total number of cones	637		62	

TABLE III. Mean seed extraction times and standard deviation (SD) by Clark's nutcrackers for each stage of cone openness and cone position for a population of southwestern white pine. Seed extraction times among the four stages of cone opening vary significantly (Multifactor ANOVA, *F*-ratio=61.62, df=3, 120, $P=0.000$).

	Extraction times in seconds per seed Mean ± SD (*n*)			
Cone position	Closed	Scales separating	Partly open	Open
Upright	43.5 ± 0.0) (1)	48.6 ± 7.0 (2)	*	*
Above horizontal	92.8 ± 62.6 (3)	32.1 ± 18.7 (4)	*	*
Horizontal	68.8 ± 40.1 (21)	53.1 ± 21.4 (31)	7.6 ± 4.6 (7)	7.9 ± 2.7 (10)
Below horizontal	80.3 ± 32.4 (9)	29.8 ± 18.1 (5)	9.5 ± 4.7 (5)	15.9 ± 12.7 (8)
Pendulous	123.0 ± 0.0 (1)	7.7 ± 0.0 (1)	6.7 ± 2.5 (5)	7.2 ± 3.4 (7)

SEED HARVEST AND PREDATION BY DIURNAL SMALL VERTEBRATES

On several occasions, we observed Steller's jays (*Cyanocitta stelleri*) eating southwestern white pine seeds. All seeds removed by jays were from frayed cones from previous nutcracker activity, open cones, or dropped seeds.

We observed red squirrels in the canopies of southwestern white pine trees throughout all study areas for a total of 79 minutes and 22 seconds. During that time, squirrels were observed removing 75 cones from trees before cones were fully open. On several occasions, the squirrels cut down entire branch tips with intact cones and foliage attached. Red squirrels required 47.8 ± 57.8 seconds cone^{-1} (mean ± SD) ($n=75$ cones, range=22 to 340 seconds cone^{-1}) to chew through the peduncle of a southwestern white pine cone, dropping the cone from the branch. Of the 75 cones we observed cut down by red squirrels, 65 cones (86%) did not have reflexed basal scales, but only 35% of our more randomly collected cone sample did not have reflexed basal scales. This difference is significant ($\chi^2=9.85$, df=1, $P < 0.01$) and suggests that red squirrels prefer cones without reflexed basal scales for cutting. Only 7% of the initial cones on monitored trees in Study Areas A and C remained on the trees at the end of the study period. Red squirrel predation was assumed to be the cause of cone removal.

We observed Colorado chipmunks (*Tamias quadrivittatus*) foraging on seeds from southwestern white pine cones throughout the study period. Typical foraging behaviour included gnawing off and removing cone scales, and subsequently eating the exposed seeds while still sitting in the tree canopy. A bare cone core remained on the tree after the chipmunk removed all of the cone scales and seeds. Chipmunks were not observed placing seeds in their cheek pouches while still in the canopy, but they may well be transporting seeds away for caching.

By the end of the study, we noted seeds occasionally falling from open cones when winds were strong and when nutcrackers were foraging on cones. Several times we observed chipmunks foraging on the ground under the canopies of southwestern white pines, possibly searching for fallen seeds, and on three occasions we saw chipmunks removing fallen seeds from the ground. We were unable to verify the number of seeds gathered by the chipmunks, but seeds were clearly held in the chipmunks' cheek pouches, presumably for transport and caching.

Discussion

Foliage, seed, and cone measurements are consistent with expectations for southwestern white pine (Steinhoff & Andresen, 1971; Farjon & Styles, 1997). However, intermediate needle length suggests possible gene flow between limber and southwestern white pine, a finding consistent with Steinhoff and Andresen's (1971) data from areas of sympatry.

SEED HARVEST AND DISPERSAL

The occurrence of seedling, sapling, and tree clusters is a signature of tree recruitment from animal caches (Tomback & Linhart, 1990). Tree clusters consist of two or more distinct individuals (different genets) that arise from a single animal cache (Linhart & Tomback, 1985; Tomback & Linhart, 1990; Tomback & Schuster, 1994; Torick, Tomback & Espinoza, 1996).

Clark's nutcracker was the most important primary disperser of southwestern white pine seeds during our study. Previous studies have documented mutualistic relationships between nutcrackers and several species of large-seeded pines (Vander Wall & Balda, 1977; Tomback, 1978; Hutchins & Lanner, 1982; Tomback, 1982; 1998; Tomback, Hoffman & Sund, 1990). In years with large cone crops, nutcrackers may harvest more seeds than are energetically required (Vander Wall & Balda, 1977; Tomback, 1982). Southwestern white pine seeds not recovered from nutcracker caches may germinate, particularly after summer rains, leading to tree recruitment. We propose that in areas of sympatry with southwestern white pine, nutcrackers are primarily responsible for seed dispersal leading to tree recruitment of southwestern white pine.

As shown previously (Tomback, 1978; Vander Wall, 1988), mean seed extraction times by nutcrackers became faster (*i.e.*, decreased) as cones ripened or opened. Extraction times later increased, when fewer seeds became available (Table III). However, extraction times did not vary significantly with cone orientation. Nutcracker harvesting efficiency was actually greatest on pendulous, partly-open cones. Because nutcrackers had difficulty foraging on closed pendulous cones and bypassed them to forage on cones of other orientations, the pendulous cones retained a full complement of seeds when they began opening. Although nutcrackers initially preferred horizontal cones, they ultimately provided seed dispersal services regardless of cone orientation.

In this study, jays and chipmunks acted as potential primary seed dispersers, *i.e.*, by harvesting seeds directly from cones and caching them away from parent trees. Steller's jays were less efficient at seed harvest, because they were unable to remove seeds from closed cones, depending instead on nutcrackers to provide access to seeds or waiting for cones to open before harvesting seeds.

Steller's jays also acted as secondary seed dispersers, taking fallen seeds from branches or the ground below tree canopies. Steller's jays typically harvest ponderosa pine seeds from the ground under trees, rather than from cones, and then cache the seeds during a narrow window of maximum seed availability (Breindel, 2000; Breindel & Tomback, unpubl. data). Although Steller's jays are not as efficient at seed harvesting as nutcrackers, and certainly cache fewer seeds than nutcrackers, they are the only seed-caching corvid that occurs at the higher elevations throughout the entire range of southwestern white pine (*i.e.*, the southwestern United States through northern Mexico, Farjon & Styles, 1997; Howell & Webb, 1995). Consequently, they may play an important role in tree recruitment, both as a primary and secondary seed disperser, particularly in geographic areas without nutcrackers.

Food-hoarding mammals quickly take the many wind-dispersed seeds that fall around a tree and may also serve as secondary seed dispersers; nocturnal rodents that cache seeds were not observed in this study, but may also contribute to secondary seed dispersal (Vander Wall, 1992; 1993). Colorado chipmunks foraged on southwestern white pine cones both in tree canopies and from the ground below tree canopies, thereby providing some primary and secondary seed dispersal services for southwestern white pine. Although the number of cached seeds that escape detection by mammals is likely to be small (Vander Wall, 1994), some seeds cached by chipmunks may lead to tree recruitment for southwestern white pine.

RED SQUIRRELS AS SEED PREDATORS

Red squirrels removed cones from southwestern white pine trees until the remaining cones were open (see Figures 1a,b, and 2), but fewer cones were removed by squirrels in the more open forests of Study Areas B and C than in the mature, closed canopy forest of Study Area A. Benkman, Balda, and Smith (1984) concluded that red squirrels were the most important seed predators at lower elevations of coniferous forests. In our study, red squirrels occurred in greatest numbers in the old-growth, mixed coniferous forest at Study Area A. Regardless of location, cone removal by red squirrels eliminated access by primary seed dispersers.

Cones removed by red squirrels are usually stored in middens and used as a food source during winter and spring. Although seeds may remain viable for a year or longer, they remain in cones (Finley, 1969). Seeds from cone middens of *Tamiasciurus* squirrels rarely are in an environment (*e.g.*, substrate) suitable for germination, and any seedlings that are produced are likely to die from root damage caused by the constant digging-up and churning of midden material by the squirrel or from lack of sunlight (Finley, 1969; Hutchins & Lanner, 1982). Furthermore, seed-dispersal distances from parent trees are restricted by squirrel home range size (Smith, 1970). We suggest that red squirrels are an important seed predator for southwestern white pine and may exert selection pressure for cone defence, such as greater resin secretion and different cone morphologies in areas of sympatry (Benkman, Balda & Smith, 1984; Benkman, 1995b).

CONE OPENING PHENOLOGY AND SEED DISPERSAL

Benkman, Balda, and Smith (1984) described four possible patterns of cone ripening phenology among tree canopies of conifers. Synchrony within a tree and asynchrony among trees was a pattern predicted by Benkman, Balda, and Smith (1984) to be the most beneficial to seed dispersers such as nutcrackers: Asynchronous ripening among trees lengthens the harvest period, preventing saturation of disperser species and thus decreasing the number of seeds that fall to the ground, where germination is less likely and predation is higher. Synchronous ripening within and among tree canopies should be limited to wind-dispersed pines; it may in effect saturate seed predators. A completely synchronous cone-opening pattern in an animal-dependent conifer would overwhelm any dispersers.

Benkman, Balda, and Smith (1984) evaluated cone ripening phenology in southwestern white pine based on the correlation between seed number and cone mass, with a high correlation (Pearson's *r*) among cones indicating synchrony. They concluded that southwestern white pine cones ripen synchronously among and within individual trees, a pattern characteristic of wind-dispersed conifers. In contrast, they found that limber pine cones ripened asynchronously among trees but synchronously within, as they had predicted for a bird-dependent species. Rather than use ripening phenology based on seed number/cone mass relationships, we used a cue more relevant to animals: seed availability. We determined cone-opening phenology for southwestern white pine by recording cone scale separation within and among trees over time.

In this study, we found an asynchronous cone-opening phenology among and within tree canopies for southwestern white pine. We suggest that trees with seeds that are primarily animal-dispersed should be expected to maintain their seeds as long as possible, thereby providing dispersal agents with ample time to harvest seeds (Vander Wall & Balda, 1977). However, the opposing selection pressure is cone removal by red squirrels, which prefer closed cones (Benkman, Balda & Smith, 1984): The longer cones remain closed, the greater the number that may be cut down by squirrels. In fact, the cone-opening phenology of southwestern white pine is far more protracted than that observed for limber pine in the Colorado

Front Range, where nearly 90% of the limber pine cones were open by the first week of September (Tomback *et al.,* unpubl. data). The longer cone-opening process in southwestern white pine provides red squirrels continuing access to closed cones and facilitates removal of the cone crop. However, since nutcrackers can remove seeds from closed cones, it also reduces competition for seeds from other avian and mammalian seed predators that remove seeds from damaged or opening cones.

We postulate that total asynchrony actually promotes avian seed dispersal. Using cone-opening phenology as a measure of seed availability, Tomback and Kramer (1980) observed that cone opening was asynchronous among limber pine trees and to a lesser extent within limber pine trees in the eastern Sierra Nevada; this was also found by Tomback *et al.* (unpubl. data) for limber pine in the Front Range of Colorado. Vander Wall (1988) noted that limber pine seed mass peaked just before cones began to open, which suggests that cone opening in fact signals seed ripeness. Vander Wall and Balda (1977) also found an asynchronous cone opening phenology in Colorado piñon pine.

Cone and seed morphology of conifers is influenced by predation pressure and mode of dispersal. This study suggests that Clark's nutcrackers are the primary seed dispersers for southwestern white pine in the San Juan Mountains of southern Colorado, whereas red squirrels are the main pre-dispersal vertebrate seed predators. Cones and seeds of southwestern white pine have characteristics that both facilitate harvest by nutcrackers and deter predation by red squirrels. The characteristics of southwestern white pine consistent with other bird-dispersed pines include large, wingless seeds, a large proportion of horizontally directed cones, and an asynchronous cone opening phenology (Tomback & Linhart, 1990). Characteristics that deter squirrel predation include reflexed basal cone scales and highly resinous cones (Smith, 1970). Short, thick cone peduncles and reflexed cone scales decrease cutting efficiency and the subsequent seed removal by pine squirrels, and resinous cones increase handling times (Smith, 1970; Benkman, Balda & Smith, 1984). In this study, red squirrels preferred to cut down cones without reflexed basal scales. However, long cone peduncles, characteristic of southwestern white pine cones, facilitate cone cutting by red squirrels (Smith, 1970). Smith (1970) argued that cone morphology largely functions to increase seed dispersal by decreasing seed predation. However, anti-squirrel defences in southwestern white pine fall short of those in limber pine, which include profuse resin secretion and shorter peduncles by about half (Steinhoff & Andresen, 1971; Benkman, Balda & Smith, 1984); this may be due, in part, to gene flow from more southern populations in which squirrels are absent, or to taxonomic constraints.

Red squirrels do not occur throughout the entire range of southwestern white pine; they are absent from northern Mexico (Hall & Kelson, 1959), southwestern New Mexico, and southeastern Arizona (Smith, 1970). This study, as well as others (Benkman, 1995b), demonstrates that in areas of sympatry, red squirrels and nutcrackers can have important and conflicting selective impacts on conifer cone and seed traits, including cone-opening phenology.

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