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ADAPTATIONS FOR SEED DISPERSAL AND THE COMPROMISES DUE TO SEED PREDATION IN LIMBER PINE¹

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Abstract: Cone and seed morphology and phenology of the closely related limber pine (*Pinus flexilis*) and southwestern white pine (*P. strobiformis*) were studied in relation to selective seed harvesting by red squirrels (*Tamiasciurus hudsonicus*) and Clark's Nutcrackers (*Nucifraga columbiana*) on two study sites in north central Arizona.

We examined possible selective influences that favor characteristics of both wind- and corvid-dispersed seeds in the limber pine. In a densely forested site, red squirrels harvested >80% of the cones of both pine species before they opened. Seeds from cones harvested by red squirrels were unlikely to germinate. Harvesting of cones and seeds by red squirrels was hindered by pitch and several other cone features. Pitch was more effective in slowing red squirrel harvesting on limber pine than on southwestern white pine. When red squirrels were absent from the open study site, >70% of the cones opened on the trees. Clark's Nutcrackers usually harvested seeds from open cones. Limber pine as compared to southwestern white pine was more evenly and completely harvested by nutcrackers, probably because the cones ripened synchronously within a tree and asynchronously among trees. Cones of southwestern white pine ripened synchronously within and among trees, thus saturating both nutcrackers and squirrels.

Differences between the two pines are most readily interpreted as adaptations for increasing seed dispersal, hindering limber pine's main seed predator (red squirrel) and facilitating seed harvest by its most important seed disperser (Clark's Nutcracker).

We conclude that squirrels in the genus *Tamiasciurus* are an important constraint on the development of cone characteristics that enable efficient seed harvest by birds. Furthermore, adaptations of pines for seed dispersal depend on the relative harvest by predators and dispersers during the different stages of cone-ripening phenology.

Key words: conifers; *Nucifraga columbiana*; pine cone morphology; *Pinus flexilis*; *P. strobiformis*; seed dispersal; seed predation; *Tamiasciurus hudsonicus*.

INTRODUCTION

Patterns of seed predation and dispersal are crucial in the reproductive ecology of plants. Studies on conifers have focused either on seed predators (e.g., Smith 1970) or seed dispersers (Vander Wall and Balda 1977, Tomback 1978). Seed predators have been investigated in wind-dispersed conifers, whereas in animal-dispersed species predators have received only minimal attention.

Conifer cone and seed morphologies are influenced by predation pressure and mode of seed dispersal. In conifers that are attacked heavily by seed predators, cone and seed morphologies tend to hinder harvest (cf.

lodgepole pine, *Pinus contorta* [Smith 1970, Elliott 1974]). In other species, such as pinon pine (*P. edulis*), cone and seed adaptations tend to increase harvest by seed dispersers (Vander Wall and Balda 1977, Ligon 1978). This occurs in two ways: (1) hindering predators so that more seeds are made available to the disperser, (2) increasing harvesting efficiency by the disperser.

Several studies on western North American conifers have shown that red squirrels (*Tamiasciurus hudsonicus*) and Clark's Nutcrackers (*Nucifraga columbiana*) are primary seed predators and dispersers, respectively (Smith 1970, 1981, Vander Wall and Balda 1977, Tomback 1978, 1982, Lanner and Vander Wall 1980). Both are specialized for feeding on conifer seeds (Mewaldt 1956, Smith 1968, 1970, 1981, Bock et al. 1973, Vander Wall and Balda 1977, 1981, Tomback 1978, Giuntoli and Mewaldt 1978). Their specialization on conifer seeds leads to emigration from their usual breeding grounds when seed crops fail and other food

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sources are unavailable (Davis and Williams 1957, 1964, Westcott 1964, Smith 1968, Bock and Lepthien 1976, Rusch and Reeder 1978, Vander Wall et al. 1981). Furthermore, red squirrel winter survival (Smith 1968, Rusch and Reeder 1978) and fecundity the following spring (Smith 1968, Kemp and Keith 1970) are often correlated with fall cone harvests.

Clark's Nutcrackers are important seed dispersers of limber pine in northern Utah and Wyoming (Lanner and Vander Wall 1980) and in California (Tomback and Kramer 1980). In the San Francisco Peaks, Arizona, nutcrackers are important seed dispersers for both limber pine (*P. flexilis*) and southwestern white pine (*P. strobiformis*) (Vander Wall and Balda 1977; their "limber" pine was actually a mixture of the two species). Limber pine is a pioneer species (Lanner 1981) frequently occupying dry, open slopes, the same habitat in which nutcrackers cache seeds (Vander Wall and Balda 1977, Tomback 1978, 1982, Lanner and Vander Wall 1980).

Limber and southwestern white pine (hereafter southwestern pine) are in the subgenus *Strobus*, subsection *Strobi* (Critchfield and Little 1966) and are so similar that some taxonomists consider them subspecies of limber pine (McDougall 1973, see Andresen and Steinhoff 1971). Limber and southwestern pines differ mainly in cone, seed, and needle characteristics (Steinhoff and Andresen 1971, Lanner 1981). These pines are syntopic on slopes above 2730 m in the San Francisco Peaks (Critchfield and Little 1966, McDougall 1973) and apparently hybridize (Steinhoff and Andresen 1971); thus, morphological and phenological differences between the species in this study probably underestimate those for allopatric populations (Steinhoff and Andresen 1971).

The objective of this study was to compare the cone and seed characteristics and patterns of seed harvest of limber and southwestern pines to determine which cone and seed characteristics hinder and which facilitate cone and seed harvest by seed predators and dispersers, respectively. Limber pine is a suitable species for this study because it has characteristics common to both wind- and bird-dispersed conifers (Smith and Balda 1979), suggesting that both seed predators and dispersers have had an important selective influence.

DESCRIPTION OF STUDY AREA

Field work was conducted on two sites on the western slopes of the San Francisco Peaks in north central Arizona. These two sites were chosen to represent the extremes of montane limber pine habitat: mid-elevation forest and open subalpine parkland.

The lower site (elevation 2770 m, 35°19'15"N, 111°42'47"W) was mixed forest dominated by aspen (*Populus tremuloides*), limber and southwestern pines, and Douglas-fir (*Pseudotsuga menziesii*). The understory was composed of herbs, grasses, sedges, and

bracken fern (*Pteridium aquilinum*). Four red squirrel territories were present, three on level ground, and the fourth on a 10° west-facing slope. Red squirrel territories were delineated by natural breaks in the conifer forest, such as openings, rocky slopes, and continuous aspen.

The upper site (elevation 2930 m, 35°19'59"N, 111°42'19"W) was 0.7 km above the lower site on an open, west-facing slope (≈20°) with scattered limber, southwestern, and bristlecone (*P. aristata*) pines. The understory consisted of mainly *Sitanion longifolium* and other grasses. Red squirrels are usually found in forest, but are often absent from subalpine parkland.

MATERIALS AND METHODS

In order to determine the relative distribution of energy in the mature seeds of both pine species, seeds from open cones on the upper site were weighed and measured to determine total mass of both viable and aborted seeds, kernel mass and seed coat thickness. Vernier calipers were used to measure seed coat thickness on the more flattened surfaces of the seed coat away from sutures and the micropylar area.

Measurements of limber and southwestern pine cones from the upper site were made in 1980. Peduncles were cut 1 cm from the cone base, and the width of the peduncle measured with vernier calipers. Cones were weighed to the nearest gram within 1 h of cutting. Cone scales were removed and the number of fully developed seed coats counted. Aborted and viable seeds were not separated since both had fully developed seed coats. Seeds damaged by insects and small inviable seeds were also tabulated. The number of scales in the seed-bearing part of each cone was counted, enabling determination of the number of seeds per scale.

Caloric values of cone tissues were measured with a Parr Semimicro Oxygen Bomb Calorimeter, following the techniques of Paine (1964). Pitch (oleoresin) content was determined by methylene chloride extraction of cones (seeds removed) dried at 60°C to a constant mass.

Observations of cone and seed harvest were made between 26 August and 6 October 1979 and 6 August and 10 October 1980. The number and distribution of cones were mapped to enable rates of seed predation by red squirrels, Clark's Nutcrackers, and insects to be determined. On the lower site, cones were mapped on 17 trees in 1979 and on 79 trees in 1980. In 1980 all cone-bearing pines were mapped on three red squirrel territories, but only four trees were mapped on the fourth territory. On the upper site, cones were mapped on five randomly chosen trees in 1979 and 1980. Trees were inspected weekly to determine the number and position of harvested cones. Red squirrels removed cones from trees, nutcrackers frayed cones, and insects caused cones to turn brown and shrivel. All observations were made with 10x50 binoculars. On the lower

TABLE 1. Seed characteristics of limber and southwestern pines.

Measurement	<i>Pinus flexilis</i>		<i>P. strobiformis</i>		<i>P</i> < *
	$\bar{x} \pm \text{SE}$	<i>n</i>	$\bar{x} \pm \text{SE}$	<i>n</i>	
Mass (g)					
Viable seeds	0.1791 $\pm$ 0.0039	44	0.2250 $\pm$ 0.0034	21	0.001
Aborted seeds	0.1083 $\pm$ 0.0017	76	0.1314 $\pm$ 0.0050	5	0.01
Kernel†	0.0776 $\pm$ 0.0014	37	0.0849 $\pm$ 0.0020	21	0.01
Mean seed coat thickness (mm)	0.471 $\pm$ 0.004	49	0.617 $\pm$ 0.011	31	0.001
Kernel mass/seed coat mass	0.431 $\pm$ 0.006	28	0.379 $\pm$ 0.005	21	0.01

* Mann-Whitney *U* test.

† Only viable seeds included.

site the distances from all mapped trees to the main cache tree on each territory were measured with a steel tape. Cores of cones eaten by squirrels (see Hatt 1943: 329, for a photograph) were gathered every week to determine locations and rates of cone consumption.

The length of foraging bouts on individual cones was measured with a stopwatch for both squirrels and nutcrackers. A foraging bout for a squirrel, including time spent removing pitch, began when the squirrel first bit pitch or scales from the cone, or when the first seed was removed, and ended when the cone was dropped. The times required to select and cut cones, retrieve cut cones on the ground, carry cones to the cache, bury them, and return to the trees were also measured. Individual squirrels were referred to by territory number. Observations were made on four squirrels but most data were gathered from squirrels I and II. Nutcracker foraging bouts included time spent peering or probing between cone scales as the bird examined a cone or cluster of cones. Juvenile foraging rates were not separated from adult rates.

Because the 1979 sample size was small and less complete, these data were used only for comparison. All data discussed are from 1980 unless otherwise indicated.

RESULTS

Cone and seed morphology

Seeds.—Seeds of both pine species are wingless or have only rudimentary wings (Mirov 1967). Seeds of limber pine have thinner seed coats than those of southwestern pine (Table 1). Furthermore, the ratio of

kernel to total seed mass is significantly greater for limber pine than for southwestern pine seeds. As Steinhoff and Andresen (1971) found, southwestern pine seeds are significantly heavier. Viable and aborted seeds are similar in appearance, but aborted seeds are only 59% as heavy.

Cones.—Limber pine cones weighed less than southwestern pine cones and contained fewer seeds (Table 2). No significant differences were found in seeds per gram of cone or per scale. Cone peduncles of the two pines were similar in thickness, but those of limber pine were significantly thicker per gram of cone (Table 2). These measurements of cone mass may not fully reflect cone size differences at maturity since the cones were gathered several weeks prior to opening. Cones also vary in time of opening (see discussion), so that these data are only an approximation of cone size differences.

Pitch.—Limber and southwestern pines had significantly more pitch on their cones than ponderosa and pinon pines (Table 3). Pitch is concentrated mainly on the cone's surface. The energy in pitch was $\approx 38\%$ of the energy in seeds for cones of limber and southwestern pines combined.

Total seed harvest

On the lower site squirrels were the most important seed predator, removing almost 83% of the cones (Table 4). Insects, including cone beetles (*Conophthorus* sp.) and a cone-boring lepidopteran larva, *Eucosma bobana*, attacked slightly more than 6% of the cones, rendering them unavailable to other seed predators

TABLE 2. Characteristics of limber and southwestern pine cones gathered in early September 1980 from the upper site ($\bar{x} \pm \text{SE}$). Sample sizes were 10 cones from six trees for *P. flexilis*; 15 cones from seven trees for *P. strobiformis*.

	Mean cone mass (g)	Mean number of seeds per cone	Seeds per gram of cone	Peduncle width (cm)	Cone mass $\div$ peduncle width	Seeds per scale
<i>Pinus flexilis</i>	138.1 $\pm$ 10.3	68.2 $\pm$ 4.3	0.52 $\pm$ 0.06	0.86 $\pm$ 0.04	159.7 $\pm$ 10.5	1.57 $\pm$ 0.08
<i>P. strobiformis</i>	167.7 $\pm$ 9.1	97.3 $\pm$ 5.9	0.58 $\pm$ 0.01	0.85 $\pm$ 0.03	192.1 $\pm$ 7.7	1.71 $\pm$ 0.04
<i>P</i> < *	.05	.01	NS	NS	.05	NS

* Mann-Whitney *U* test.

TABLE 3. The energy value of pitch on pine cones. The *Pinus flexilis* and *P. strobiformis* pine cones were gathered from the upper site in September 1979. The *P. ponderosa* and *P. edulis* cones were gathered near Flagstaff, Arizona in 1979.

Species	Mean energy content per cone (J)	Energy content of pitch per cone (J)	% of cone energy content in pitch	No. cones
<i>P. ponderosa</i>	334.1	13.3	4.0	19
<i>P. edulis</i>	176.9	13.3	7.5	30
<i>P. flexilis</i> and <i>P. strobiformis</i>	1324.2	128.4	9.7	8

(Smith and Balda 1979). Nutcrackers harvested seeds from $\approx 1\%$ of the closed cones. Nearly 10% of the cones opened on both pine species, making them unsuitable for squirrel harvest (Smith 1981) and thus available to many seed harvesters. Similar results were obtained in 1979: 570 (89.0%) cones were removed by squirrels, 16 (2.5%) were attacked by insects, 51 (8%) opened on the trees, and none were harvested by nutcrackers prior to opening.

At the upper site, 74% (82% of 268 cones in 1979) of the cones on two limber pines were harvested by a juvenile squirrel (Table 4). On the other three trees $\approx 70\%$ (62% of 360 cones in 1979) of the cones opened on the tree. Observations in other open areas on the San Francisco Peaks indicate this is the general pattern of cone harvest. For sixteen other pines on the upper site where squirrels were absent, most cones opened on the tree. In 1980, most of the cones opened on trees in a more extensive open area ≈ 2 km north of the upper site.

Insect damage was roughly the same at both study sites (Table 4). Of 237 seeds gathered from open cones

between 26 September and 5 October 1980, 4 (1.7%) seeds, all from one cone, were parasitized by *Megastigmus* sp., a seed chalcid (Hymenoptera). For 13 limber and 18 southwestern pine cones gathered on the upper site, 57 (6.8%) and 29 (1.8%) of the seeds were damaged by insects, respectively ($n = 841$ limber, 1661 southwestern pine seeds). Insect damage amounted to an estimated 10% of the seed crop.

Clark's Nutcracker as well as Stellar's Jay (*Cyanocitta stelleri*), Williamson's Sapsucker (*Sphyrapicus thyroideus*), Mountain Chickadee (*Parus gambeli*), and Red-breasted Nuthatch (*Sitta canadensis*) were seen foraging for seeds in open cones. Terrestrial mammals, including golden-mantled ground squirrel (*Spermophilus lateralis*), and gray-collared chipmunk (*Eutamias cinereicollis*) foraged for seeds in open cones, seeds that fell into needle clusters, and seeds on the ground. Chipmunks are limited to seeds from open cones because they cannot open large cones (Smith and Balda 1979).

Red squirrel behavior

Red squirrels actively defended individual year-round territories. Each squirrel cached unopened cones in a central midden and consumed them from late fall to early spring; this behavior is typical (Smith 1968, 1970, Rusch and Reeder 1978). All squirrels cached most of their cones at the base of large (> 55 cm dbh) limber or southwestern pines. The caches were located in deep (> 0.3 m) litter consisting mainly of cone scales. The same middens were used in both years, and all four territories had middens of about equal size.

Seed extraction and consumption.—Red squirrels required more time to extract and eat a seed (eating includes removing the seed coat and consuming the kernel) from a limber than a southwestern pine cone (Table 5). Significantly more time was spent by red squirrels removing pitch from the cone per seed for

TABLE 4. Total predation on limber and southwestern pine cones between 6 August and 10 October 1980. See text for explanation.

	Total no. cones on trees	No. cones mapped	Fate of mapped cones							
			Predation on closed cones							
			Removed by squirrels		Nutcrackers		Insects		Opened on tree	
			No.	%	No.	%	No.	%	No.	%
Lower site	2117	1925	1593	82.8	21	1.1	123	6.4	188	9.8
<i>Pinus flexilis</i>	1262	1165	957	82.2	17	1.5	81	7.0	110	9.4
<i>P. strobiformis</i>	855	760	636	83.7	4	0.5	42	5.5	78	10.3
Upper site	783	523	151	28.9	58.5	11.2	59.5	11.4	254	48.6
<i>P. flexilis</i>										
with squirrels caching cones	296	191	146	74.4	3	1.6	30	15.7	16	8.4
without squirrels caching cones	261	167	6	3.6	19.5	11.7	24.5	14.7	117	70.1
<i>P. strobiformis</i>	226	165	3	1.8	36	21.8	5	3.0	121	73.3

TABLE 5. Red squirrel feeding rates on cones between 22 August and 29 September 1980, when time spent grooming and removing pitch is not included. Cones that had insect damage were not included. Red squirrels obtained and ate seeds from closed *P. strobiformis* cones more rapidly than from closed *P. flexilis* cones ($P < .001$, Mann-Whitney U test).

	Mean time per seed (s)	Sample size	
		Seeds	Cones
Cones closed			
<i>Pinus flexilis</i>	14.1	1063	32
<i>P. strobiformis</i>	11.3	1959	32
Cones opening			
<i>P. flexilis</i>	16.8	165	4

limber than southwestern pine (Table 6). Squirrels required only 3–5 s to eat a seed from either pine species ($n = 17$ cones). Thus, the differences in total time squirrels spent per seed between the two pine species was due to differences in cone morphology which made limber pine seeds more difficult to obtain, and due to differences in the effectiveness of pitch which required squirrels to spend relatively more time removing pitch from limber pine cones as compared to southwestern pine cones. Although limber and southwestern pines were combined for pitch energy determination (Table 3), limber pine probably has a greater proportion of pitch than southwestern pine.

Squirrels acquired energy $\approx 1.5 \times$ faster by foraging on southwestern pine cones, due to larger seeds and faster foraging rate, compared to limber pine cones ($0.051 \text{ seeds/s} \times 0.080 \text{ g/seed} = 0.004 \text{ g/s}$ for limber pine; $0.072 \text{ seeds/s} \times 0.085 \text{ g/seed} = 0.006 \text{ g/s}$ for southwestern pine). In addition, there were $1.6 \times$ more seeds in southwestern pine cones (limber pine had 48.2 and southwestern pine 75.6 seeds per cone).

Cone harvest.—Squirrels harvested southwestern pine cones 8–10 d earlier than those of limber pine and concentrated their cone harvesting between 29 August and 26 September (Fig. 1). Many of the cones started to open by 19 September and most were open by 26 September. The fastest harvest rates were 32.3 cones/d by squirrel I between 6 and 12 September, and 29.3 cones/d by squirrel II between 19 and 26 September.

Timing of the cone harvest differed for the three squirrels (Fig. 1). Relatively early completion of cone caching resulted in fewer cones opening in the cache. The temporal order of cache completion was squirrel I, II, and IV, and on 6 November they had 1, 10, and 60 open cones atop their caches, respectively. Cones that opened in the cache were not utilized by red squirrels, and as cone scales opened squirrel feeding rates decreased (Table 5).

Caching cones: the effect of pitch.—Pitch increased travel time from the harvest tree to the cache because

of additional time spent removing pitch and grooming (Table 7). The effect of pitch on travel time was greater for limber pine than for southwestern pine cones (Table 7). The relatively long travel time for squirrel II was due, in part, to its later harvest of cones which had accumulated more pitch.

Squirrels could have harvested cones faster if they had been free of pitch (Table 8). We estimated the time to select, cut, retrieve, and cache a cone, from the time that squirrel I took to cut 11 cones from its midden tree (where travel time equals zero), retrieve, and cache them. An average of 105.6 s per cone was required with an additional 7.2 s to remove pitch. Squirrels I and II were observed during 164 caching trips. Travel time was significantly correlated with the distance of the harvest tree from the cache for both limber and southwestern pine cones ($r > 0.96$; $P < .01$). Travel times were estimated for each tree by using regression equations derived from these data. When carrying a cone, squirrel I took $1.75 \times$ longer to travel to the cache than when not carrying a cone. This ratio was used to estimate return times to the harvest tree. The time spent removing pitch was linearly related to the distance traveled, suggesting that squirrels remove pitch from cones during rests; thus, the actual increase in harvest time because of pitch may be overestimated.

The total time to cache cones, without considering pitch removal time, was determined by estimating the total time spent traveling to and from the cache plus the 105.6 s per cone to complete the caching process. The number of cones cached from each tree was determined by subtracting the number of cone cores beneath the tree from the number of cones harvested by squirrels. The total time spent removing pitch was found by multiplying the number of cones brought to the cache by 7.2 s, and adding the estimated time spent removing pitch while traveling (Table 8).

The time required to remove pitch increased squirrel I's caching time 19.9% and squirrel II's time 32.2% (Table 8).

TABLE 6. Feeding rates of three red squirrels between 22 August and 26 September 1980. A squirrel was timed from the initial removal of pitch or cone scales until the cone was dropped. The increase in time due to pitch was greater for *P. flexilis* than for *P. strobiformis* ($P = .012$, Mann-Whitney U test). The number of viable seeds per cone differed between *P. flexilis* ($\bar{x} = 48.2$) and *P. strobiformis* ($\bar{x} = 75.6$) ($P < .01$, Mann-Whitney U test).

	Mean time per seed (s)		Percent increase due to pitch	Sample size	
	With pitch	With- out pitch		Seeds	Cones
<i>Pinus flexilis</i>	19.6	16.6	18.7	289	6
<i>P. strobiformis</i>	13.8	12.4	10.7	1059	14

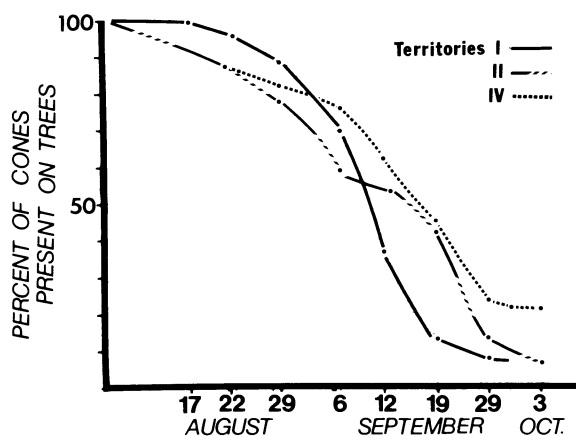


FIG. 1. Percent of limber and southwestern pine cones present on trees through autumn on three red squirrel territories.

Clark's Nutcracker foraging behavior

When they foraged on closed cones, nutcrackers were selective with regard to pine species and cone orientation, but not cone height on the tree. On the upper site, nutcrackers foraged preferentially on closed southwestern pine cones (chi-squared = 4.52, $df = 1$, $0.05 < P < .025$, Table 4), suggesting that features of closed limber pine cones that hindered red squirrels also deterred nutcrackers (a similar result was found in 1979). Nutcrackers preferred closed cones that were not pendulous; of 58 cones shredded in 1980 on the upper site, 42 (72%) had their axis above 45° below horizontal (chi-squared = 34.83, $df = 1$, $P < .005$; using a random sample of 99 cones, with 75 pendulous). Nutcrackers preferentially shredded the basal portion of cones, probably due to the difficulty of hammering on closed cones while hanging upside down. Closed cones were harvested randomly in relation to height of cones on the trees ($P > .10$ for each of the four pines with more than two 1.6-m levels. The comparison was made using a contingency table with expected values of equal proportions harvested from each layer).

The mean time that nutcrackers required to extract

TABLE 8. Estimated caching time and the effect of pitch on the caching efficiency of two red squirrels in 1980. See text for explanation.

	No. cones brought to cache	No. cones cached by 3 October	Total time required for completed cache	
			To cut, carry and cache (h)	To remove pitch (h)
Territory I	287	281	13.8	2.5
Territory II	339	247	17.6	5.7

a given number of seeds decreased as cones opened and exposed their seeds and later increased when seed availability dropped. Mean extraction time per seed on closed cones was $5.7 \times$ greater than when cones were open (Table 9). After 4 October, when all cones on the upper site were open, seed extraction time increased, probably due to a decrease in the number of available seeds. This decrease in the number of seeds in the cones was due to both seed harvest and seeds falling from the open cones. The proportion of viable seed decreased from 83.3% on 27 September ($n = 60$ seeds, four trees) to 47.8% on 3–5 October ($n = 111$ seeds, two trees) (comparing the number of viable to aborted seeds at these times yielded chi-squared value of 25.8, $df = 1$, $P < .005$). The increase in cones visited per foraging bout during 9–10 October, compared to earlier periods (Table 9) further indicates that seeds were less available.

Nutcracker seed extraction rates on open limber ($n = 249$ seeds, 69 bouts) and southwestern pine cones ($n = 152$ seeds, 46 bouts) did not differ, averaging 5.5 s/seed from 27 September to 6 October. Extraction rates also varied little among individual trees during this period (4.3 to 6.6 s/seed for seven trees).

Foraging intensity increased from 20 September to early October. On 20 and 22 September nutcrackers foraged for seeds on the upper site an average of 1 of every 210.5 min of observation, whereas between 27 September and 10 October they foraged on average for

TABLE 7. The effect of cone pitch on time spent carrying cones from harvest trees to cache for red squirrels in 1980.

	Mean travel time (s)	Mean time spent removing pitch (s)	Increase in time due to pitch (%)	Sample size		Mean date
				Trees	Trips	
Territory I						
<i>Pinus flexilis</i>	42.0	18.9	45.0	5	62	Sep 12.5
<i>P. strobiformis</i>	70.1	24.3	34.5	3	22	
Territory II						
<i>P. flexilis</i>	47.5	59.5	125.1	4	57	Sep 22
<i>P. strobiformis</i>	52.6	49.2	93.5	3	23	

TABLE 9. Nutcracker seed extraction rates through autumn 1980. These data were gathered on the upper site except for six foraging bouts between 29 August and 7 September, which were observed on the lower site. The mean time per seed differed between both the first and the second time periods, and the second and the third time periods ($P < .01$, Mann-Whitney U test).

Cone status	Time period	Mean time per seed (s)	No. seeds	No. cones	No. foraging bouts	Cones per bout
Closed	23 Aug–7 Sep	37.0	93	15	15	1.0
		when seeds were eaten				
		43.9	44	9	9	
Open	27 Sep–6 Oct	when seeds were pouched				
		31.5	49	6	6	
		5.6	573	182	143	1.3
Open	9–10 Oct	7.8	73	60	31	1.9

1 of every 18.3 min. This increase was associated with cone opening and increased seed availability.

The time spent foraging on trees was positively correlated with the number of cones on each tree ($r^2 = 0.85$, $df = 9$, $P < .01$). The correlation was stronger for limber pine ($r^2 = 0.98$, $df = 3$, $P < .01$) than southwestern pine ($r^2 = 0.52$, $df = 5$, $0.10 > P > .05$). Furthermore, nutcrackers spent more time foraging on limber pine than expected, considering the number of cones and seeds on the trees, resulting in a given limber pine seed being $2.5 \times$ more likely to be harvested by a nutcracker than a southwestern pine seed.

Limber and southwestern pine seeds occasionally have small wings. When nutcrackers encountered winged seeds, they quickly broke off the wing by wiping the seed across a needle cluster. The general lack of wings, therefore, increased nutcracker foraging efficiency (Tomback 1978).

Although limber pine had a thinner seed coat than southwestern pine (Table 2), nutcrackers required the same time to remove the seed coat and eat the kernel for both pines. The rate on limber pine seeds was 17.0 s/seed ($n = 37$ seeds, 19 bouts), whereas for southwestern pine seeds the rate was 16.4 s/seed ($n = 88$ seeds, 22 bouts). Tomback (1978) also noted that nutcrackers required an average of 17 s/seed for whitebark pine (*P. albicaulis*). Pitch did not appreciably lengthen the seed harvesting time for nutcrackers, and they were only occasionally seen bill-wiping as if to remove pitch.

DISCUSSION

Red squirrels and nutcrackers occur commonly throughout most of the range of limber pine, but are absent from much of southwestern pine's range. Limber pine occurs from northern Arizona and New Mexico north through the Rocky Mountains to south Canada (Critchfield and Little 1966). Southwestern pine is found from northern Arizona and southern Colorado south to north central Mexico (Critchfield and Little 1966); thus, it is found mainly south of the ranges of red squirrels (Hall and Kelson 1959) and Clark's Nut-

crackers (American Ornithologists' Union 1957). The main seed predators and dispersers of southwestern pine throughout most of its range are undoubtedly squirrels in the genus *Sciurus* (Hall and Kelson 1959) and Steller's Jays (Miller 1955, Marshall 1957), respectively. Limber pine is thus predicted to be better adapted for seed dispersal by nutcrackers than southwestern pine.

Tree characteristics

Seed Coat.—Seed coat thickness in *Pinus* is generally proportional to seed size (Vander Wall and Balda 1977, Balda 1981). The thinner seed coat of limber pine in comparison with southwestern pine is consistent with the pattern found in other corvid-dispersed pines, which have thinner seed coats than do wind-dispersed pines (Vander Wall and Balda 1977, Smith and Balda 1979, Balda 1981). Thin seed coats in nutcracker-dispersed pinon pine have been hypothesized to decrease the time required by nutcrackers to break open the seed coat and obtain the kernel (Vander Wall and Balda 1977). Contrary to this hypothesis, nutcrackers in this study did not remove the thinner coat of limber pine seeds more rapidly than those of southwestern pine.

Nutcrackers may benefit from thinner seed coats because the amount of food per unit of seed mass is increased. Since caching flights are the most energetically costly part of the harvesting process (Vander Wall and Balda 1981), a decrease in the amount of inedible seed material should benefit nutcrackers. Kernels of southwestern pine are only 85% as large as those of limber pine for seeds of the same size; thus, nutcrackers can carry $1.2 \times$ more food per caching trip by selecting limber pine seeds. This results in caching (1) more energy, and (2) more seeds per unit time, since a given number of limber pine seeds weighs less. The greater energy stored should benefit the nutcracker, whereas the more seeds cached presumably benefits the tree. Although seed coats of limber pine are proportionately thinner than those of southwestern pine, they are not thinner than that expected for a similarly sized wind-

dispersed seed (see Balda 1931). This suggests that there is counter-selection against thin seed coats.

Selection against thin seed coats is probably exerted by generalized seed predators (Janzen 1971). Benkman (1982) found that the foraging rate of a captive *Peromyscus maniculatus* was slowed significantly by thicker seed coats. Seed coat thickness may, therefore, depend in part on the relative intensity of harvest by seed predators and dispersers.

Cone.—Seed dispersal can be promoted by increasing disperser harvesting efficiency and/or by increasing the number of seeds available to the disperser. Lanner (1981) studied limber pine from the Clark's Nutcracker's viewpoint and concluded that its cones "have no obvious structural modifications that aid nutcrackers in their harvest." However, Lanner looked only for modifications that increased nutcracker harvesting efficiency. Features of cone morphology that slow squirrel harvesting rates also increase the number of cones that remain on the tree, open, and become available to nutcrackers.

Pitch increased limber pine seed dispersal by nutcrackers by hindering the harvest rate of its major seed predator, the red squirrel, without hindering nutcracker harvest. Red squirrel foraging behavior indicates that limber pine devotes relatively more energy to pitch than southwestern pine. Pitch is energetically expensive, and the relatively large amount of pitch on limber and southwestern pine cones suggests that much of the pitch is devoted to predator defense.

Thick cone peduncles deter squirrel predation. Smith (1970) found that a thicker core of vascular tissue in the peduncle decreased the rate of lodgepole pine cone removal by red squirrels. Limber and southwestern pine had equally thick cone peduncles, but for a given cone mass, those of limber pine were thicker. Peduncle thickness may have reached an upper limit because peduncles were nearly as thick as the branch from which they arise. Squirrels sometimes cut through the branch adjacent to the cone, and then presumably spent additional time to cut the cone from the branch.

Lanner (1981) postulated that the upright position of limber pine cones is an adaptation favoring seed harvest by nutcrackers. We have found that nutcrackers preferentially harvest seeds from nonpendulous cones. One important characteristic of other corvid-dispersed conifers is retention of seeds in the cone after maturity, which increases the time seeds are available to dispersers (Vander Wall and Balda 1977, Tomback 1978, Smith and Balda 1979). Limber pine does not have any seed-arresting mechanisms, such as "flanges" that hold seeds in the erect cones of pinon pine (Vander Wall and Balda 1977).

Cone ripening.—The pattern of cone ripening on and among trees should affect seed dispersal. Cones of wind-dispersed conifers, such as ponderosa (Balda 1981) and sugar pine (*P. lambertiana*) (Tevis 1953), usually open synchronously throughout a local region. Wind-dis-

persed conifers with massive cones, e.g., Coulter pine (*P. coulteri*), or with small, few-seeded cones, e.g., western hemlock (*Tsuga heterophylla*), are not easily harvested by squirrels (Smith 1970), and seeds are released slowly (USDA 1974) after a long period on the tree (Smith 1970). The cones of animal-dispersed conifers should ripen when dispersal agents are abundant, since rapid harvest decreases predation and increases the number of seeds dispersed. Seeds that fall to the ground are rapidly removed by ground foragers (Lanner 1981), and if cached their survival is probably low (Abbott and Quink 1970).

Four patterns of cone opening are possible depending on combinations of synchrony and asynchrony within and among trees. Each pattern has different consequences for animal dispersers. The first pattern, synchrony within and among trees, should be limited mainly to wind-dispersed species. Total synchrony of an animal-dispersed species would likely saturate the dispersal agent and increase seed loss to predators. The second pattern, total asynchrony, should also not be found in animal-dispersed conifers, because although it increases the time for dispersers to harvest seeds, it would reduce harvesting efficiency. This cone-ripening pattern should only occur if cones ripen in a predictable pattern on the trees and ripe cones are readily recognized by dispersers. These same conditions apply to the third pattern, synchronous ripening among trees and asynchronous ripening within a tree, though to a lesser degree.

The last pattern is synchrony within a tree and asynchrony among trees, a pattern predicted to be most beneficial to dispersers such as nutcrackers. Synchronous ripening within a tree allows a disperser to recognize profitable food trees, and to return to a given tree and remove the most seeds while revisiting the fewest cones. This is important to wide-ranging corvids such as nutcrackers, since tracking the ripening of individual trees may be difficult. Asynchronous ripening among trees lengthens the harvest period, preventing saturation of disperser species, which decreases the number of seeds that fall to the ground where germination is less likely and predation is higher.

Limber pine cones appear to ripen synchronously on a tree and asynchronously among trees (C. W. Benkman, *personal observation*, S. B. Vander Wall, *personal communication*, Tomback and Kramer 1980). The pattern of cone ripening can be determined from the relationship between seed number and cone mass. As cones ripen, cone mass increases, but the number of seeds remains the same. In mature cones, the number of seeds per gram of cone is nearly constant (Table 2), and a strong correlation should exist between cone mass and seed number. If cones ripen synchronously, the correlation of cone mass to seed number should be very high, and if asynchronously the correlation should be weaker. Using the cones from Table 2, it was found that in limber pine there was almost no correlation

between cone mass and seed number ($r = 0.01$, $df = 8$, NS) for 10 cones from six trees, whereas in southwestern pine cones from seven trees correlation was high ($r = 0.95$, $df = 13$, $P < .01$). (Only cones with $>90\%$ of their seed coats fully developed were used.) This suggests that southwestern pine cones ripened synchronously among and within individual trees. For limber pine the correlation was approximately zero, suggesting that the cones opened randomly or asynchronously among trees. Within one limber pine, where three cones were suitable for analysis, a high correlation ($r = 1.00$) was found between cone mass and seed number. This supports the observations that limber pine cones ripen synchronously on a tree, but asynchronously among trees. (Another interpretation of these data is that among limber pine trees, mass per seed differed, not ripening phenologies).

Nutcrackers harvested cones more completely on limber than on southwestern pine. Nutcracker harvest patterns support the hypothesis that synchrony of ripening on a tree and asynchrony among trees increases seed harvest and dispersal by nutcrackers.

If squirrels can accurately assess cone ripeness (which they apparently do by repeatedly "inspecting" cones on trees), the pattern of synchrony within and asynchrony among trees benefits squirrels by lengthening the harvest period. This may be the reason that equal proportions of limber and southwestern pine cones were harvested by squirrels even though southwestern pine cones were preferred.

Harvest and cone ripening pattern

For limber pine, costs of seed predation by red squirrels and the benefits of seed harvest by nutcrackers can be estimated if several assumptions are made. First, we assume that equal proportions of limber pine cones (and seeds) exist in habitats where red squirrels are present and absent (which appears roughly true). Second, we estimated that nutcrackers harvest 12% of the seeds from open cones in areas with and without squirrels. To emphasize the benefit to the squirrels of asynchronous ripening among trees, we assume that 10% of the cones open on squirrel territories (as actually found) if the trees ripen in complete synchrony, but that none open if they ripen synchronously within and asynchronously among trees. Where squirrels are absent it is assumed that all cones open. Finally, since nutcrackers were $2.5\times$ more likely to harvest a given limber pine seed than a given southwestern pine seed, we assume conservatively that nutcrackers harvest only half as many seeds from trees that ripen in complete synchrony as from trees ripening asynchronously.

We therefore estimate that the number of seeds harvested when cones ripen synchronously within trees and asynchronously among trees is 6.6% of the total seed crop. If the cones were to ripen in complete synchrony a total of only 3.7% of the seeds would be

harvested. This suggests that the pattern in which limber pine cones ripen increases nutcracker harvest. By varying the assumptions one can get a rough idea of the range of values under which limber pine's cone ripening pattern would be beneficial. When the proportion of limber pine habitat occupied by red squirrels is increased to $>90\%$, or when the cone-ripening pattern of synchrony within a tree and asynchrony among trees increases the likelihood of a limber pine seed being harvested by only $1.4\times$, the synchronous ripening pattern results in more seeds harvested by nutcrackers. If limber pine only occurred in red squirrel habitat, cones should ripen synchronously to saturate the squirrels and increase the number of cones opening on the trees. Because limber pine occurs frequently in open habitats free of squirrels, the gain by ripening asynchronously among trees outweighs the cost. It should be noted that linearity is assumed in the above model, yet as theorized, the advantage of asynchrony among trees should increase nonlinearly as the density of cones opening increases. This should increase the advantage of asynchronous cone ripening among trees as cone density increases and/or squirrel density decreases.

We conclude that limber pine's cone-ripening pattern increases the number of seeds dispersed. Likewise, on forested sites at lower elevations, where limber and southwestern pines overlap (Steinhoff and Andresen 1971), southwestern pine's synchronous cone-ripening pattern reduces seed predation by squirrels.

Seed predation as a constraint to avian seed dispersal

Species in the genus *Tamiasciurus* are major predators on conifer seeds in North America (Smith 1970, 1981). Accordingly, where *Tamiasciurus* reside there should be selective pressure on conifers, especially large-seeded species, to defend seeds (Smith 1970). Large-seeded conifers are found mainly in open, dry habitats where alternative food resources for *Tamiasciurus* (such as fungi [Smith 1981]) are rare and predation on squirrels may be intense. *Tamiasciurus* are absent or relatively rare in pinon-juniper woodlands in the southwest United States where large-seeded pinon pines are found. In this habitat, therefore, it is not surprising to find a multitude of avian-dispersed characteristics in these large-seeded pines.

Where *Tamiasciurus* occurs, large-seeded conifers may be unable to evolve cone features that permit reliable avian dispersal. Sugar pine has larger seeds than either whitebark or limber pine (Lanner 1981), yet its seeds are winged and wind-dispersed. It is almost always a forest species, and in habitats suitable for Douglas squirrels (*T. douglassi*) it suffers heavy seed predation (Tevis 1953). Jeffrey pine has large seeds and occupies forests where Douglas squirrels are common (C. W. Benkman, *personal observation*). Predation by squirrels may limit both sugar and Jeffrey pines to wind

dispersal, although avian seed caches also may not be favorable germination sites for these pines (D. F. Tomback, *personal communication*). The taller growth form of sugar and Jeffrey pines also makes for more effective wind dispersal of seeds than for pinon pine.

Limber pine occurs in forests where *Tamiasciurus* is found, but it also occurs where these squirrels are absent (Lanner and Vander Wall 1980) or uncommon (this study). Limber pine is a pioneer species (Lanner 1981) in habitats not suitable for year-round occupation by *Tamiasciurus*. Accordingly, limber pine's possession of both wind-dispersed and animal-dispersed characteristics (Smith and Balda 1979) is not unexpected.

Seed density and dispersal adaptations

The higher the density of seeds, the more likely it is that dispersers will be saturated, reducing effectiveness of dispersal. The ability to produce abundant seed crops places a higher premium on features of the cones and seeds that facilitate seed harvest by potential dispersers. Because southwestern pine occurs at lower densities than limber pine (Potter and Green 1964, Balda 1967, Carothers et al. 1973), southwestern pine produces fewer seeds per year in a given area, which decreases the probability of disperser saturation. The asynchronous pattern of cone ripening among limber pine and the thinner seed coats have probably been important adaptations decreasing disperser saturation. The very high density of pinon pine seeds intermittently produced over large areas may be one reason (in addition to the absence of *Tamiasciurus* in its habitat) why pinon pines have a wide array of features increasing seed harvest by corvids.

Cone adaptations

The types of adaptations of pine cones for seed dispersal are contingent upon the relative harvest by predators and dispersers during the different stages of the ripening. Furthermore, cone characteristics may not equally affect different seed harvesters (e.g., spines on cone scales may hinder squirrels but not insects). Features benefiting avian seed dispersers may not increase wind dispersal.

We distinguish three stages in cone-ripening phenology that influence adaptations for dispersal. In the first stage, prior to seed maturation, all adaptations should decrease harvesting rates by both predators and dispersers. Adaptations important in this stage include rapid seed maturation, which decreases the period when seeds are energetically profitable, and structural defenses such as thick cone scales. Cone pitch is an adaptation of limber pine to decrease seed harvest at this stage.

A closed cone with mature seeds represents the second stage of ripening phenology. During this stage seeds can be dispersed, but also present the most profitable

energy packet for predators such as red squirrels that harvest whole cones. Predation is therefore likely to be intense in this stage. Nevertheless, cone adaptations should depend on the relative intensity of harvest by predators and dispersers. If predation is higher, adaptations should mainly deter predators. High red squirrel predation on limber pine at this stage is correlated with increase in pitch on cones. At this stage nutcrackers preferentially harvested seeds from southwestern pine, suggesting that the characteristics of closed limber pine cones that decreased seed harvest by red squirrels also hindered nutcrackers. If harvest by dispersers is higher, adaptation should favor such harvest. Whitebark pine is an example of facilitation of seed harvest by dispersers after seed maturation: before seeds ripen nutcrackers extract a seed, on average, every 31 s, whereas after seeds mature nutcrackers extract a seed from closed cones every 7 s (Tomback 1978). These foraging rates are comparable to those of nutcrackers on limber pine before and after cone opening, respectively. The thin seed coats of limber pine increase nutcracker harvest in this stage as well as during the following stage. In our study, the timing of cone harvest by red squirrels was crucial in determining the number of cones that remain closed and useable in the squirrel's cache. The later a red squirrel completed caching cones, the larger the number of cones opening in the cache. This suggests that the pattern of cone ripening and harvest are integrally related, and that brief ripening periods adversely affect red squirrel harvesting abilities.

The third stage, when the cones open, is the primary dispersal stage. Predation by animals that remove the whole cone is reduced after the cones open. This is when adaptations increasing the dispersal agent's seed harvesting efficiency are likely to be most pronounced. Limber pine has adaptations to increase nutcracker harvest in this stage, such as the cone-ripening pattern within and among trees.

Smith (1970) has argued that cone morphology largely functions to increase seed dispersal by decreasing seed predation. Now it appears that cone morphology also varies with the dispersal agent. We suggest that cone morphology and phenology vary due to the timing and intensity of seed predation and dispersal. It should be possible to predict qualitatively the types of adaptations found in cones by knowing the patterns of predation and dispersal.

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