

Evolutionary interactions between tree squirrels and trees: A review and synthesis

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Tree squirrels, by virtue of their arboreal niches, granivorous (or herbivorous) feeding habits, and long, relatively unchanged history have shared a close evolutionary relationship with many of the woody plants on which they feed. As such, many tree and flying squirrels may be keystone consumers that serve as indicators of the stability of forested ecosystems. Herein, I review the evidence for evolutionary interactions between squirrels and seed trees, and provide a brief overview of the general ways in which the two influence each other's evolutionary history. I review three systems in which detailed studies have demonstrated strong evolutionary interactions between squirrels and trees: one in which squirrels act primarily as seed predators, another as herbivores, and a third in which squirrels act as both seed predators and dispersal agents. I show the detailed methodology required to uncover such interactions and the potential implications of these studies.

Keywords: Coevolution, herbivory, sciuridae, seed dispersal, seed predation.

Introduction

TREE squirrels, especially those residing in temperate regions, are important granivores that have been long known to exert a significant impact on the seeds and seed trees on which they feed¹. Likewise, the evolution of tree squirrels has been shaped by plant resources on which squirrels depend for food, nests and escape from predators. The family Sciuridae (tree, flying and ground squirrels) first appeared in the fossil record in the late Eocene, and the tree squirrels (*Sciurus* and *Tamiasciurus*), present by the early Miocene, have remained virtually unchanged to the present². During that time, most tree squirrels shared a close association with nut-producing trees, providing ample time for both plants and squirrels to impact each other's evolutionary history³.

Evolutionary impact of squirrels on trees

The evolutionary influences of tree squirrels on woody plants (primarily nut-bearing trees but also numerous

tropical species, including lianas) result primarily from their activity as either herbivores or granivores. Herbivory usually takes the form of twig clipping, bark stripping, a combination of the two^{4,5}, or consumption of leaves, flowers and floral nectar (R. M. Borges, pers. commun.). As granivores, tree squirrels impact seed, fruit and nut crops either as seed predators or in their dual role as both seed predators and dispersal agents^{5,6}.

Evidence that tree squirrels are important selective agents in the origin of specific tree characteristics (adaptations) falls into three major groups: physical, chemical and life history traits (Table 1)⁵. Physical (or morphological) adaptations of plants that likely evolved in response to squirrels include the woody protection of many nuts and seeds (e.g. hickories⁷, walnuts^{8,9}, Table 1). Evidence of chemical adaptations may include the lipids and tannins of oaks^{10,11}, and most certainly the xylem and phloem properties of ponderosa pine that have evolved in direct response to the specialized feeding habits of Abert's squirrel (*Sciurus aberti*)¹²⁻¹⁵. Life-history responses refer to behaviour of masting in trees, or the episodic and synchronized production of seeds followed by years of mast failure^{16,17}. Common in many nut-bearing species, masting increases the probability of seed dispersal and establishment by squirrels during high mast years, and reduces squirrel populations during mast failures⁶.

Evolutionary impacts of trees on tree squirrels

Table 2 summarizes adaptations of tree squirrels posited to result from selective pressures exerted by trees. Not shown are general morphological and behavioural adaptations that are widely interpreted as general adaptations for exploiting an arboreal niche. Well-documented adaptations of the squirrels are limited to only a few behavioural and morphological traits (Table 2), although many more (e.g. physiological traits) are likely to be discovered in the future.

In his detailed studies of interactions between *Tamiasciurus* and conifers, Smith advanced a strong argument for the evolution of larder-hoarding behaviour in which squirrels store large quantities of cones in a central midden that is vigorously defended via territorial behaviour¹⁸⁻²⁰. Later, Smith advanced an equally convincing argument that nuts of many deciduous trees, which are not well stored in a larder, gave rise to the scatter-hoarding behaviour of many species of *Sciurus* and, in turn, their overlapping

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Table 1. Putative evolutionary effects of tree squirrels on seed trees for which there exists strong circumstantial evidence or direct empirical support

Squirrel (genus or species) and common name	Tree (genus or species) and common name	Selective pressure ^a	Tree trait	Reference
<i>Tamiasciurus</i> spp. (red and Douglas' squirrel)	<i>Pinus contorta</i> Lodgepole pine	P	More woody protection per cone Fewer seeds per cone Cones asymmetrical at base Stronger point of attachment of cone to branch Cone shape (i.e. wider at the base)	18–20, 27, 28, 30–32, 46
<i>Tamiasciurus</i> spp.	<i>P. flexilis</i> Limber pine	P	More woody protection per seed	47, 48
<i>T. hudsonicus</i>	<i>P. contorta</i>	P	Reduced serotiny	29
<i>Sciurus vulgaris</i> European red squirrel	<i>P. halepensis</i> Aleppo pine	P	Larger cones Disproportionately larger scales	34
<i>S. aberti</i> Abert's squirrel	<i>P. ponderosa</i> Ponderosa pine	H	Xylem composition Xylem flow rate Phloem nutrient composition	12–15
<i>S. niger niger</i> Southeastern fox squirrel	<i>P. palustris</i> Long-leaf pine	P	Cone size	21
<i>S. carolinensis</i> / <i>S. aureogaster</i> Easter gray squirrel/ Mexican gray squirrel	<i>Quercus</i> (section <i>Quercus</i>) Oaks (white oak group)	P/D	Non-dormancy, early germination Multiple-seeded acorns	23–25, 38, 39
<i>S. carolinensis</i>	<i>Quercus</i> spp.	P/D	Chemical gradients of acorns	10, 11, 41
<i>S. niger</i> Fox squirrel	<i>Juglans niger</i>	P/D	Thick husk of nut High energy content per nut	8

^aP, Seed predation; H, Herbivory; D, Seed dispersal.

Table 2. Putative evolutionary effects of woody plants (primarily seed trees) on tree squirrels for which there exists strong intuitive or empirical support

Tree type or species and common name	Squirrel (genus or species) and common name	Selective pressure ^a	Squirrel trait	Reference
Conifers	<i>Tamiasciurus</i>	CMS	Larder-hoarding behaviour Territorial behaviour	18–20, 27
Deciduous trees	<i>Sciurus</i>	NMS	Scatter-hoarding behaviour Overlapping home ranges Dominance hierarchy	20, 27
<i>Pinus contorta</i> Lodgepole pine	<i>Tamiasciurus</i> spp. Red and Douglas' squirrel	CM	Stronger jaw musculature Stronger lower jaw Larger body size	19, 20
<i>P. palustris</i> Long-leaf pine	<i>S. niger</i> Fox squirrel	CM HT	Body size Pelage colour	21 17, 22
<i>Quercus</i> Both red and white oak species	<i>Sciurus</i>	NG	Selective consumption of white oaks Selective dispersal/hoarding of red oaks	23–25
<i>Quercus</i> (section <i>Quercus</i>) White oak species	<i>S. carolinensis</i> Eastern gray squirrel <i>S. aureogaster</i> Mexican gray squirrel Possibly <i>S. niger</i>	NG	Embryo excision	26
<i>Quercus</i> (section Lobato) Primarily red oak species	<i>S. carolinensis</i>	NC	Partial consumption/dispersal of acorns	10, 11
<i>P. ponderosa</i> Ponderosa pine	<i>S. aberti</i>	XPC	Selective herbivory	12–15
<i>Juglans niger</i> Black walnut	<i>S. niger</i>	NMS	Scatter-hoarding Selective consumption	8

^aCMS, Cone morphology and storability; NMS, Nut morphology and storability; CM, Cone morphology; HT, Habitat type; NG, Nut germination; NC, Nut chemistry and XPC, Xylem and phloem chemistry.

home ranges and non-territorial social structure²⁰. Other examples of adaptations of tree squirrels that likely evolved in direct response to nut-bearing trees include primarily morphological (i.e. increased body size, jaw musculature^{19–21} and pelage colouration²²) or behavioural adaptations (e.g. selective herbivory^{12–15}, granivory^{10,11,23–25} and embryo excision of oaks²⁶).

Interactions between *Tamiasciurus* and conifers

One of the most thoroughly documented examples of selection between a tree squirrel and its seed tree is that of *Tamiasciurus* and lodgepole pine (*Pinus contorta*). Smith^{19,27} showed that squirrels on either side of the Cascade Mountain Range in southwestern British Columbia, Canada, exhibit characteristics that match closely with contrasting characteristics of lodgepole pine, especially in the frequency of serotiny (i.e. cones that open only after intense fires). West of the range, a wet, maritime climate limits forest fires, and thus provides ideal conditions for a race of non-serotinous lodgepole pines that produce cones with a soft surface, weak point of attachment, and many more seeds per cone. In contrast, to the east, the rain shadow results in frequent lightning strikes, regular forest fires and serotinous cones. The squirrels on either side of the Cascades show strikingly different traits, presumably in response to these cone characteristics. West of the range, *Tamiasciurus douglasii* is smaller in size and has a smaller jaw with weaker jaw muscles; to the east, the closely related *T. hudsonicus* is larger in size and has stronger jaw muscles with a particularly strong lower jaw^{19,27}. Morphology of squirrels in these two locations allows them to better exploit their cone resources, especially on the eastern slopes. Furthermore, these adaptations of the squirrels appear to have further influenced cone morphology^{19,20,27}. The serotinous cones in the east exhibit a hard surface, a stronger point of attachment on the branch, an asymmetrical shape (especially pronounced at the point of attachment) and many fewer seeds per cone²⁷, all characteristics shown elsewhere to evolve in response to the highly selective feeding behaviour of *Tamiasciurus*²⁸.

Although Smith¹⁹ first interpreted the larger jaw musculature of *T. hudsonicus* as the cause of the harder cones of the lodgepole pine, he later concluded that it was the physical environment acting as the independent variable driving cone characteristics that subsequently spurred many of the squirrel characteristics²⁰. He noted, however, that this evolutionary trajectory did not preclude the possibility of feedback between species and that in the *Tamiasciurus*–lodgepole pine system, the physical environment only determined the level at which coevolutionary interactions between squirrels and cones may equilibrate²⁰.

However, the interaction between squirrel and pines may be far more complicated. A recent study in the southern

Rocky Mountains²⁹, for example, suggests that the seed predation by *T. hudsonicus* may actually select against serotiny. A comparison of five locations where *T. hudsonicus* is absent with 344 where it occurs, revealed that the frequency of serotiny was nearly 100% at all sites where the squirrels were not found. At the other 344 sites, serotiny rarely reached these high frequencies and averaged only 50% across all sites. It should be noted, however, that frequency of fire, a key selective pressure for serotiny, was not considered in this analysis. Although Smith argued that frequency of fire and serotiny will enhance the level to which this coevolutionary interaction will escalate, Benkman and Siepielski²⁹ suggest that selection against serotiny by tree squirrels will serve as a stabilizing force in the escalation of this arms race.

The evolutionary impact of *T. hudsonicus* on lodgepole pine is further complicated by the geographic mosaic of selection created by the distribution of the squirrel, coupled with its interaction with the common crossbill (*Loxia curvirostra*)^{30–32}, which is typically left to forage on cones rejected by the squirrels. Such geographic mosaics of coevolution may be the rule rather the exception³³. On the Iberian peninsula, for example, where the Eurasian red squirrel, *Sciurus vulgaris* is common, the efficient exploitation of Aleppo pine (*Pinus halepensis*) by *S. vulgaris* results in strong selection for larger cones with more pronounced scales³⁴. In contrast, on islands in the Mediterranean where *S. vulgaris* is absent, cone size is reduced. Accordingly, cone use by crossbills is uncommon on the peninsula, but not on these islands. Moreover, on the islands where crossbills are found, cones are smaller and exhibit thicker scales, a likely adaptation to deter crossbills³⁴. On one island, however, where both crossbills and squirrels are absent, cones are smaller and possess smaller scales³⁴.

Interactions between *Sciurus* and *Quercus*

The close interactions between *Sciurus* and the oaks (genus *Quercus*) is another system where several studies suggest strong evidence of a squirrel–plant mutualism. Although many of the evolutionary interactions between oaks and their seed consumers (mammals and corvid birds) represent diffuse interactions by an entire guild of granivores, some involving the tree squirrels may be more direct.

Oaks (*Quercus*) are dominant in many temperate and subtropical forests; and, wherever oaks are found, generally so too are tree squirrels. Oaks produce acorns that appear adapted for both preventing pre-dispersal predation (with primarily chemical defences, i.e. tannins) and for encouraging dispersal by seed-consuming mammals and birds^{9,23–25,35}.

In the Central Hardwoods region of North America, the basis of these interactions follows from the physical and chemical composition, germination schedules and pack-

aging of acorns and from the feeding and caching responses of tree squirrels. Here, and throughout many other regions, oaks comprise two major groups (sections): the white oaks (WO, section *Quercus*) and the red oaks (RO, section *Lobatae*³⁶). Acorns of WO generally exhibit lower levels of lipid (ca. 10% by dry mass) and tannin (<2%) and consistently exhibit precocious germination²⁵. The ROs produce acorns that are higher in both lipid (ca. 20%) and tannin (5–15%), and remain dormant through a portion of the winter²³.

Several species of *Sciurus* and other rodents show considerable sensitivity to these traits and selectively cache RO acorns over those of WO^{24,25} during autumn seed-fall. Behavioural studies with free-ranging *S. carolinensis* further show that the preference to cache RO acorns is due to their lower perishability, a consequence of delayed germination³⁷.

Additional experiments, in which the internal composition of the acorn cotyledon was experimentally modified, showed that squirrels consistently cache RO acorns that are constructed of RO shells regardless of their internal composition (e.g. white oak cotyledon, unpublished). It thus appears that squirrels rely on a chemical cue in the shell to determine which acorns are suitable for hoarding (i.e. dormant acorns). Recent experiments further show that naïve squirrels raised in captivity with no previous experience with acorns still show a strong tendency to cache RO (*Q. rubra*) acorns over those of WO (*Q. alba*²⁶).

Moreover, the potential reciprocal impact of these decisions on the dispersal and establishment of ROs and WOs suggests strong selection by tree squirrels on the oaks. Such interactions, however, are likely more accurately characterized as a response to diffuse selective pressures from an entire assemblage of granivorous mammals. The interaction between squirrels and acorns, however, appears more akin to coevolution when one considers two additional aspects of oak–squirrel interactions. One of these involves the precocious germination of WO acorns, characterized by rapid conversion of the cotyledon into a fleshy taproot (mostly cellulose). It is widely interpreted as an adaptation of the WOs to escape seed predation by small granivorous mammals (mice, *Peromyscus*; chipmunks, *Tamias*; and tree squirrels^{38–40}). The trait renders WO acorns a highly perishable food source, inappropriate for long-term storage. And, indeed, the selective caching of RO acorns by at least five or more species of small mammals indicates a high level of sensitivity to this trait.

Early germination of WO acorns appears to have selected for a specific behavioural strategy that allows tree squirrels to circumvent this problem. Gray squirrels and at least one additional member of the genus *Sciurus* will frequently cache WO acorns, but only after they have excised the embryo, killing the seed^{23,24,39}. With a few scrapes of the incisors, squirrels are able to permanently arrest germination and produce an acorn that stores well up to six months or more²⁴. Moreover, squirrels possess

an innate ability to perform embryo excision without previous experience with acorns, suggesting a behavioural adaptation, unique to the genus *Sciurus* that evolved in direct response to precocious germination²⁶.

Embryo excision by *Sciurus* spp. places strong selection on the WOs and may have influenced a counter adaptation in the oaks to prevent embryo excision. Many oak species produce multi-seeded acorns that produce two or more radicles, only one of which emerges from the apical end of the acorn, the way a single-seeded acorn would normally germinate⁴¹. Acorns of *Quercus* produce six ovules, five of which typically abort. However, in at least 14 species of oaks (both RO and WO species) in North and central America, such abortion is not complete and can result in multiple seeds and radicles⁴¹. And, indeed, for acorns in which squirrels attempt embryo excision, multi-seeded acorns often successfully germinate and develop into healthy seedlings⁴¹. Although it would seem that these traits satisfy the conditions of a coevolutionary arms race⁴², such a contention is less convincing when one considers other predator species (e.g. *Curculio*) that may have influenced this trait.

Evolutionary interactions between squirrels and oaks also appear to involve the chemical composition of acorns. Although many aspects of acorn chemistry do not influence the decision to cache RO acorns over those of WO, the chemical composition of the cotyledon may influence squirrel behaviour and subsequent dispersal of oaks in subtle but equally important ways. When acorns are abundant, grey squirrels consume only 10–60% of the acorn cotyledon from the basal (proximal) end of the fruit, frequently caching the remaining acorn fragment¹¹. Both field (unpublished) and greenhouse experiments indicate that partially eaten seeds can germinate, and in some situations do so at rates comparable to that of whole acorns¹⁰. Chemical analyses of several species of acorns indicate that within the cotyledon there are chemical gradients that may promote this behaviour. Specifically, tannins are significantly lower in the basal end of the acorn than in the distal end surrounding the seed. However, in contrast, results of recent unpublished studies (pers. obs.) indicate that lipids and some key nutrients (e.g. sodium) show an opposite gradient with higher levels in the basal portion eaten by the animals. The result is a suite of chemical gradients that may divert feeding activity by squirrels (and other seed predators) away from the distal end where the food source is comprised of key nutrients, higher energy and more palatable and/or digestible tissue.

Abert's squirrel (*Sciurus aberti*) and ponderosa pine (*Pinus ponderosa*)

The Abert's squirrel from the southwestern US and northern Mexico, is an example of an extreme habitat specialist that exerts strong directional selection on a single tree

species, the ponderosa pine^{12,13,15,43}. Across its natural range the species is entirely dependent on this pine. Active the year round, Abert's squirrels are highly selective with respect to both the individual trees and the site and position within trees where they construct leaf nests^{15,44}. The chemical composition of the phloem of nest trees also influences nest site selection, with nest trees having higher levels of sodium and non-structural carbohydrates and lower levels of copper, iron and silica than trees not selected for nesting⁴⁴. Abert's squirrel also feeds heavily on the seeds of the cones of ponderosa pine just prior to their maturation, an energy-rich but seasonally available food. Once cones open and seeds are dispersed, squirrels switch to feeding on nutrient-poor inner bark (phloem and cambium) of the terminal twigs of the tree¹⁵.

Abert's squirrels are highly selective in their use of inner bark, returning each year to feed on the same tree^{12,43}. Other trees are consistently avoided; and the distinction between preferred and avoided trees is based on differences in the xylem and phloem characteristics. The xylem oleoresin of preferred trees has significantly lower levels of β -pinene and β -phellandrene as well as significantly slower flow rates. Phloem of preferred trees has significantly higher levels of sodium and non-structural carbohydrates, and significantly lower levels of iron^{12,15}. These phloem and xylem characteristics within individual trees appear to be under strong genetic control and show little variation in response to long-term herbivory by the squirrels^{12,15}. Moreover, repeated defoliation of ponderosa pine trees clearly reduces the fitness of preferred trees by causing reduced growth, lower production of both male and female cones, and reduced seed quality^{13,15}. The result is a strong directional selection by this specialized mammalian herbivore on its host plant. Further biogeographic comparisons suggest a strong coincidence of genetically distinguishable subspecies of *S. aberti* and biochemical characteristics of ponderosa pine⁴³, although more research is needed on this subject.

Despite the apparent simplicity of this system, and such clear evidence for directional selection by Abert's squirrel, the evolutionary story is far more complex when community-level interactions with ponderosa pine are considered. In the southern Rocky Mountains, two other herbivores, the mountain pine bark beetle (*Dendroctonus ponderosae*) and the North American porcupine (*Erethizon dorsatum*), and one plant, the parasitic dwarf-mistletoe (*Arceuthobium vaginatum*), all feed on the phloem of ponderosa pine¹⁵. Each, however, selects trees based on different, genetically-based biochemical properties. The result is multi-directional (diversifying) selection by this community of consumers that likely serves to increase, rather than decrease, genetic diversity in ponderosa pine¹⁵.

Finally, the importance of hypogeous fungi in the diet of Abert's squirrels, a critical food resource that often appears to satisfy nutrient deficits during food shortages

deserves mention^{5,43}. Squirrels consume the sporocarps, defecate their spores, and thereby disperse the fungi that form an obligate mutualism with the roots of ponderosa pine^{5,43}.

Conclusions

To date, approaches proven most effective in testing evolutionary interactions between trees squirrels and trees include (1) detailed behavioural experiments^{24,26,35}, (2) well-controlled field manipulations (e.g. those that simulate seed damage)^{13,37}, (3) landscape comparisons that focus on the biogeographic 'matrices' of evolutionary (or coevolutionary) hot and cold spots^{31,32}, (4) multifaceted studies that consider the diffuse effects of all members of an ecological guild¹⁵, and (5) a consideration for the history of the system^{19,29,30}. Tree squirrels and their seed trees impact each other's evolutionary history in profound ways; and some of these interactions have clearly escalated to coevolutionary arms races. With the exception of studies on herbivory by Abert's squirrels, however, little is known about the impact of squirrels on the fitness of individual trees. This is one area where future research is needed. Finally, the studies discussed here are almost entirely from the Holarctic region. More studies are needed from the tropics, especially southeast Asia⁴⁵ where the diversity of tree and flying squirrels is the highest in the world.

1. Thoreau, H. D., *Faith in a Seed*, Island Press, California, 1993.
2. Emry, R. J. and Thorington, R. W., The tree squirrel *Sciurus* (Sciuridae, Rodentia) as a living fossil. In *Living Fossils* (eds Eldridge, N. and Stanley, S. M.), Springer-Verlag, New York, 1984, pp. 22–31.
3. Vander Wall, S. B., The evolutionary ecology of nut dispersal. *Bot. Rev.*, 2001, **67**, 74–117.
4. Gurnell, J., *The Natural History of Squirrels*, Facts on File Publications, New York, 1987.
5. Steele, M. A. and Koprowski, J. L., *North American Tree Squirrels*, Smithsonian Institution Press, Washington DC, 2001.
6. Steele, M. A., Wauters, L. A. and Larsen, K. W., Selection, predation and dispersal of seeds by tree squirrels in temperate and boreal forests: Are tree squirrels keystone granivores? In *Seed Fate: Predation, Dispersal and Seedling Establishment* (eds Forget, P.-M. et al.), CAB International, Wallingford, 2005, pp. 205–221.
7. Tamura, N., Katsuki, T. and Hayashi, F., Walnut seed dispersal: Mixed effects of tree squirrels and field mice with different hoarding abilities. In *Seed Fate: Predation, Dispersal and Seedling Establishment* (eds Forget, P.-M. et al.), CAB International, Wallingford, 2005, pp. 241–251.
8. Stapanian, M. A. and Smith, C. C., A model for scatterhoarding: Coevolution of fox squirrels and black walnuts. *Ecology*, 1978, **59**, 884–896.
9. Smith, C. C. and Follmer, D., Food preferences of squirrels. *Ecology*, 1972, **53**, 82–91.
10. Steele, M. A., Knowles, T., Bridle, K. and Simms, E. L., Tannins and partial consumption of acorns: Implications for dispersal of oaks by seed predators. *Am. Midl. Nat.*, 1993, **130**, 229–238.
11. Steele, M. A., Gavel, K. and Bachman, W., Dispersal of half-eaten acorns by gray squirrels: Effects of physical and chemical seed

- characteristics. In *Ecology and Evolutionary Biology of Tree Squirrels* (eds Steele, M. A., Merritt, J. F. and Zegers, D. A.), Spec. Publ., Virginia Museum of Natural History, Martinsville, 1998, pp. 223–232.
12. Snyder, M. A., Selective herbivory by Abert's squirrel mediated by chemical variability in ponderosa pine. *Ecology*, 1992, **73**, 1730–1741.
 13. Snyder, M. A., Interactions between Abert's squirrel and ponderosa pine: The relationship between selective herbivory and host plant fitness. *Am. Nat.*, 1993, **141**, 866–879.
 14. Snyder, M. A. and Linhart, Y. B., Barking up the right tree. *Nat. Hist.*, 1993, **102**, 44–49.
 15. Snyder, M. A., Abert's squirrel (*Sciurus aberti*) in ponderosa pine (*Pinus ponderosa*) forests: Directional selection, diversifying selection. In *Ecology and Evolutionary Biology of Tree Squirrels* (eds Steele, M. A., Merritt, J. F. and Zegers, D. A.), Spec. Publ., Virginia Museum of Natural History, Martinsville, 1998, pp. 195–202.
 16. Koenig, W. B. and Knops, J. M. H., The behavioral ecology of mast seeding in oaks. In *Oak Forest Ecosystems: Ecology and Management for Wildlife* (eds McShea, W. J. and Healy, W. M.), Johns Hopkins University Press, Baltimore, USA, 2002, pp. 129–148.
 17. Kiltie, R. A. and Edwards, R., Interspecific correlates of squirrel coat patterns: Ecology, taxonomy, and body size. In *Ecology and Evolutionary Biology of Tree Squirrels* (eds Steele, M. A., Merritt, J. F. and Zegers, D. A.), Spec. Publ., Virginia Museum of Natural History, Martinsville, 1998, pp. 161–170.
 18. Smith, C. C., The adaptive nature of social organization in the genus of tree squirrels *Tamiasciurus*. *Ecol. Monogr.*, 1968, **38**, 31–63.
 19. Smith, C. C., The coevolution of pine squirrels (*Tamiasciurus*) and conifers. *Ecol. Monogr.*, 1970, **40**, 349–371.
 20. Smith, C. C., The evolution of reproduction in trees: Its effect on squirrel ecology and behaviour. In *Ecology and Evolutionary Biology of Tree Squirrels* (eds Steele, M. A., Merritt, J. F. and Zegers, D. A.), Spec. Publ., Virginia Museum of Natural History, Martinsville, 1998, pp. 203–210.
 21. Weigl, P. D., Sherman, L. J., Williams, A. I., Steele, M. A. and Weaver, D. S., Geographic variation in the fox squirrel (*Sciurus niger*): A consideration of size clines, habitat vegetation, food habits, and historical biogeography. In *Ecology and Evolutionary Biology of Tree Squirrels* (eds Steele, M. A., Merritt, J. F. and Zegers, D. A.), Spec. Publ., Virginia Museum of Natural History, Martinsville, 1998, pp. 171–184.
 22. Kiltie, R. A., Test of hypotheses on predation as a factor maintaining polymorphic melanism in coastal-plain fox squirrels (*Sciurus niger* L.). *Biol. J. Linn. Soc.*, 1992, **45**, 17–37.
 23. Smallwood, P. D. and Peters, W. D., Grey squirrel food preferences: The effects of tannin and fat concentration. *Ecology*, 1986, **67**, 168–174.
 24. Steele, M. A., Turner, G., Smallwood, P. D., Wolff, J. O. and Radillo, J., Cache management by small mammals: Experimental evidence for the significance of acorn embryo excision. *J. Mammal.*, 2001, **82**, 35–42.
 25. Steele, M. A. and Smallwood, P. D., Acorn dispersal by birds and mammals. In *Oak Forest Ecosystems: Ecology and Management for Wildlife* (eds McShea, W. J. and Healy, W. M.), Johns Hopkins University Press, Baltimore, 2002, pp. 182–195.
 26. Steele, M. A., Manierre, S., Genna, T., Contreras, T., Smallwood, P. D. and Pereira, M., The innate basis of food-hoarding decisions in grey squirrels: Evidence for behavioural adaptations to the oaks. *Anim. Behav.*, 2006, **71**, 155–160.
 27. Smith, C. C., The coevolution of seeds and seed predators. In *Coevolution of Animals and Plants* (eds Gilbert, L. E. and Raven, P. H.), University of Texas Press, Austin, 1975, pp. 53–77.
 28. Elliot, P. F., Evolutionary responses of plants to seed-eaters: Pine squirrel predation on lodgepole pine. *Evolution*, 1974, **28**, 221–231.
 29. Benkman, C. W. and Siepielski, A. M., A keystone selective agent? Pine squirrels and the frequency of serotiny in lodgepole pine. *Ecology*, 2004, **85**, 2082–2087.
 30. Benkman, C. W., The selection mosaic and diversifying coevolution between crossbills and lodgepole pine. *Am. Nat.*, 1999, **153**, S75–S91.
 31. Benkman, C. W., Holiman, W. C. and Smith, J. W., The influence of competitors on the geographic mosaic of coevolution between crossbills and lodgepole pine. *Evolution*, 2001, **55**, 282–294.
 32. Benkman, C. W., Parchman T. L., Favis, A. and Siepielski, A. M., Reciprocal selection causes a coevolutionary arms race between crossbills and lodgepole pine. *Am. Nat.*, 2003, **162**, 182–194.
 33. Thompson, J. N., *The Coevolutionary Process*, University of Chicago Press, Chicago, Illinois, 1999.
 34. Mezquida, E. T. and Benkman, C. W., The geographic selection mosaic for squirrels, crossbills and Aleppo pine. *J. Evol. Biol.*, 2005, **18**, 348–357.
 35. Smallwood, P. D., Steele, M. A. and Faeth, S. H., The ultimate basis of caching preferences of rodents and the oak-dispersal syndrome: Tannins, insects, and seed germination. *Am. Zool.*, 2001, **41**, 840–851.
 36. Nixon, K. C., Infrageneric classification of *Quercus* (Fagaceae) and typification of sectional names. *Ann. Sci. For.*, 1993, **50**, 258–348.
 37. Hadj-Chikh, L. Z., Steele, M. A. and Smallwood, P. D., Caching decisions by grey squirrels: A test of the handling-time and perishability hypotheses. *Anim. Behav.*, 1996, **52**, 941–948.
 38. Barnett, R. J., The effect of burial by squirrels on germination and survival of oak and hickory nuts. *Am. Midl. Nat.*, 1977, **98**, 19–30.
 39. Fox, J. F., Adaptation of gray squirrel behavior to autumn germination by white oak acorns. *Evolution*, 1982, **36**, 800–809.
 40. Vander Wall, S. B., *Food Hoarding in Animals*, University of Chicago Press, Chicago, 1990.
 41. McEuen, A. B. and Steele, M. A., Atypical acorns appear to allow seed escape after apical notching by squirrels. *Am. Midl. Nat.*, 2005, **154**, 450–458.
 42. Janzen, D. H., When is it coevolution? *Evolution*, 1980, **34**, 611–612.
 43. States, J. S. and Wettstein, P. J., Food habits and evolutionary relationships of tassel-eared squirrels (*Sciurus aberti*). In *Ecology and Evolutionary Biology of Tree Squirrels* (eds Steele, M. A., Merritt, J. F. and Zegers, D. A.), Spec. Publ., Virginia Museum of Natural History, Martinsville, 1998, pp. 172–185.
 44. Snyder, M. A. and Linhart, Y. B., Nest-site selection by Abert's squirrel: Chemical characteristics of nest trees. *J. Mammal.*, 1994, **75**, 136–141.
 45. Borges, R. M., Figs, Malabar Giant squirrels, and fruit shortages within two tropical Indian forests. *Biotropica*, 1993, **25**, 183–190.
 46. Elliot, P. F., Foraging behavior of a central-place forager: Field tests of theoretical predictions. *Am. Nat.*, 1988, **131**, 159–174.
 47. Benkman, C. W., Balda, R. P. and Smith, C. C., Adaptations for seed dispersal and compromises due to seed predation in limber pine. *Ecology*, 1984, **65**, 632–642.
 48. Benkman, C. W., The impact of tree squirrels (*Tamiasciurus*) on limber pine dispersal adaptations. *Evolution*, 1995, **49**, 585–592.

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