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THE ADAPTIVE SIGNIFICANCE OF SPINES ON PINE CONES

Kimberly Coffey, Craig W. Benkman,[1] and Brook G. Milligan

Department of Biology, New Mexico State University, Las Cruces, New Mexico 88003 USA

Abstract. Besides woody cone scales, certain species of wind-dispersed pines (*Pinus*) have spines on their scales as a putative form of defense against seed predators. We tested whether spines differentially deterred seed predators foraging on closed and open pine cones. Red Crossbills (*Loxia curvirostra*) were selected as the seed predator because they commonly forage on these cones. We timed crossbills foraging on closed and open pine cones with and without spines. Crossbills did not require more time to remove seeds from closed ponderosa pine (*P. ponderosa*) cones with spines. However, crossbills required significantly more time (18–34%) to remove seeds from open ponderosa pine and Table Mountain pine (*P. pungens*) cones with spines than from cones whose spines had been removed. Moreover, experiments designed to isolate the effect of spines on the perching and probing behavior of crossbills revealed that spines hindered both activities additively. These experimental results were consistent with our phylogenetic analyses of 21 species of hard pines (subgenus *Pinus*). Whereas the evolution of changes in the length of time seeds are retained in closed cones and that of changes in the presence of spines appear independent, changes in the length of time seeds are retained in open cones were associated with changes in the presence or development of spines. Therefore, pines that retain seeds in open but not closed cones for extended periods tend to have well-developed spines. This illustrates the complementarity of experimental approaches and explicit phylogenetic models in elucidating ecological processes.

Key words: adaptation; evolutionary models; foraging behavior; hard pines; Loxia curvirostra; *phylogenetic analysis; pine cone spines;* Pinus; *predation; seed defenses; seed retention.*

INTRODUCTION

Plants have adaptations to defend themselves and their seeds against enemies (Cavers 1983). Pines (*Pinus*), for example, have cones with woody scales that help protect their seeds from seed predators such as birds, squirrels, and other rodents (Smith 1970, Elliott 1974, Linhart 1978, Benkman 1987*b*). Besides cone scales, most hard pines (subgenus *Pinus*) have spines located on the abaxial or exposed surface of each cone scale (McCune 1988). These spines are believed to act as an impediment to seed predators by making it more difficult to reach seeds inside the cone. However, no researchers have tested whether spines hinder seed predators. Moreover, not all cones have well-developed spines, and some species lack spines (McCune 1988) even in the presence of known seed predators. Finally, there is little discernible pattern among the species of wind-dispersed pines regarding the presence or absence of spines on the scales. This has led McCune (1988) to suggest that spines might be an ineffective defense against predation.

Many mammals and birds eat pine seeds (Smith and Balda 1979). Tree squirrels (*Sciurus* and *Tamiasciurus*) feed mostly on seeds in closed cones (Smith and Balda 1979), whereas some birds forage for seeds in both closed and open cones (Benkman et al. 1984, Benkman 1987*a*, *b*). Important defenses against red squirrels (*Tamiasciurus hudsonicus*) include thicker cone scales and a reduction in the number of seeds per cone (Smith 1970). Spines, however, are unlikely to have a substantial impact on squirrel foraging efficiency because squirrels bite off scales at their base, away from the spine, even on cones that lack spines (Benkman 1995). Birds and some less specialized mammals (e.g., chipmunks *Tamias* spp.), on the other hand, often reach between the scales of open pine cones to obtain the seeds at the bases of the scales (Stallcup 1968, Smith and Balda 1979, Benkman 1993). Thus, birds are the most likely seed predators to be inhibited by the presence of spines on the scales.

We used a boreal finch, the Red Crossbill (*Loxia curvirostra*), in experiments to test the effect of spines on foraging rates, because crossbills forage on seeds in both closed and open cones (Benkman 1987*a*, *b*, Benkman and Lindholm 1991). Crossbills have bills specialized for separating conifer scales to reach the seeds within closed and open cones (Benkman and Lindholm 1991). We used ponderosa pine (*P. ponderosa* var. *scopularum*) cones in the experiments because these cones have well-developed spines (McCune 1988), and crossbills forage on both closed and open ponderosa pine cones (Benkman 1993). Table Mountain pine (*P. pungens*) was used in experiments as a representative of a species of pine exhibiting extremely

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[1] Corresponding author; E-mail: cbenkman@nmsu.edu

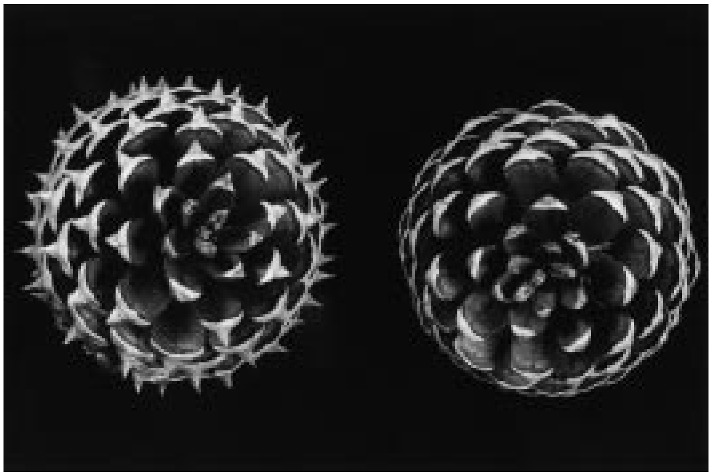

PLATE 1. Photograph of two open Table Mountain pine cones viewed from their distal ends. The cone on the right has its spines removed.

well-developed spines (McCune 1988). Only open Table Mountain pine cones were used as experimental cones because crossbills could not pry open the scales of the closed cones. Crossbills forage on both pine species in the wild (Benkman 1993, Groth 1993).

We tested two hypotheses regarding the effects of spines of pine cone scales on foraging behavior by Red Crossbills. The first hypothesis was that the presence of spines would decrease the foraging rate of seed predators that forage on closed (green) cones. A prediction of this hypothesis was that crossbills foraging for seeds in closed cones should have required more time to obtain seeds from pine cones with spines than from cones without spines. A related hypothesis was that well-developed spines should be present on cones of pine species that retain seeds in closed cones for extended periods (e.g., serotinous-coned species).

The second hypothesis was that the presence of spines would decrease the foraging rate of seed predators that forage on seeds held in open cones. If this was true, crossbills should have required more time to obtain seeds from open pine cones with spines than from cones without spines. A related hypothesis was that more developed spines should be present on pine species that retain seeds for extended periods in open cones compared to those that release their seeds soon after opening.

METHODS

Experiments

We conducted experiments in a 1.6 × 2.7 × 2.2 m aviary in the New Mexico State University Animal Care Facility. We maintained the seven Red Crossbills (type 2 of Groth [1993]) used in the experiments at a low mass several days before and during the experiments by monitoring their diet of seeds of closed pine (*P. eldarica*) cones and Mazuri Chow (PMI Seeds Incorporated, St. Louis, Missouri, USA). To ensure consistent and high motivation for foraging on the experimental cones, we removed all food from the aviary 14 h before the experiments. On the mornings of the experiments all seven crossbills were caught, placed in a cloth bag and weighed to the nearest 0.1 g on a portable electronic balance. We released all crossbills except the experimental bird into the adjacent aviary separated from the experimental side by 1.3-cm mesh screen. The presence of the other crossbills eliminated variation that might arise from time spent scanning for predators (Benkman 1997).

We collected ponderosa pine (*Pinus ponderosa* var. *scopularum*) cones in Colorado and Table Mountain pine (*P. pungens*) cones in North Carolina to use in the experiments. We measured the length of the spines on both closed and open cones to the nearest 0.01 mm with digital calipers to detect whether variation in spine length had an impact on foraging performance and to ensure that any differences observed were due to treatments rather than natural difference in spine length. In addition, we measured the lengths of scales and gaps between overlapping scales in open cones to ensure consistency among cones. Experimental cones were attached to a screw at the end of a wooden dowel. This dowel was then placed at the front of the aviary ~1 m from the viewing window. The experimental crossbill was released into the aviary once the cone had been secured. The crossbill then flew to the cone and started foraging, while one of us (K. Coffey) observed through a glass window.

Closed cone experiments.—We used green ponderosa pine cones, gathered in late July 1996, in experiments to test the effect of spines on closed cones. These cones were stored for up to 7 mo in a freezer (−3°C) until the afternoon before the experiments, when they were placed in a refrigerator (4°C) to thaw. We gave each crossbill a pair of similar-sized cones from each of nine trees. Only one cone was given to a bird at a time, and spines were removed from one of each pair of cones with clippers (Plate 1). Each crossbill foraged on no more than three pairs of cones (a total of 66 seeds) on any single day, to prevent satiation during the experiments; crossbills require >100 seeds per day. The order in which cones in a pair (spines present and spines removed) were presented to each crossbill was alternated between pairs to eliminate any order effects.

We timed foraging crossbills to the nearest 0.1 s with a stopwatch from when they finished eating the first seed from a cone until they had eaten the 11th seed (i.e., time to extract and eat 10 seeds). Any time not spent actively foraging was not included in the analyses; crossbills usually foraged continuously until we terminated the trial.

Open cone experiments.—All seven crossbills were given 10 pairs of open ponderosa pine cones and 10 pairs of open Table Mountain pine cones (Plate 1). Experiments were conducted in essentially the same fashion as for closed cones, alternating cones with and without spines. Open cones of both species were emptied of all seeds and stocked in specific scales with 10 Douglas-fir (*Pseudotsuga menziesii*) seeds (one seed per scale). We used Douglas-fir seeds because most of the Table Mountain seeds in the cones were empty, Douglas-fir seeds are of similar size, and we had access to large numbers of full Douglas-fir seeds. The gaps between the stocked scales ranged from 0.4 to 1.0 cm, and the depth of these scales ranged from 1.8 to 2.5 cm. We used these dimensions because the crossbills could reach the seeds only with some difficulty but without damaging the cones. We timed crossbills foraging from when they finished eating the first seed until they had eaten the sixth seed.

Crossbills are large enough that, when perching on a cone, they are foraging on an area of the cone away from their feet. Consequently, we conducted two additional experiments on open cones to determine whether spines reduced foraging rates because it was difficult for the crossbills to perch or because it was difficult to reach between the cone scales. In each of these experiments we used five pairs of open ponderosa pine cones, with all of the spines removed from one cone in each pair (we used the same cones as those used in the first experiments on open cones). To test whether the presence of spines on the cone made it difficult for the birds to perch, we removed only the spines immediately above and below the scales where the seeds were placed from one cone. To test whether spines interfered with the birds reaching for seeds between the scales, we removed all the spines but those immediately above and below the scales where the seeds were placed.

We used one-tailed paired t tests to analyze the data, because we predicted that cones with spines would decrease crossbill foraging rates.

Phylogenetic analyses

Experimental tests of the response of birds to cone spines can reveal whether or not spines currently function as a deterrent to potential seed predators. By themselves, however, they cannot reveal whether the evolutionary origin of spines was in response to predation pressure. To quantify the evolutionary change we performed a phylogenetic analysis of spines and potential predation pressure. Opportunity for predation of pine seeds is directly related to the length of time seeds are retained in cones prior to dispersal. As a result, if spines have evolved as a protective mechanism, their elaboration should be phylogenetically associated with high predation risk or long periods of retention in cones.

We restricted these analyses to 21 species of North American hard pines (subgenus *Pinus*; Fig. 1) for which we could obtain data on both cone structure and seed retention time from the literature. When possible, we used the most widespread subspecies when more than one subspecies occurred. These pines have winged seeds that are presumably dispersed at least initially by wind (Tomback and Linhart 1990).

McCune (1988) ranked spine development on a scale from 0 (no spines) to 1.5 (extremely well-developed spines). We considered species with spine scores ≥1.0 to have well-developed spines, and species with scores <1.0 to lack well-developed spines. The species we used in the foraging experiments, ponderosa and Table Mountain pines, have spine scores of 1.0 and 1.5, respectively (McCune 1988), which represent the extremes of what we considered were cones with well-developed spines.

The phenology of cone maturation and seed dispersal in most North American pines consists of several clearly identifiable phases of differing length among species. Cones generally mature their seeds in autumn (Krugman and Jenkinson 1974). Once seeds are mature, they are retained within closed cones for a period of time. Subsequently, the cone scales open and seeds are retained for a period of time prior to dispersal. Thus, species of pines can be characterized by the length of time cones remain closed once seeds mature, and by the length of time seeds remain within the cone once the cones open.

Most species of North American pines open their cones shortly after seed maturation (Krugman and Jenkinson 1974), whereas some species, especially serotinous ones, have cones that remain closed for longer periods. Pines that open their cones within 2 mo of seed maturation were considered to have a closed-cone phase of short duration, while those that take longer than 2 mo to open their cones were considered to have a closed-cone phase of long duration.

Once the cones open, variation in the time seeds are retained is less discrete; however, two categories of seed retention time can be recognized. Based on seed dispersal times in Krugman and Jenkinson (1974) and Fowells (1965), we used 2 mo as the dividing time between species that retain their seeds for short and long periods once cones open. In case of conflicting times in these two sources, we relied on additional

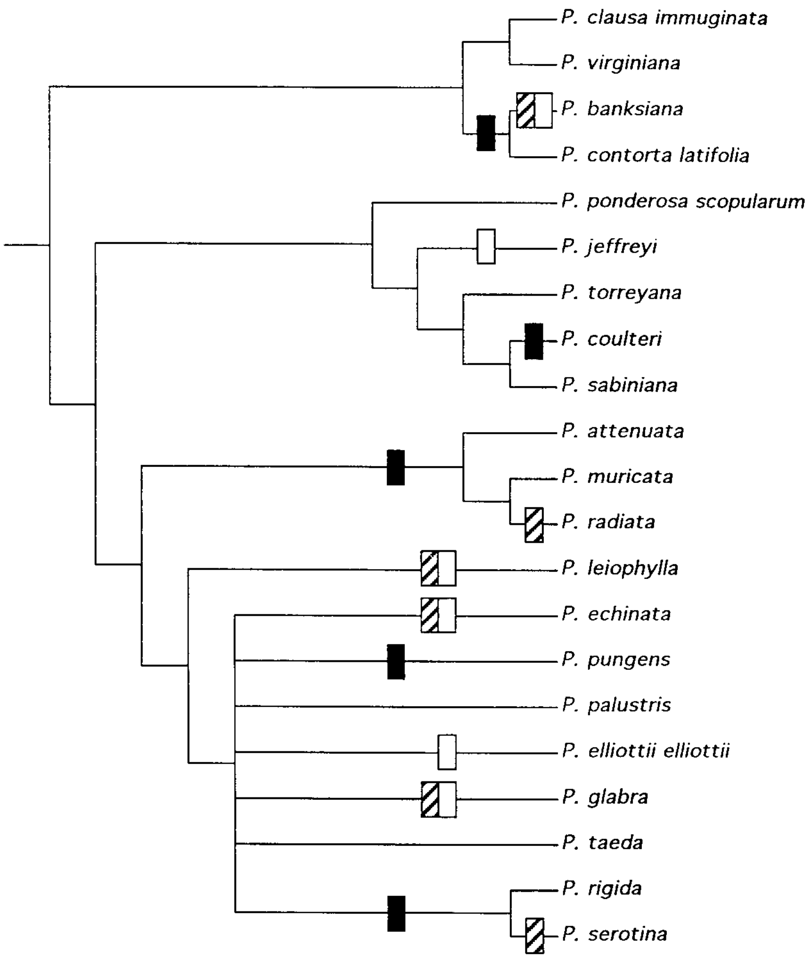

FIG. 1. Cladogram showing the traits and relationships used to estimate rates of morphological evolution among 21 species of hard pines (subgenus *Pinus*). We assumed equal branch lengths for all species. The reconstructed ancestral condition was cones with well-developed spines with short and long periods in closed and open cone phases, respectively. The loss of well-developed spines is indicated by a hatched bar. Transitions of the duration of the closed cone phase from short to long are indicated by solid bars. Transitions of the duration of the open cone phase from long to short are indicated by open bars (see *Phylogenetic analyses*).

sources (Crossley 1955, Givnish 1981, McMaster and Zedler 1981, Critchfield 1985) to determine seed dispersal times.

The pine phylogeny (Fig. 1) used in the analyses was based on phylogenies and data in Hong et al. (1993) and Price et al. (1998). We assumed equal branch lengths for all species. Two phylogenetic analyses were performed to determine whether an evolutionary relationship exists between spine development and seed retention time (a surrogate for predation risk). First, the ancestral states for each character were reconstructed using MACCLADE version 3.03 (Maddison and Maddison 1992). The locations of ancestral-state transitions were examined for concordance between changes in duration of phases of closed cones with mature seeds and open cones before seed dispersal and changes in spine elaboration.

To assess quantitatively whether or not the dynamics of evolutionary change in these traits involve a dependence of spine loss on predation risk, we used the approach described by Milligan (1994) and independently developed by Pagel (1994) to contrast several alternative models of cone evolution. In all cases, we modelled the transitions between the four joint combinations (Fig. 2) of cone-phase duration (short and long) and spine elaboration (short and long); the same analyses were performed for both the closed and open phases of cone development. Our adaptive model was based on the twin assumptions that predation risk (hence the benefit of spines) increases with the duration of seed retention, and that there exists an energetic cost to elaborating spines. We further assumed that the benefit of spines exceeds the cost of producing spines when seeds are retained for long periods, whereas the reverse is true when seeds are retained for short periods.

These assumptions lead to the transition diagram pre-

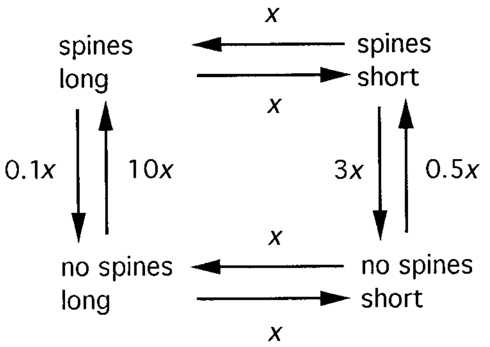

FIG. 2. A model of morphological evolution assuming that the benefits of spines increase with length of time seeds are retained in cones. The relative rates of the transitions are next to the transition arrows. ''Long'' and ''short'' refer to the periods seeds are retained in cones.

sented in Fig. 2, which describes the evolutionary dynamics of our adaptive model. There is a baseline rate of transition (*x*) between long and short duration phases, irrespective of whether cones exhibit well-developed spines (pairs of horizontal transitions). However, when cones retain seeds for only a short period of time, there is an increased rate of spine loss (3*x*) compared with spine gain (0.5*x*) because of the relatively high cost of spines compared to the low benefit (righthand vertical transitions). Finally, when cones retain seeds for long periods of time, there is a large increase in the rate of spine gain (10*x*) compared with spine loss (0.1*x*) because of the relatively high benefit due to protection from predation (lefthand vertical transitions). The ratio of transitions in the latter case (100:1) is greater than in the former (6:1). These transition values were chosen a priori because we assumed that the loss in fitness from having no spines when seeds are held in cones for long periods is much greater than the loss in fitness from producing spines when seeds are held for only short periods of time. Overall, this model describes the evolutionary dynamics of cone morphology and phenology in terms of a single rate parameter, *x*, with adjustments to each transition made to reflect the relative benefits and costs of each trait combination.

Given the evolutionary model depicted in Fig. 2 and the phylogeny depicted in Fig. 1, the probability of observing the morphological and phenological data summarized in Fig. 1 can be obtained as a function of the rate parameter *x* (Milligan 1994). This probability is proportional to the likelihood of the evolutionary model (Edwards 1992). The maximum likelihood estimate of the transition rate *x* (and the associated likelihood of that model) may be obtained using software developed by Milligan (1994).

To determine whether or not this adaptive model is supported by the data, we contrast it with a model in which the two characters evolve independently of each other, each with its own basal rate of transition between the two states. The likelihood of the adaptive model compared with the likelihood of the independent model is an indication of the degree of support given by the data to the former (Edwards 1992). This contrast between models was performed for both the closed and open cone phases of the phenology.

RESULTS

Closed cone experiments

Only five of the seven crossbills would forage on closed ponderosa pine cones. Two of the crossbills took longer on average to remove and eat 10 seeds from closed cones with spines, while the other three crossbills took longer on average on cones without spines (Fig. 3A). Overall, the foraging times (time per 10 seeds) were not significantly greater on cones with spines than on cones without spines ($t = 1.14$, df = 4, $P = 0.32$).

Open cone experiments

Ponderosa pine.—All seven crossbills took longer on average to remove and eat five seeds from open ponderosa pine cones with spines than from cones without spines (Fig. 3B). In contrast to the closed cone experiments, the mean foraging times of the seven crossbills on open cones were significantly greater on cones with spines than on cones from which spines had been removed ($t = 7.28$, df = 6, $P = 0.0003$). The overall mean time per seed increased 18.2%, from 5.0 s on cones with spines removed to 5.9 s on cones with spines. The difference between the results of the experiments on open and closed cones was not due to differences in spine lengths. Spines did not differ significantly in length ($t = 1.30$, df = 18, $P = 0.21$) between closed ponderosa pine cones (mean ± 1 SE = 4.2 ± 0.1 mm, $n = 9$ trees) and open ponderosa pine cones (3.8 ± 0.2 mm, $n = 10$ trees).

Spines hindered crossbills' perching on the cone and reaching for seeds between the scales. First, crossbills required significantly more time to obtain seeds when spines were only where birds perched than when spines were absent entirely ($t = 2.81$, df = 6, $P = 0.03$). The overall mean time per seed increased 10.6%, from 3.9 s on cones with no spines to 4.3 s on cones with spines only where crossbills perched. Second, spines affected the ability of crossbills to reach seeds when probing between scales. Crossbills took significantly longer to obtain seeds in cones with spines remaining only on the scales surrounding where the seeds were placed than in cones without spines ($t = 3.46$, df = 6, $P = 0.01$). The overall mean time per seed increased 6.9%, from 4.5 s on cones without spines to 4.8 s on cones with spines remaining only where crossbills probed between scales to reach the seeds.

Table Mountain pine.—Experiments using Table Mountain pine yielded results similar to those of the experiments with open ponderosa pine cones (Fig. 3C).

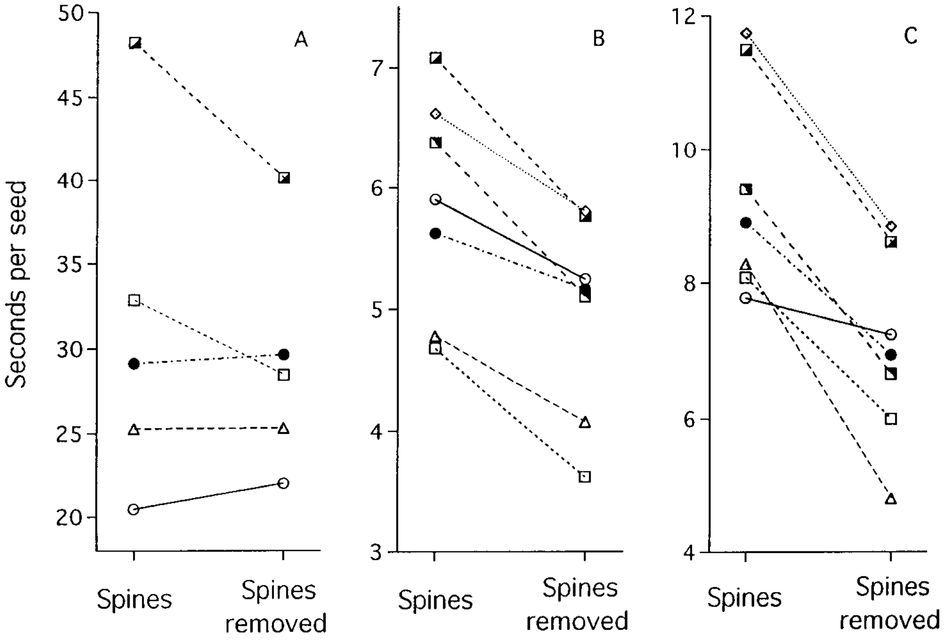

FIG. 3. The mean number of seconds per seed for individual crossbills foraging on (A) closed ponderosa pine cones, (B) open ponderosa pine cones, and (C) open Table Mountain pine cones with and without spines. Each symbol represents a different crossbill.

Again, all seven crossbills took longer on average to obtain seeds from cones with spines than from cones without spines. Overall, foraging times on cones with spines were significantly greater than those on cones without spines (t = 6.55, df = 6, P = 0.0006). The overall mean time per seed increased 33.8%, from 7.0 s on cones with spines removed to 9.4 s on cones with spines.

The larger percentage increase in time per seed for crossbills foraging on open Table Mountain pine cones compared to those foraging on open ponderosa pine cones may have been related to the significantly longer spines on Table Mountain pine cones (4.6 ± 0.2 mm, n = 10 trees; t = −2.88, df = 19, P = 0.01). However, spine length was not correlated with variation in the time spent foraging on cones with spines within a given species (ponderosa pine: r = 0.2, df = 69, P = 0.09; Table Mountain pine: r = 0.2, df = 69, P = 0.10).

Phylogenetic analyses

For the joint evolution of seed retention time in closed cones and the elaboration of cone spines, the likelihood of the model of independent change was 4850 times greater than the likelihood for the model of adaptive evolution depicted in Fig. 2. Thus, there was no evidence supporting the adaptive model relating spine development to duration of seed retention in closed cones. In distinct contrast, however, the likelihood of the adaptive model relating spine development to the duration of seed retention in the open cone phase was 6.9 times greater than that of the independent model. An association between reductions in spine development and reductions in the length of time seeds are retained in open (but not closed) cones was also evident from visual inspection of Fig. 1. This indicates that pines that retain seeds for extended periods in open cones tend to have spines (13 of 15 species), whereas those species that retain seeds for brief periods in open cones tend to lose spines (4 of 6 species).

DISCUSSION

Spines have the potential to act as an important defense against seed predators foraging on seeds in open cones. This is supported by the consistent and substantial percentage increase in time (18–34%) required by crossbills to reach seeds in open ponderosa and Table Mountain pine cones compared to cones with their spines removed (Fig. 3). Such increases in time to remove seeds from cones are likely to serve as a deterrent to seed predators because, for example, crossbills select and use conifer cones so that feeding rates are maximized (Benkman 1987*a*, 1989). As a result, crossbills would likely either leave cones earlier, before seeds are depleted, delay the use of cones, or completely avoid trees with cones with more developed spines. In all of these cases, an increase in spine development presumably increases the probability of seeds dispersing from cones by wind. This will provide a selective advantage to trees having cones with more developed spines.

The location on the cone where spines are most developed is also consistent with spines functioning primarily to deter animals reaching between open scales. Spines tend to be most developed in the area of the cone where seeds are concentrated and where animals like crossbills reach between the scales for seeds. The basal scales of many pines lack seeds (e.g., Smith 1970) and these scales often lack spines, or, if present, the spines are of reduced size (e.g., lodgepole pine *P. contorta* var. *latifolia*). Instead of having spines, the basal scales of lodgepole pine, for example, are enlarged. Enlarged knobby scales may act more effectively as a deterrent to animals foraging on closed cones. The thick and knobby basal scales of lodgepole pine are effective deterrents to red squirrels, which have to bite through these scales to reach the seed-bearing distal scales (Smith 1970, Elliott 1974).

Spines make it difficult to perch on the cone and also hinder animals reaching for seeds between cone scales. Moreover, at least for crossbills foraging on ponderosa pine cones, spines act to hinder perching and probing additively. That is, the combined percentage increase in foraging time (17.5%) from the two experiments testing whether spines interfere with perching or probing is similar to the percentage increase when spines could interfere with both perching and probing (18.2%). Variation between pines in spine orientation may also influence the relative impact of spines on perching and probing. Spines curve down and out from the ends of the scales on ponderosa, Table Mountain (Plate 1), and many other pine species. This likely hinders both perching and probing. On the other hand, spines on Jeffrey pine (*P. jeffreyi*), for example, curve down on open cones (Munz 1959) and likely inhibit probing behavior most.

Although spines had no significant impact on foraging time on closed cones, crossbills did devote time to removing spines with their bills from the closed ponderosa pine cones. Because time was spent removing spines, perhaps the reason there was no significant effect from the spines is that the spines on ponderosa pine are small compared to some species of pines. For example, if we could have used the large-spined Table Mountain pine cones in the closed cone experiments, there might have been a significant effect of the presence of spines. Another possible reason that we did not detect a significant effect of spines on closed cones could be variation in other traits among cones within a tree (e.g., variable number of seeds per cone). This would confound our ability to detect an effect of spines. Such variation was reduced in the open cone experiments by placing the same number of seeds in each cone, and locating them between scales with similar characteristics. Finally, the difference between the results on closed and open cones could have arisen from recording the foraging times to remove different numbers of seeds (10 seeds from closed cones and 5 seeds from open cones). However, based on extensive observations of foraging crossbills (e.g., Benkman 1987*a*, *b*, 1993) it is difficult for us to provide a plausible explanation that would support this alternative. In sum, although spines are likely to hinder at least some seed predators on closed cones, spines are likely to be much more effective at deterring seed predators foraging on open cones.

The phylogenetic analyses are consistent with the experimental results. Namely, the degree of spine development appears to have evolved in concert with the length of time seeds are retained in open, but not closed, cones. A result is that the degree of spine development is related to the length of time seeds are retained in open cones, so that pines that retain seeds in open cones for extended periods tend to have the most developed spines. In contrast, the degree of spine development is unrelated to the length of time seeds are retained in closed cones. This is consistent, first, with the hypothesis that the benefit of spines increases with the duration of time seeds are retained in open cones. Second, the cost of spines to the plant can outweigh the benefits when seeds are retained in open cones for only a brief period. Additionally, by deterring seed predators, longer spines may increase the time seeds remain in open cones before dispersing. This likely contributes to the observed patterns, but is insufficient alone, because then all pines with well-developed spines should hold seeds in open cones for extended periods. This was not the case (Fig. 1: *P. jeffreyi* and *P. elliottii elliottii*). Moreover, if the duration of time seeds are retained in open cones is simply the result of the timing of seed removal by predators, then selection should strongly favor rapid release of seeds, and all open cones should hold seeds for a short period of time. We suggest that the most plausible hypothesis is that variation in seed retention is likely an important life history trait, and when long seed retention times in open cones are favored, large spines that deter seed predators are also favored.

Finally, we also believe that the various adaptations of crossbills likely reduce the impact of cone spines on their foraging performance. These adaptations include strong legs for perching on or near the cones at various angles and their ability to spread open scales farther apart with the tips of their mandibles and probe between scales with long protrusible tongues to remove seeds (Newton 1972, Benkman 1987*b*, Benkman and Lindholm 1991). Consequently, many of the more generalized conifer-seed eaters, including chickadees (*Parus* spp.), nuthatches (*Sitta*), cardueline finches other than crossbills (e.g., *Carpodacus* spp.), and chipmunks, which lack specializations for probing between open scales, are likely to be more adversely affected than crossbills by cone spines. Thus, cone spines are likely an important general defense against the large assemblage of seed predators that forage on seeds in open cones.

In conclusion, this study illustrates the power of combining experimental and phylogenetic approaches to answering ecological and evolutionary questions.

Further, it illustrates the importance of explicitly contrasting alternative evolutionary models in order to clarify the dynamics of evolutionary change. Experiments can reveal the current function(s) of ecological traits (Sinervo and Basolo 1996); for example, ours revealed that cone spines can function as a deterrent to seed predators. However, experiments alone cannot reveal information about the evolutionary origin of those same traits (Harvey and Pagel 1991). In contrast, a phylogenetic analysis can provide insight into the pattern of origin of ecological traits, but cannot identify the processes involved unless the processes are explicitly included in the analysis (Larson and Losos 1996).

The phylogenetic analysis used here directly investigates alternative evolutionary processes leading to the ecological traits currently observed. It does so by comparing a specific adaptive with a specific nonadaptive process of evolution and determining which is better supported by the data (Edwards 1992). Contrasts such as this are an important use of explicit models (Wimsat 1987), and are what ultimately link our experimental and phylogenetic analyses. The experimental results suggest an adaptive evolutionary process that can be directly compared with an alternative nonadaptive one to determine whether the current function identified by the experiments was responsible for the evolutionary origin of the traits. We hope that future studies will adopt the complementary and powerful ecological and evolutionary approaches exemplified here.

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