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*Evolution*, Vol. 49, No. 4 (Aug., 1995), 585-592.

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# EVOLUTION

INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION

PUBLISHED BY  
THE SOCIETY FOR THE STUDY OF EVOLUTION

Vol. 49

August, 1995

No. 4

*Evolution*, 49(4), 1995, pp. 585–592

## THE IMPACT OF TREE SQUIRRELS (*TAMIASCIURUS*) ON LIMBER PINE SEED DISPERSAL ADAPTATIONS

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**Abstract.**—Tree squirrels (*Tamiasciurus*) are important selective agents on conifer reproductive strategies (Smith 1970, 1975). Although this is well established for wind-dispersed pines, the impact of tree squirrels on bird-dispersed pines has been largely ignored. I assessed the impact of tree squirrels on the allocation of reproductive energy in the bird-dispersed limber pine (*Pinus flexilis*) by comparing its cone and seed traits from three sites in the Rocky Mountains where tree squirrels (*Tamiasciurus*) are present to those from three mountain ranges in the Great Basin where tree squirrels are absent. As predicted, differences between the two regions in individual cone and seed traits are consistent with the hypothesis that tree squirrels are important selective agents on these traits. In the absence of tree squirrels, limber pine allocates more than twice as much energy to kernel compared with that invested in putative seed defenses (cone, resin, and seed coat) as does limber pine where tree squirrels are present. Such a large difference is particularly striking, because tree squirrels may have become extinct in the Great Basin in only the last 12,000 yr. Although many factors influence the allocation of energy to cones and seeds, no single factor other than the presence of tree squirrels is compatible with the large and consistent differences between limber pine in the Rocky Mountains and Great Basin. These results show that tree squirrels are an important constraint on the evolution of cone and seed traits that promote the dispersal of seeds by birds.

**Key words.**—*Nucifraga columbiana*, *Pinus flexilis*, seed dispersal, seed predation, *Tamiasciurus*.

Received May 27, 1994. Accepted June 21, 1994.

Early life stages are often particularly vulnerable to predation (e.g., Howe and Smallwood 1982). Consequently, predators have a strong effect on the timing and allocation of resources to reproduction (e.g., Reznick et al. 1990). Plant seeds, especially, are subject to intense predation (Cavers 1983), because at this stage nutrients and energy are concentrated (Smith 1970, 1975; Janzen 1971) resulting in high-quality resources that also can be hoarded (Smith and Reichman 1984; Vander Wall 1990). Seed predators, not surprisingly, are well recognized as affecting the evolution of seed-ripening phenology, morphology, and associated defenses (Smith 1970, 1975; Janzen 1971), as well as plant distributions (Louda 1982) and community structure (Brown et al. 1986).

Even though the heavy cones that protect the seeds of wind-dispersed conifers provide an outstanding example of the effect of selection by predators (Smith 1970, 1975; Elliott 1974; Linhart 1978; Benkman 1989), studies of bird-dispersed conifers have tended to ignore the importance of seed predators. Instead, these studies have focused on cone and

seed characteristics that ease seed harvest and dispersal by birds, particularly Clark's nutcrackers (*Nucifraga columbiana*) (e.g., Vander Wall and Balda 1977; Tomback 1978, 1983; Lanner 1980, 1982; Tomback and Linhart 1990; but see Benkman et al. 1984). Indeed, a recent and lengthy review of the evolution of avian seed dispersal in pines included only one sentence on the possible impact of seed predators (Tomback and Linhart 1990). Such a narrow view, however, is unwarranted considering that studies of fruit dispersal show that predators alter the interactions and coevolution between plants and their seed dispersers (Herrera 1985).

A study (Benkman et al. 1984) on red squirrels (*Tamiasciurus hudsonicus*) and Clark's nutcrackers led to the suggestion that selection by red squirrels increased cone defenses in limber pine (*Pinus flexilis*). This, in turn, reduced the effectiveness with which nutcrackers harvest and disperse the seeds. For example, a reduction in the number of seeds per cone acts as a defense against squirrels because they would have to bite through more cone scales to gain access to underlying seeds (e.g., Smith 1970); squirrels remove cones from the tree and then starting at the base of the cone bite off successive scales. However, a decrease in the number of seeds per cone would also reduce seed harvest rates by nut-

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crackers (e.g., Vander Wall 1988). Here, I test the hypothesis that tree squirrels (*Tamiasciurus hudsonicus* and *T. douglasi*) have had an impact on the evolution of seed defenses of limber pine. This is a reasonable hypothesis since tree squirrels have been found to selectively harvest cones in relation to the effect of different cone traits on tree squirrel foraging efficiency (e.g., Smith 1970; Elliott 1974); furthermore, tree squirrels have been found to harvest over 80% of the limber pine cones on their territories, from which few if any seeds germinate and become trees (Benkman et al. 1984). I hypothesize that, in the absence of *Tamiasciurus*, limber pine should have reduced its allocation of energy to the cone compared with the amount it invests in seed kernel (embryo and female gametophyte). Of course, cones and seeds are more than just energy. However, because I am comparing the same structures from different trees, energy provides a good measure of resource allocation to the different components (see Smith 1970).

Limber pine usually co-occurs with *Tamiasciurus* (Benkman et al. 1984), except in the Great Basin (fig. 1). Throughout the Great Basin limber pine is widespread on mountain ranges (fig. 1; Critchfield and Little 1966; Arno and Hammerly 1984), but *Tamiasciurus*, although probably formerly present (Heaton 1990; see also Wells 1983; Grayson 1987), may have gone extinct in the last 12,000 yr (Grayson 1987; Heaton 1990). In this period, the geographic range of limber pine changed little in the Great Basin, although it has shifted to higher elevations (Wells 1983; Axelrod and Raven 1985; Thompson 1988). Clark's nutcrackers occur throughout the range of limber pine (see Peterson 1990), and act as limber pine seed dispersers (Vander Wall and Balda 1977; Lanner 1980; Lanner and Vander Wall 1980; Tomback and Kramer 1980; Benkman et al. 1984; Lanner et al. 1984). Except for the absence of *Tamiasciurus* from the Great Basin, the conifer-seed predator assemblages are very similar in the two regions. Insect cone and seed predators are widespread in both the Great Basin and Rocky Mountains (Hedlin et al. 1980), and insects have been found to damage less than 10% of the cones in both regions (Lanner and Vander Wall 1980; Benkman et al. 1984). Other mammalian seed predators such as *Sorex* spp., *Tamias* spp., *Spermophilus lateralis*, and *Peromyscus* spp. (see Smith and Balda 1979) occur in many of the Great Basin ranges, including those from which cone collections were made (Hall 1981; Heaton 1990). These mammalian seed predators are less specialized for harvesting conifer seeds and have much less of an impact on limber pine than *Tamiasciurus* (see Smith and Balda 1979); they harvest individual seeds from open cones or fallen seeds, which accounts for a small percentage of the total seed crop because *Tamiasciurus* and nutcrackers harvest between 80% and 90% of the cones before they even open (Lanner and Vander Wall 1980; Benkman et al. 1984). In sum, the only known important biotic factor that might influence limber pine seed and cone traits, and that differs between the Great Basin and the Rocky Mountains, is the presence of *Tamiasciurus*. The possible impact of abiotic factors will be addressed in the Discussion section.

Predicted changes for limber pine in the Great Basin in comparison to limber pine in the Rocky Mountains include: (1) an increase in the number of seeds per cone, and (2) a

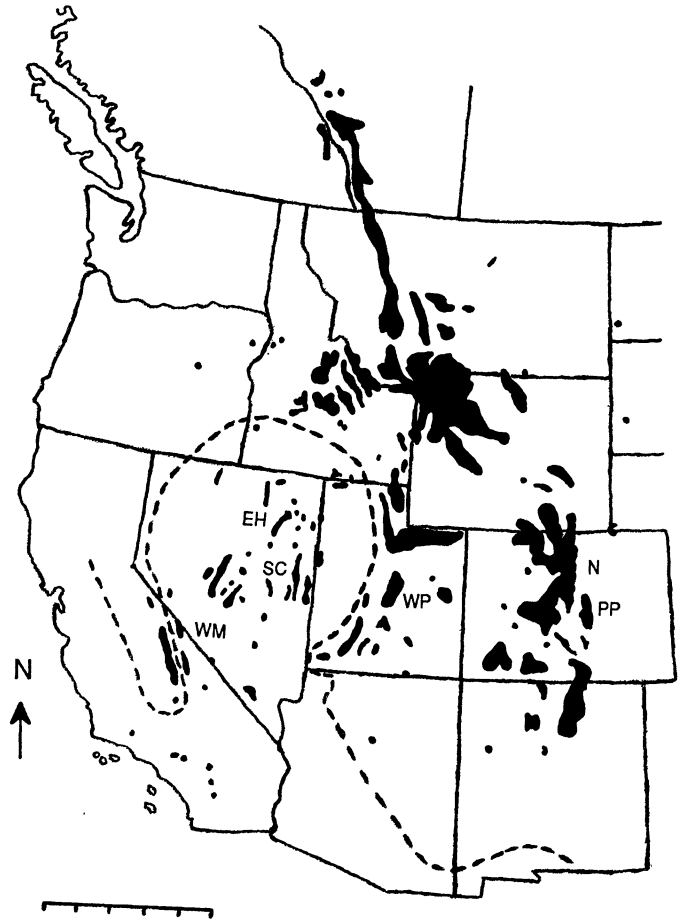


FIG. 1. A map of western North America showing the distribution of limber pine (*Pinus flexilis*; in black) and the location of study sites. *Tamiasciurus* occur to the north of the dashed line (i.e., *Tamiasciurus* are absent from most of Nevada). The letters represent the initials of the different study sites. The White Mountains, Wasatch Plateau, Nederland, and Pikes Peak study sites are west of their respective initials, whereas the East Humboldt Mountains and Schell Creek Range study sites are east of their respective initials. The distribution of limber pine is based on Critchfield and Little (1966).

reduction in cone mass so that the percentage of the total energy devoted to kernel is increased. Both an increase in the number of seeds per cone and a reduction in cone mass would enhance nutcracker foraging rates by reducing the time required to extract seeds from the cones (see Benkman et al. 1984; Vander Wall 1988), which would presumably benefit the trees because more seeds could be dispersed. (3) A reduction in resin is predicted in the absence of tree squirrels, because resin on the surface of limber pine cones hinders harvest by *Tamiasciurus* (Benkman et al. 1984; see also Smith 1970). (4) Seed-coat thickness is predicted to decline in the absence of *Tamiasciurus*. No evidence suggests *Tamiasciurus* select for thicker seed coats; variation in seed-coat thickness is minor compared to the much greater thicknesses of cone scales that *Tamiasciurus* bite through to get seeds (see also Smith 1970). However, if limber pine is more efficiently and completely harvested by nutcrackers, then fewer seeds fall to the ground where ground-foraging seed predators (e.g.,

rodents, including *Peromyscus*) gather most of the seeds (see Lanner 1980; Hutchins and Lanner 1982; see also Benkman et al. 1984). Increased seed-coat mass and thickness may act to deter predation from ground-foraging rodents (see Smith 1970; Janzen 1971; Smith and Balda 1979; Benkman et al. 1984). These rodents are less likely to prey on seeds harvested by nutcrackers, because nutcrackers often cache seeds (buried at depths of about 2 cm in soil) in open areas having low rodent densities (Tomback 1978, 1982; Vander Wall 1988; see also Ligon 1978; Hutchins and Lanner 1982; Vander Wall 1990). (5) Kernel mass is not expected to change (Smith 1970; Elliott 1974), especially because limber pine has large seeds compared to other co-occurring conifers (see Smith 1970).

The comparison of limber pine in the Great Basin to limber pine in the Rocky Mountains is suitable for testing an additional hypothesis. Although nutcrackers disperse large wingless pine seeds (e.g., Vander Wall and Balda 1977; Tomback 1978, 1982, 1983; Lanner 1980, 1982; Lanner and Vander Wall 1980; Hutchins and Lanner 1982), Price and Jenkins (1986) suggested that nutcrackers might be the lesser of "several evils" and have a net negative effect because they also eat a large number of seeds. Price and Jenkins (1986) pointed out that whether nutcrackers are mutualists can be determined depending on whether pines evolve traits that deter nutcrackers in the absence of squirrels. Because many cone features hinder both nutcrackers and squirrels (Benkman et al. 1984), reductions in these seed defenses in the absence of squirrels, but in the presence of nutcrackers, imply that nutcrackers act as mutualists.

#### METHODS

I gathered limber pine cones from three sites in Colorado and Utah (hereafter, collectively the Rocky Mountains) where *Tamiasciurus* are present (August 25–28, 1990), and from three sites in Nevada and California (hereafter, collectively the Great Basin) where *Tamiasciurus* is absent (August 29–30, 1990) (fig. 1). I attempted to reduce the latitudinal range of collections and differences in latitude between the two regions, because there is some latitudinal variation in cone size (Steinhoff and Andresen 1971). The mean difference in latitude between sites from the two regions was only 4'. The Rocky Mountain sites were on the north slope of Pikes Peak (38°55' lat., 2820 m elev.) and about 8 km north of Nederland (40°01' lat., 2770 m elev.), Colorado, and on the Wasatch Plateau (38°59' lat., 2910 m elev.), Utah. The Great Basin sites were in the Schell Creek Range (39°11' lat., 2950 m elev.) and East Humboldt Mountains (41°02' lat., 2770 m elev.), Nevada, and the White Mountains (37°30' lat., 3070 m elev.), California. I gathered cones from large stands of limber pine at each site so that a similar and high frequency of ovules was likely to be pollinated and would initiate seed-coat development (see Smith et al. 1988).

Cones were gathered from each of ten trees at each site. Each cone was sealed in a uniquely labeled plastic bag and placed on dry ice. Cones remained frozen until I analyzed them in March and April 1991. I chose the first ten trees that had within easy reach at least several cones with no apparent insect or other damage. The one cone trait that I could easily

observe was the amount of resin on the cone surface. To counter a potential bias in tree selection, I selected trees whenever possible from a distance beyond which I could assess the amount of resin.

I analyzed one cone from each tree to determine the total amount of energy invested in seed kernels relative to all the energy devoted to putative structural defenses (resin, cone, and seed coat) and seed kernel (i.e., percent kernel). First, I measured the amount of resin on the cone's surface. Each cone was thawed; I then used two or three washes of dichloromethane to remove and isolate resin from the cone's surface (two washes were sufficient to remove virtually all resin from the cone's surface). The dichloro-methane was evaporated, and the resin was dried and weighed to the nearest 0.01 g (all other masses were weighed to the nearest 0.001 g). Then the cones were oven-dried (60°C) for over 5 d. I removed the seeds and then weighed each cone (cone scales and axis). I then removed the seed coats from the kernels of five randomly chosen seeds and weighed the seed coats. I used digital calipers to measure the thickness to the nearest 0.01 mm on the more flattened surfaces of the seed coats of each of the five seeds. Next, I estimated the mass of seed coats for each cone as the number of seeds times the mean seed-coat mass per seed. From each cone, I counted only the number of seeds of sufficient size to contain kernels. I did not count small and incompletely developed seeds that occur, for example, at the base of the cone where seeds rarely contain a kernel. To estimate the total caloric values of the cone exclusive of kernels, I multiplied each of the total masses (resin, cone, and seed coat) by its specific caloric value (8206.7, 4766.8, and 4660.6 cal/g, respectively; C. C. Smith pers. comm. 1981; see also Benkman et al. 1984), and summed these products.

I estimated the potential mass of kernel per cone as the mean kernel mass of the five seeds chosen above from each cone times the number of seeds as counted above. I used seeds with fully developed seed coats, whether full or empty of kernel, rather than only those containing seed kernels, because seed coats better represent the potential for each cone (see Smith 1970). Seed coats grow after both self- and cross-pollination, but the female gametophyte is more likely to be reabsorbed after self-pollination (Smith et al. 1988, and references therein).

Cones and seed coats were fully developed when I gathered them, and I thought kernels would be mature because in northern Utah, for example, kernel mass reached maximum size by the first week of September (Vander Wall 1988). Unfortunately, I was unaware that in some areas, such as in the White Mountains, limber pine may mature later in September (see Lanner et al. 1984). Kernels from two Great Basin sites, the Schell Creek Range and White Mountains, were unusually small, shriveled, and immature. Seed coats, however, were fully developed (see Westoby and Rice 1982). For these two sites, I estimated kernel mass based on the relationship between the cube root of kernel mass ( $KM$ ), square root of seed-coat mass ( $SCM$ ), and seed-coat thickness ( $SCT$ ) from the Rocky Mountain sites:

$$KM = 2.607 + 0.478(SCM) - 6.402(SCT)$$

( $R^2 = 0.85$ ,  $df = 27$ ,  $F = 75.14$ ,  $P < .0001$ ). This relationship implies, quite reasonably, that kernel mass increases as seed-

TABLE 1. Cone and seed measurements ( $\bar{x} \pm SE$ ) for cones gathered in the Rocky Mountains and in the Great Basin. The *F* and *P* values give the significance of the differences between regions (i.e., Rocky Mountains and Great Basin) and for differences among sites within regions based on two-level nested ANOVAs (ln-transformed data). Also shown is the relative percentage of the total variation accounted for by variation between regions and among sites within regions.

Measurement	Rocky Mountain sites ( <i>Tamiasciurus</i> present)						Great Basin sites ( <i>Tamiasciurus</i> absent)				Between regions			Among sites within regions		
	Pike Peak	Nederland	Wasatch Plat.	Schell Creek	E. Humboldt	White Mts.	<i>F</i> (df = 1, 4)			<i>P</i>	% of variation	<i>F</i> (df = 4, 52)		<i>P</i>	% of variation	
	7.50 (0.69)	5.05 (0.78)	9.02 (0.55)	20.11 (1.08)	15.71 (0.67)	13.06 (0.42)	134.79	<0.025	70.0	10.49	<0.001	14.8				
<b>Cone</b>																
No. seeds	49.4 (4.2)	26.5 (5.2)	39.6 (3.2)	79.8 (4.3)	82.7 (5.6)	67.1 (3.8)	10.97	<0.05	58.4	6.32	<0.001	14.8				
Cone mass, g	34.78 (2.54)	29.49 (2.26)	42.97 (1.44)	24.56 (1.28)	26.19 (2.07)	24.72 (1.82)	7.17	<0.10	44.1	5.39	<0.005	17.4				
Resin mass, g	2.78 (0.26)	1.93 (0.21)	2.83 (0.26)	0.96 (0.19)	2.66 (0.33)	1.64 (0.36)	1.82	=0.25	11.1	7.35	<0.001	35.2				
<b>Seed</b>																
Kernel mass, mg	44.90 (1.87)	47.98 (3.04)	82.15 (3.04)	59.66 (3.15)	50.31 (3.55)	43.05 (2.00)	0.16	>0.50	0	22.74	<0.001	69.2				
Seed-coat mass, mg	60.27 (3.71)	53.01 (2.49)	56.85 (2.46)	38.31 (1.33)	41.20 (2.77)	35.23 (1.65)	26.56	<0.01	70.9	3.45	<0.025	5.9				
Seed-coat thickness, mm	0.43 (0.01)	0.38 (0.01)	0.30 (0.01)	0.26 (0.01)	0.28 (0.01)	0.30 (0.01)	8.49	<0.05	55.6	8.73	<0.001	20.0				

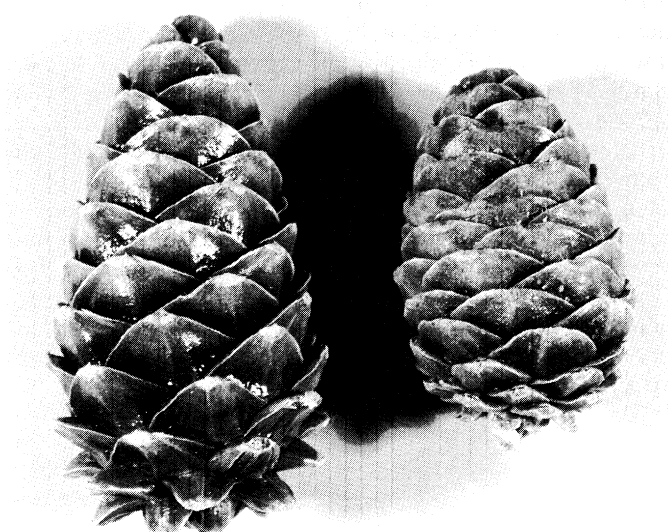


FIG. 2. A photograph of limber pine cones from the Great Basin (right) and Rocky Mountains (left) (see text). These cones were chosen to represent some of the general traits from each region, and are not atypical.

coat mass increases but is discounted by increases in seed-coat thickness. I multiplied the specific caloric value of limber pine seed kernels (7362.8 cal/g; C. C. Smith pers. comm. 1981) by total kernel mass per cone to estimate total calories of kernel per cone.

I used a two-level nested ANOVA (Sokal and Rohlf 1981) on each trait (ln-transformed) to determine the significance, and the relative amount of variation, due to differences between the two regions (i.e., Rocky Mountains and the Great Basin), and to differences among sites within regions. Because of insect damage to single cones from both the Schell Creek Range and White Mountains the sample size was nine cones for each of these sites, but ten for the other sites. I used nested ANOVAs with unequal sample sizes (Sokal and Rohlf 1981).

RESULTS

The percent of total cone energy devoted to seed kernels in the Great Basin averaged over twice of that in the Rocky Mountains (16.3% and 7.2%, respectively; table 1). Of the total variation in this ratio, 70% was from differences between the two regions, whereas only 15% of the variation was attributable to differences among sites within regions (table 1). Contributing most to the difference between the two regions was the number of seeds per cone. Cones from the Great Basin contained an average of twice as many seeds as those from the Rocky Mountains (table 1). The number of scales per cone (not counted) appeared similar between sites (fig. 2), with a linear transect along the cone axis often crossing about ten large scales. The increase in number of seeds per cone in the Great Basin appeared to result from a reduction in the number of sterile scales at the base of the cone. Sterile basal scales increase the time taken by squirrels to reach full seeds because squirrels begin foraging at the base of the cone and bite off successive scales (see Smith

1970). An increase in the number of sterile basal scales with increases in seed predation by squirrels is what is predicted based on studies of lodgepole pine (*P. contorta* var. *latifolia*) (Smith 1970; Elliott 1974).

Cones tended to be smaller in the Great Basin (table 1; fig. 2), and averaged only about 0.7 as much in mass as those from the Rocky Mountains. Assuming, as argued above, that the number of scales per cone was similar among sites, the decrease in cone mass implies that individual cone scales were smaller in the Great Basin than in the Rocky Mountains. This was obvious from visual inspection as well (fig. 2). In addition, the basal scales of cones from the Rocky Mountains tended to have larger and more reflexed apophyses than those from the Great Basin (fig. 2). Large reflexed apophyses may impede squirrels from removing cones from the trees and from biting off the basal scales to gain access to the seeds (see Smith 1970; Elliott 1974). Small cones and only slightly reflexed scales have been noted previously for limber pine from the White Mountains (Steinhoff and Andresen 1971).

Resin mass per cone did not differ significantly between the Rocky Mountains and Great Basin (table 1). Variation among sites within regions, however, was significant and accounted for 35% of the total variation in resin mass (table 1). The amount of resin on cones from the Great Basin was especially variable (table 1).

Seed-kernel mass (per seed) did not differ between the Rocky Mountains and the Great Basin (table 1). In contrast, variation among sites within regions was highly significant and contributed nearly 70% of the total variation in kernel mass (table 1). Limber pine occupies sites differing in climatic and edaphic characteristics (Lepper 1974), and most of the variation in seed (and kernel) mass is probably related to factors other than seed predation. Similarly, within the Rocky Mountains of Colorado total seed mass varies tremendously among sites (14 sites in Colorado had a range in mean total seed masses of 67 to 143 mg; Steinhoff and Andresen 1971).

Seed coats were significantly lighter and thinner in the Great Basin than in the Rocky Mountains (table 1). Furthermore, seed-coat thickness decreased as calories allocated to cone and resin relative to kernel declined (fig. 3;  $r^2 = 0.67$ ,  $df = 4$ ,  $F = 7.98$ ,  $P < .05$ ). This correlation was strongest among the three Great Basin sites (fig. 3). Such a correlation should occur if declines in the relative amount of energy devoted to defenses enables nutcrackers to harvest and cache more seeds so that fewer seeds become available to generalist seed predators (see Introduction). A decline in seed-coat thickness might also occur if generalist seed predators were absent from the Great Basin. Many generalist seed predators (e.g., *Tamias*, *Spermophilus*, and *Peromyscus*), however, occur in the mountains of the Great Basin including those sampled (Hall 1981; Heaton 1990).

In sum, in the absence of *Tamiasciurus*, cone masses tend to be smaller, the number of seeds per cone is nearly double, seed coats are thinner, and the proportion of total cone energy devoted to kernel averages over twice of that devoted by limber pine where *Tamiasciurus* is present. Resin and seed kernel masses, however, do not differ between the two regions.

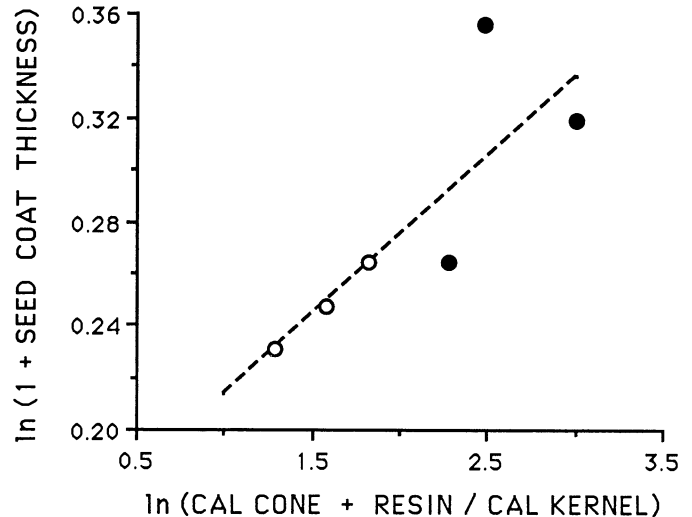


FIG. 3. Seed-coat thickness in relation to the amount of calories devoted to cone and resin relative to kernel. Open circles, Great Basin sites; filled circles, Rocky Mountain sites; dashed line, linear regression line (see text).

#### DISCUSSION

Differences in energy allocation to cone and seeds between the Great Basin and Rocky Mountains are consistent with the hypothesis that *Tamiasciurus* has had a major selective impact on limber pine (Benkman et al. 1984). The smaller cone size ( $P < .10$ ) and the greater number of seeds per cone in the Great Basin, where *Tamiasciurus* is absent (table 1), are differences predicted as selection pressure from *Tamiasciurus* is relaxed (Smith 1970; Elliott 1974; Benkman et al. 1984). For instance, wind-dispersed lodgepole pines have more cone scale mass and fewer seeds in the basal part of the cone in apparent response to increases in seed predation by *Tamiasciurus* (Smith 1970; Elliott 1974; for similar examples in other wind-dispersed conifers, also see Linhart 1978 and Benkman 1989). Moreover, because nutcrackers preferentially harvest and cache seeds from trees with more seeds per cone (Vander Wall and Balda 1977), and nutcrackers harvest most of the seeds and cones in sites where *Tamiasciurus* are absent (Lanner and Vander Wall 1980), nutcrackers may have hastened changes in limber pine. In fact, directional selection by nutcrackers might have been critical for such large changes to occur in the Great Basin, especially if *Tamiasciurus* became extinct only 12,000 yr ago (and limber pine cones in the Great Basin were similar to those in the Rocky Mountains); 12,000 yr represents at most 400 limber pine generations, assuming a generation time of 30 yr (limber pine begins producing cones at 20 to 40 yr of age; Schopmeyer 1974). Such rapid evolution would be strongly supported if fossil limber pine cones are found in the Great Basin.

Particularly striking is the convergence of energy allocation by limber pine in the Great Basin to other pines considered more typical of those dispersed by birds (Smith and Balda 1979). For example, the percent of total cone energy (cone, seed coats, and kernel, but excluding resin) devoted to kernel is 14.1% (assuming 76% of the seeds are full [Vander Wall 1988]). This is similar to the average whitebark pine

(*P. albicaulis*) cone from a site in Wyoming (17%; Lanner 1982; resin was excluded). These values are much larger than those for limber pine in the Rocky Mountains (6.3%) or wind-dispersed ponderosa pine (8%; Lanner 1982, estimated from Smith 1970). In addition, this change in energy allocation in limber pine is consistent with nutcrackers acting as effective seed dispersers (e.g., Vander Wall and Balda 1977), and not just the lesser of "several evils" (Price and Jenkins 1986).

In contrast to the other traits, the difference in seed-coat thickness and mass between the Great Basin and Rocky Mountains was predicted to result as a consequence of the reduction in seed defenses against *Tamiasciurus* (see the Introduction). As seed defenses against *Tamiasciurus* decline, the accessibility of seeds to nutcrackers should increase (traits that reduce access of seeds to *Tamiasciurus* tend to do the same to nutcrackers; Benkman et al. 1984) so that fewer seeds fall to the ground. For example, on the San Francisco Peaks in north-central Arizona (*Tamiasciurus* present; see fig. 1), nutcrackers, in local sites where *Tamiasciurus* were absent, harvested only about 10% of the cones before they opened, and many limber pine seeds fell to the ground unharvested by nutcrackers (Benkman et al. 1984; C. W. Benkman pers. obs.). In contrast, in the Raft River Mountains in northwestern Utah (Great Basin range where *Tamiasciurus* is absent; see fig. 1), nutcrackers harvested over 90% of the cones, and few limber pine seeds fell to the ground (Lanner and Vander Wall 1980; S. B. Vander Wall pers. comm. 1991).

With fewer seeds falling to the ground, predation by ground-foraging seed predators declines along with selection pressure for thick seed coats. Moreover, thinner seed coats would benefit trees if the trees could thus devote more energy to kernel, and if thinner seed coats increase the amount of energy (and seeds) that can be carried per caching trip (Benkman et al. 1984). Thinner seed coats may also reduce seed-handling times (Vander Wall and Balda 1977), which benefits both nutcrackers and trees because more time is available for caching seeds. Seed-handling time averages nearly one-half for nutcrackers on limber pine seeds in the Raft River Mountains ( $9.7 \pm 4.6$  s (mean  $\pm$  SD); Vander Wall 1988) as on the San Francisco Peaks ( $17.4 \pm 5.5$  s; mean seed-coat thickness = 0.47 mm; Benkman et al. 1984).

The presence or absence of *Tamiasciurus* does not account for all the variation in the traits predicted to differ. In particular, resin on the cone surface was predicted to decline in the absence of squirrels (see Benkman et al. 1984), yet no difference was found between the Great Basin and the Rocky Mountains. Although cones from two of the Great Basin sites (Schell Creek Range and White Mountains) had little resin on their cone surfaces (table 1), these low values may have occurred because cones from these two sites were gathered before their seed kernels had fully matured (see Methods); pitch seems to increase on the cone surface during kernel maturation (C. W. Benkman pers. obs.). Thus, the variation in resin mass among sites may be even less than that suggested from data in table 1. This argues further that the presence or absence of *Tamiasciurus* alone has not had an impact on resin production. Resin may be a general defense against vertebrate and invertebrate seed predators or may be unrelated to them (see Langenheim 1990). Although I did not sample systematically for insect damage, the two sites (Schell

Creek Range and White Mountains) that had smaller cone samples because of insect damage were also the sites with the least amount of resin. This is consistent with the hypothesis that resin acts to reduce seed predation by invertebrates.

Kernel mass was the one trait predicted to be unaffected by *Tamiasciurus*, and it did not differ between the two regions (table 1). This supports Smith's (1970) hypothesis that seed (kernel) mass, especially of large-seeded species, should be little affected by selection from *Tamiasciurus*. Moreover, this shows that the different cone and seed traits can vary independently of each other (see table 1).

The physical conditions during germination have an important selective influence on seed-kernel mass (Westoby et al. 1992), and variation in these conditions may be related to kernel-mass variation among sites. However, the lack of a consistent difference in kernel mass between the Great Basin and the Rocky Mountains suggests that the abiotic factors that affect kernel mass do not differ consistently between the areas sampled in these two regions. This is further supported by data on mean annual precipitation near the different study sites. At the Great Basin sites, mean annual precipitation ranges from less than 36 cm at the White Mountains to 80 cm near timberline in the Schell Creek Range, and 100 cm in the East Humboldt Mountains (Arno and Hammerly 1984). A similar, but narrower range of annual precipitation has been recorded near the Rocky Mountain sites. Annual precipitation averages only about 54 cm near the Pikes Peak site and 58 cm near the Nederland site (Bates 1924; Barry 1973), but on the southern end of the Wasatch Plateau, it may reach 100 cm (Arno and Hammerly 1984).

Weather conditions could have affected pollination and the number of seeds per cone. Although variation in pollination was in all likelihood responsible for some variation in the number of seeds per cone, this is an inadequate explanation for the large difference between the two regions. Seeds were not just fewer per cone in the Rocky Mountains than in the Great Basin, but they also differed in their distribution within the cone. Seeds were consistently absent from the basal scales in the Rocky Mountains, but present near the base in the Great Basin.

It is harder to envision how variation in limber pine cone structure might be related to abiotic factors (see Smith 1970). One possibility is that thicker cone scales protect seeds from heat damage during fires (Smith 1970; Linhart 1978). This alternative, although not mutually exclusive with the predation hypothesis, can be eliminated for limber pine: its cones are not serotinous, and limber pine experiences fire only infrequently (see McCune 1988). Furthermore, except for fire-adapted conifers, I know of no example in which variation in conifer cone structure is related to abiotic factors.

#### CONCLUSION

Because selection pressures on plants from seed predators and dispersers often conflict (e.g., Jordano 1987; but see Whelan et al. 1991), adaptations for seed dispersal are often compromised by counter-selection from seed predators. The convergence in energy allocation of limber pine cones in the Great Basin to that of other more exemplary bird-dispersed

pinus demonstrates that both squirrels and nutcrackers have important and conflicting selective impacts on conifer cone and seed structure. Moreover, this convergence may have occurred in the last 12,000 yr or so since the extinction of *Tamiasciurus* in the Great Basin (see Heaton 1990). Because all of the recognized adaptations of pines for seed dispersal by birds can be thought of as increasing seed availability to birds (e.g., Vander Wall and Balda 1977), *Tamiasciurus* has, in effect, acted to constrain the evolution of some cone traits that aid seed dispersal by birds. For some pines, *Tamiasciurus* may have even precluded the evolution of seed dispersal by birds (Benkman et al. 1984).

## ACKNOWLEDGMENTS

B. Blohm showed me how to remove and measure resin, and he also graciously provided materials, equipment and space for me to measure resin. A. Holbert at Cabrillo College kindly provided access to computers and printers. C. Whelan, S. B. Vander Wall, G. J. Vermeij, D. F. Tomback, C. C. Smith, M. Price, R. Lanner, and two anonymous reviewers provided helpful comments on the manuscript. I am most grateful to D. Schluter who encouraged this research while I was supported by a National Science and Engineering Research Council of Canada International Fellowship.

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