

Frequency-dependent selection by tree squirrels: adaptive escape of nondormant white oaks

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Frequency-dependent selection is theoretically predicted to have an important impact on predator–prey dynamics, but little is understood about this process in nature. We investigated oak–squirrel interactions to test the hypothesis that tree squirrels predate/disperse white oak acorns based on the frequency of their germination phenotypes (dormancy, i.e., delayed germination vs. nondormancy, i.e., immediately germinating), which in turn influences dispersal and establishment of these oaks. In Central China, we manipulated the relative frequency of dormant and nondormant acorns available to Père David's Rock squirrel (*Sciurotamias davidianus*) with 2 white oaks (QAA, *Quercus aliena* var. *acutesevata* and QSB, *Quercus serrata* var. *breviptiolata*) that exhibit considerable variation in acorn germination between and within oak species throughout the fruiting season. We predicted that dispersal success (i.e., the probability of a viable acorn being hoarded) of each germination phenotype would vary with the phenotype frequency and hence show either positive or negative frequency-dependent selection. We found that acorn-embryo removal by squirrels may select for the dormant phenotype but is more likely to occur for early germinating acorns. We also found that both absolute and relative dispersal success of each germination phenotype increased with their frequency in the 2 white oaks, thus demonstrating positive frequency-dependent selection. Our results reveal that the frequency of germination phenotypes can account for as much as 40.5% and 21.4% of the observed dispersal success in QAA and QSB, respectively. We show that behavioral preferences of scatter-hoarding animals could result in frequency-dependent selection in nature, and such selection may help maintain variation in germination phenotypes in prey species. **Key words:** behavioral preference, dispersal success, frequency-dependent selection, oak–squirrel system, predator–prey dynamics, seed germination/dormancy. [*Behav Ecol* 21:169–175 (2010)]

Frequency-dependent selection is predicted in principal to have an important impact on predator–prey dynamics: selection can be either negative, leading to a rare-morph advantage or positive if common morphs are favored (Ayala and Campbell 1974; Allen 1988; Sinervo and Calsbeek 2006). Positive frequency-dependent selection and common-morph advantage, for example, is predicted to lead to monomorphism (Thompson 1984) or convergent evolution among prey species (Greenwood 1985), whereas negative frequency-dependent selection and rare-morph advantage is often proposed to maintain phenotypic diversity in prey populations (Clarke 1962; Allen 1988; Olendorf et al. 2006). However, there are few studies that demonstrate how such frequency-dependent selection influences predator–prey dynamics in nature.

Similar to the interactions between predator and prey, those between seed plants and animals (i.e., seed predation and/or animal-mediated dispersal) provide a model system for testing frequency-dependent selection on specific seed phenotypes, their fitness consequences, and their effects on population/community dynamics (Greenwood 1985). For plant seeds, seed size, seed chemistry, and patterns of dormancy (germination behavior) are all common phenotypic traits that can influence

behavioral preferences of seed predators and dispersers, which in turn can directly influence plant demography and distribution (Crawley 1992; Hulme 1998). Many studies have considered how seed predators or dispersers select fruits or seeds based on specific fruit/seed traits, but few studies have tested the effects of the relative frequency of specific seed traits (e.g., seed size or germination phenotype) on seed selection by animals and how such behavioral choices in turn influence plant reproductive success (Greenwood 1985; but see Hulme and Hunt 1999; Celis-Diez et al. 2004; Celis-Diez and Bustamante 2005). Aside from a phenotypic trait, the germination schedule of seeds is also one critical factor influencing seed fate (Harper 1977). In this study, we used oak–squirrel interactions as a model system to investigate how variation in seed germination schedules influences population dynamics in nondormant white oaks during selection by tree squirrels acting as both seed predators and seed dispersers.

Although there are many germination phenotypes among different plant species, oak species (*Quercus* sensu, Fagaceae family) typically exhibit 2 relatively distinct germination phenotypes: they can either germinate immediately or shortly after maturity or undergo a period of dormancy (without visible sign) and germinate weeks, several months, or even longer after maturity. Germination phenotypes are quite distinct among the 3 extant oak groups. Acorns from most white oaks (subgenus *Quercus*, WO), distributed across the Northern Hemisphere, often germinate soon after maturity prior to dispersal by animals and sometimes even while still attached to

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the tree. However, some WO species and individual trees also appear to exhibit a polymorphism in germination phenotypes in which some of their acorns germinate immediately but others exhibit a short but variable period of dormancy. Acorns from the other 2 oak groups, that is, red oaks (subgenus *Erythrobalanus*, RO) in North America and ginkgang oaks (subgenus *Cyclobalanopsis*, QG) in South and Southeast Asia, show extended dormancy usually until the following spring (e.g., Fox 1982; Smallwood et al. 2001; Xiao Z, unpublished data).

The evolution of the nondormant phenotype in WO species is hypothesized to be a general adaptation for escape from both pre- and postdispersal rodent predation because rapid germination allows transfer of energy into an indigestible taproot before acorns are recovered (Barnett 1977; Fox 1982). However, at least one group of acorn predators/dispersers, tree squirrels (e.g., several *Sciurus* species in North America), exhibit what appears to be a counter adaptation to early germination in which they frequently remove acorn embryos prior to hoarding (Fox 1982; Steele, Turner, et al. 2001; Steele et al. 2006). In many WO species, however, the nondormant phenotype will not result in germination of all mature acorns at the same time, which may serve to counter this behavioral adaptation exhibited by tree squirrels. The fruiting season for mature acorns often lasts 1–3 months (Fox 1982). Thus, some acorns can remain dormant at variable frequencies relative to germinating acorns at least during the fruiting season. Maintenance of natural populations in WO species requires that at least part of acorn crops are dispersed (i.e., scatter-hoarded) with their embryos remaining intact before germination and that some of these hoarded acorns develop and survive as seedlings (Fox 1982). Therefore, the relative frequency of dormant and germinating phenotypes may be extremely important in determining whether some acorns could escape embryo removal by tree squirrels. However, no one to date has explored whether acorn selection by tree squirrels is dependent on the frequency of these germination phenotypes, and how such selection may influence population dynamics in oak species and as well as the evolution of acorn germination and dormancy.

For this study, we relied on the variation of germination frequency among different parent plants from 2 common white oaks (*Quercus aliena* var. *acutesevata*, hereafter QAA; *Quercus serrata* var. *breviptiolata*, hereafter QSB). We determined the extent to which the relative frequency of dormant and germinating acorns occurred during the fruiting season. After our new finding that Père David's Rock squirrel (*Sciurotamias davidianus*) frequently removes the embryos of WO acorns in a manner similar to tree squirrels from North America, we conducted field experiments in which we manipulated the relative frequency of dormant and germinating acorns from the 2 WO species in a deciduous broadleaf forest in Central China to determine dispersal success of WO species under these varying conditions. Our goal was to quantify dispersal success as a function of the frequency of each germination phenotype during dispersal and predation by free-ranging squirrels. Here, dispersal success is defined as the probability of hoarded acorns remaining viable after being dispersed and hoarded.

We hypothesized that the squirrels consume or hoard WO acorns based on the relative frequency of germination phenotypes thereby influencing variation in dispersal patterns of WO species. We further sought to determine whether 1) dispersal success of each germination phenotype would decrease with the phenotype frequency (negative frequency-dependent selection) or 2) dispersal/survival advantage would be favored for common germination phenotypes (positive frequency-dependent selection). In addition, we also predicted that dormant acorns should have a dispersal/survival advantage over germinating acorns because tree squirrels frequently remove

embryos of nondormant/germinating acorns compared with those remaining dormant (Fox 1982; Steele, Smallwood, et al. 2001; Xiao et al. 2009).

MATERIALS AND METHODS

We performed all field experiments during the autumn (September–November) of 2008 in the Foping National Nature Reserve (ca. 293 km²; 1100–1300 m; 35°0'N, 105°30'E) in Shaanxi Province, Central China, established in 1978 to conserve the endangered giant panda and its habitat. The total annual rainfall is about 920 mm with frequent rainfall from May to October. The average annual temperature is about 13 °C with lowest temperatures (–3 °C) in January and highest temperatures (28 °C) in July. The main natural vegetation types in the reserve include deciduous broadleaf forests (below 2000 m), birch forests (2000–2500 m), and conifer forests (above 2500 m) (Liu and Zhang 2003). In deciduous broadleaf forests, several oak species (e.g., WO species, QAA, QSB, *Quercus variabilis*, *Q. serrata*; and QG species, *Cyclobalanopsis* spp.) and other nut-bearing plants (e.g., *Castanea mollissima*, *Corylus* spp. and *Juglans* spp.) are most common (Liu and Zhang 2003). At the study site, several rodent species, including Père David's Rock squirrel (*S. davidianus*), Swinhoe's striped squirrel (*Tamias swinhoei*), white-bellied rats (*Niviventer confucianus*), South China field mouse (*Apodemus draco*), and greater long-tailed hamster (*Tscheskia triton*) (Liu and Zhang 2003; Xiao Z, unpublished data) rely on acorns and other nuts as an important food source. According to our survey in 2007 and 2008, Père David's Rock squirrels were found to not only scatter-hoard acorns and other nuts but also to frequently remove acorn embryos in several Fagaceae species (e.g., *Quercus* spp., *Cyclobalanopsis* spp., and *C. mollissima*) (Figure 1); other rodents did not selectively remove acorn embryos but instead acted primarily as seed predators by consuming the entire nut and scatter hoarding relatively few acorns.

Acorn germination

We investigated variation in acorn germination from different parent plants in 2 WO species (QAA, QSB). In our study site, QAA acorns are mature in late September, a little earlier than QSB acorns. Like most WO species, acorns from these 2 oak species often germinate soon after falling to the ground. After maturity, at least 200 acorns were collected on the tree from each of 5 fruiting plants of each oak species. One hundred sound acorns per plant were randomly selected and buried in wet sand as arrays in a separate chamber (diameter, 40 cm) at room temperature (ca. 10 °C). By simulating frequent rainfall during the fruiting season, adequate water was added everyday so that some water was visible at the bottom of each chamber box. We inspected each acorn for germination status once weekly (total = 5 weeks). Acorn germination was determined by whether the radicle was protruding from the pericarp. Because the germination frequencies were proportional data and because the data collection involved temporal pseudoreplication (repeated measures on the same arrays), we used a generalized linear mixed model with family as a binomial (using Package lme4 in R 2.8.0) to test for differences in acorn germination among different parent plants for each oak species and for differences between the 2 oak species.

Frequency-dependent selection by tree squirrels

From late September to mid-November in 2008, we conducted a series of field experiments with 5 frequency treatments for each oak species. We collected mature acorns

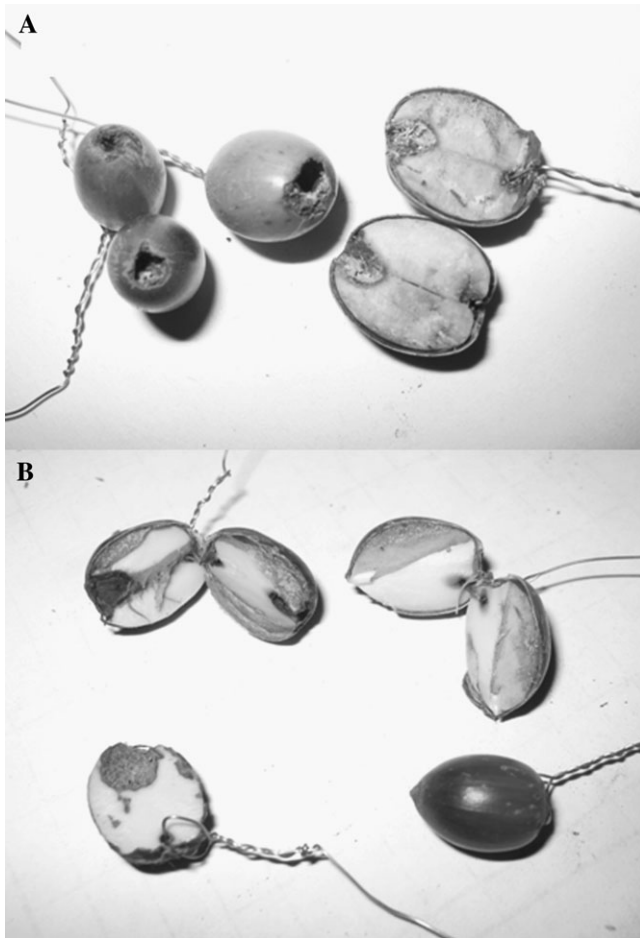


Figure 1
Acorn embryos removed by tree squirrels: (A) QAA and (B) QSB (both photographs were from the tagged acorns).

from 6 fruiting QAA plants and 5 QSB plants and stored these acorns in separate chambers with wet sand. Each frequency treatment represented a different ratio derived by varying proportions of a combined sample of 50 dormant (D) and germinating (G) sound acorns from the same plant. We used the following proportions (D:G) of nuts: 0.1 (5:45), 0.3 (15:35), 0.5 (25:25), 0.7 (35:15), and 0.9 (45:5). Here, germinating acorns had radicles protruding from the pericarp, whereas dormant acorns showed no visible signs of germination. For each frequency treatment, we conducted one bout for each plant from each oak species depending on the availability of the germinating acorns. The result was 1–5 replicates of each frequency treatment for each oak species (total: QAA, $n = 19$; QSB, $n = 24$). All feeding bouts were performed randomly in 6 different stands (separated by a minimum distance of 100 m); each feeding bout was conducted at a different location to avoid any biases that would result from the squirrels' experience.

Individual acorns were labeled with a numbered plastic tag attached by a thin stainless steel wire 10 cm long, similar to the procedures reported by Xiao et al. (2006). This seed-tagging method permitted us to follow the exact fate and spatial pattern of caches over time until the seeds germinated and emerged as seedlings (Xiao et al. 2004, 2006, 2008, 2009). Because squirrels are diurnal, we began at 8:30–9:30 AM and monitored nuts until 15:30 PM. For each bout, we placed the appropriate ratio of 50 D- and G-acorns randomly distrib-

uted in a circle (diameter, ca. 0.5 m) on the ground. At each feeding station, acorn fate was determined from the center of the station to a radius of approximately 30 m. Acorns at each station were categorized as 1) remaining or 2) not removed but eaten and those removed from the station were categorized as 3) hoarded, 4) eaten (tags and seed fragments found), or 5) missing (not retrieved). Hoarded acorns were also excavated to identify whether their embryos were removed by squirrels. Distances to the source were also measured for the hoarded and eaten acorns. To precisely identify which animals were most responsible for the hoarding and embryo removal of the tagged acorns, we used a digital video camera (Sony DCR-SR85E) for some bouts ($n = 5$ bouts, for 1–3 h depending on camera power and weather). According to video camera documentation and daily experiments, we found that Père David's Rock squirrel (1–3 individuals per station) was the only animal species to harvest nearly all the tagged acorns at the sites videotaped.

Data analysis

Acorns with embryos removed by squirrels have an extremely low probability of establishment (Fox 1982; Steele, Turner, et al. 2001; McEuen and Steele 2005; Xiao et al. 2009). Thus, successful seed dispersal of WO species is most dependent on whether a hoarded acorn remains viable, that is, with embryo intact. In this study, we examined 2 variables for each germination phenotype and each frequency treatment: 1) hoarding success (i.e., the probability of hoarding), calculated by dividing the total number of hoarded acorns by the total number of available acorns and 2) absolute dispersal success (i.e., the probability that a hoarded acorn remain viable in a given trial), calculated by dividing the total number of viable acorns that were hoarded (i.e., embryos not removed by tree squirrels) by the total number of acorns available. Both variables involved proportional data and thus were analyzed using generalized linear regression models (GLM) with a logit link function. Here, family = quasibinomial instead of a binomial because there was some overdispersion of the residual deviances (Crawley 2007). In the analysis, germination phenotype was treated as a categorical factor and phenotype frequency as a covariate.

We also estimated relative dispersal success for each germination phenotype (see Gigord et al. 2001). For each frequency treatment and each phenotype, the relative dispersal success was calculated by dividing the total number of viable acorns hoarded by the total number of those hoarded. The relative dispersal success of the dormant phenotype for each frequency treatment was calculated as $RRDS_d = 2 RDS_d / (RDS_d + RDS_g)$. $RRDS_d$ is the relative dispersal success of the dormant phenotype, whereas RDS_d and RDS_g are the relative dispersal success of D- and G-acorns, respectively. Linear regression and correlation were used to test the relationships between phenotype frequency (natural-log scale) and the relative dispersal success of the dormant/germinating phenotype.

In addition, we used linear mixed-effects model to test the differences of dispersal distance (log-transformed to meet assumptions of normality) with fate category and germination phenotype as fixed factors and bout as a random factor. Here, 3 fate categories were considered for analysis: 1) whole, hoarded acorns with embryos intact; 2) embryo removed, hoarded acorns with embryos removed; and 3) eaten acorns, with marks and acorn fragments found some distance from the source. The analysis of dispersal distance was performed only on trials involving equal proportions of G and D acorns (i.e., 25:25, the 0.5-ratios) because of the potential for different G:D ratios to bias by the squirrels' behavior.

RESULTS

The probability of acorn germination varied considerably among different parent plants for both QAA ($Z = -5.293$, $P < 0.001$) and QSB ($Z = -4.986$, $P < 0.001$). QSB acorns, however, germinated much earlier (mean \pm standard error [SE], $52.8 \pm 3.8\%$ after 5 weeks) than those of QAA ($39.4 \pm 2.8\%$ after 5 weeks) ($Z = 12.451$, $P < 0.001$) (Figure 2).

For all bouts, squirrels harvested nearly all the tagged acorns: very few (0–7) acorns remained at the stations after each trial but more G-acorns remained than D-acorns for pooled data (QAA: 29 [7.53%] vs. 14 [2.48%], respectively, $\chi^2 = 13.537$, degrees of freedom [df] = 1, $P < 0.001$; QSB: 10 [1.72%] vs. 2 [0.32%], respectively, $\chi^2 = 5.94$, df = 1, $P = 0.015$; Pearson Chi-square tests).

For both WO species, the proportion of acorns hoarded was not affected by either germination phenotype (QAA: $t = 0.515$, $P = 0.610$; QSB: $t = 0.246$, $P = 0.807$; GLM with family = quasibinomial) or phenotype frequency (QAA: $t = 0.041$, $P = 0.967$; QSB: $t = 1.002$, $P = 0.321$; GLM with family = quasibinomial) (Figure 3). In QAA, absolute dispersal success increased as each germination phenotype became more common (Figure 3A,3C). This was also the case for the germinating phenotype in QSB (Figure 3D). Phenotype frequency had a significant effect on dispersal success for either QAA ($t = 2.267$, $P = 0.0299$) or QSB ($t = 1.989$, $P = 0.0528$; GLM with family = quasibinomial) but germination phenotype did not (QAA: $t = 1.031$, $P = 0.3100$; QSB: $t = 1.3010$, $P = 0.1998$; GLM with family = quasibinomial). In addition, the interaction between germination phenotype and phenotype frequency also had a significant effect on

dispersal success in QAA ($t = 2.098$, $P = 0.0434$; GLM with family = quasibinomial). This also indicates that a high proportion of hoarded acorns had their embryos removed for each phenotype frequency in each oak species but was much higher for the germinating phenotype (over 70% for most phenotype frequencies) (Figure 3). For the 2 white oak species tested here, the relative dispersal success of each germination phenotype was significantly positively correlated with phenotype frequency (QAA: $F_{1,17} = 27.58$, $P < 0.0001$; QSB: $F_{1,22} = 15.47$, $P = 0.0071$) (Figure 4). In addition, dormant acorns were dispersed farther than germinating acorns of either QAA ($t = 2.1259$, $P = 0.0351$) or QSB ($t = 2.9916$, $P = 0.0032$). However, the whole acorns were dispersed a shorter distance than either embryo-removed (QAA: $t = 1.5174$, $P = 0.1312$; QSB: $t = 1.2119$, $P = 0.2274$) or eaten acorns (QAA: $t = 1.7527$, $P = 0.0816$; QSB: $t = 2.5267$, $P = 0.0125$) for each oak species (Figure 5).

DISCUSSION

In this study, we first demonstrated that Père David's Rock squirrels, similar to several *Sciurus* species (i.e., *Sciurus carolinensis*, *Sciurus aureogaster* and *Sciurus niger*) in North America, frequently removed acorn embryos from several Fagaceae species, including several WO species in the Foping National Nature Reserve. Similar behavior has also been observed in the scatter-hoarding red agouchi (*Myoprocta exilis*) feeding on seeds of *Carapara procera* (Meliaceae) in French Guiana (Jansen et al. 2006) and the agouti when scatter-hoarding acorns in Costa Rica (Steele MA, personal observation). Because animal species and related plants vary considerably across different continents, and they are often faced with similar selective pressures, convergence of such behavioral adaptations can be expected (Forget and Vander Wall 2001). Our new record of acorn-embryo removal by Père David's Rock squirrels in China suggests that acorn-embryo removal by tree squirrels may be more widespread than presently documented. In fact, we found that another tree squirrel species, Pallas's squirrel (*Callosciurus erythraeus*), displayed embryo removal behavior from acorns from several WO species and other Fagaceae species in Qingcheng Mt. in Sichuan Province, Southwest China (Xiao et al. 2009).

Here, we provide strong evidence that as seed predators and seed dispersers, Père David's Rock squirrels can cause positive frequency-dependent selection in the wild: both absolute and relative dispersal success for each germination phenotype increased as it became more common (Figures 3 and 4). Frequency-dependent selection by predators is well studied under experimental or seminatural conditions (Allen 1988). According to foraging theory, selection by predators will be negative if common phenotypes maximize their energy intake or feeding efficiency (Hubbard et al. 1982; Allen 1988). However, some studies using artificial prey indicate that prey density may change the magnitude and direction of frequency-dependent selection. Predators should tend to consume disproportionately more common prey when prey density is low, whereas at high prey densities rare prey tend to be consumed more due to their conspicuousness in relation to common prey (e.g., Horsley et al. 1979; Allen and Anderson 1984; Allen 1988; Allen et al. 1998). In addition, positive frequency-dependent selection or frequency-independent selection is expected to occur if one prey type is more profitable (e.g., larger seeds, Celis-Diez and Bustamante 2005) or highly unprofitable (e.g., fatally toxic to predators, Thompson 1984).

Unlike true predators in many predator-prey systems, however, many scatter-hoarding animals not only serve as seed predators but also as seed dispersers. Thus, the selective

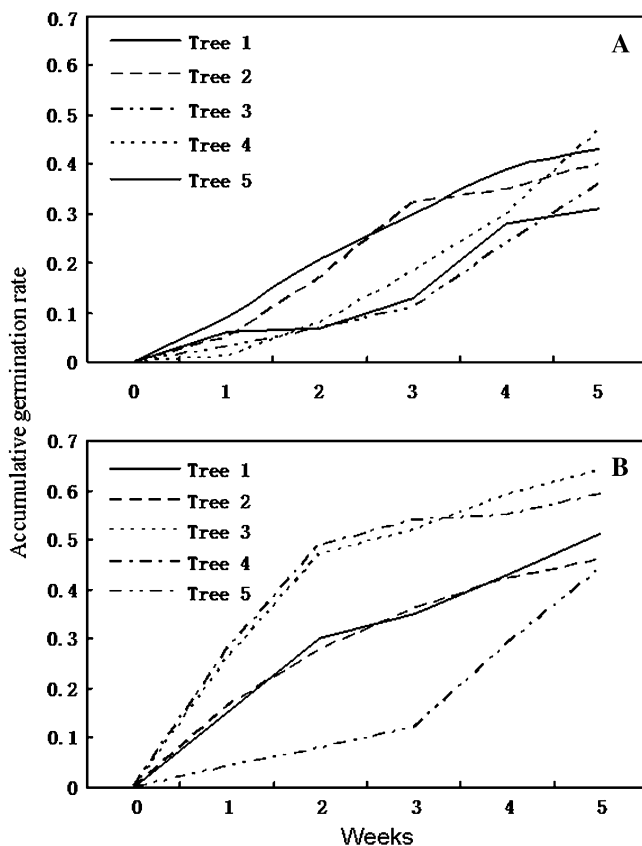
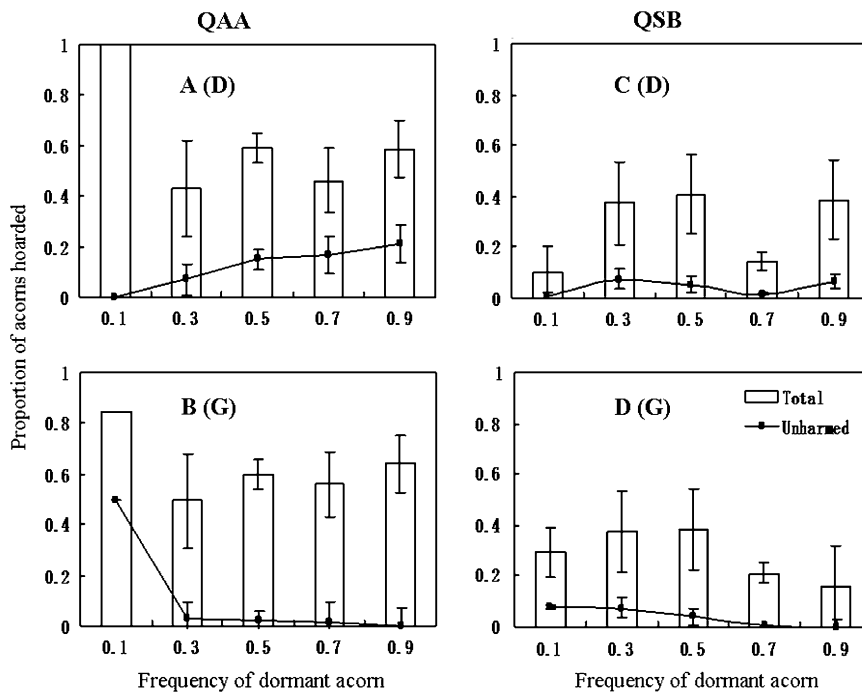


Figure 2
Variation of acorn germination among different parent plants in (A) QAA ($n = 5$) and (B) QSB ($n = 5$).

**Figure 3**

Mean proportion of acorns hoarded in total (total, i.e., hoarding success) and unharmed (i.e., absolute dispersal success, see text for details) for each germination phenotype in QAA and QSB. Panel (A) and (C) for dormant phenotype (D) and panel (B) and (D) for germinating phenotype (G). Data displayed are means \pm SE.

direction and its fitness consequences to prey populations (here plant seeds) caused by seed dispersers (as mutualists) would be opposite to those operating for nondispersing seed predators (Greenwood 1985). Generally, behavioral preferences of seed scatter-hoarding animals are complicated by feeding/hoarding decisions, the resolution of which is considered essential for optimizing survival and reproductive success (Vander Wall 1990). For tree squirrels, hoarding behavior is even more complex because embryo-removed acorns are also hoarded (Steele et al. 2001; Xiao et al. 2009; Xiao Z, unpublished data). On the one hand, germinating acorns, compared with dormant acorns, are more perishable and less valuable for subsequent use, thus they are more likely consumed, as predicted by the food perishability hypothesis (Hadj-Chikh et al. 1996; Smallwood et al. 2001; Steele, Smallwood, et al. 2001, 2006). This may be the case for QSB acorns here, which germinated much faster than QAA acorns (Figure 2). On the other hand, loss of food reserves because of germination is a relatively slow physiological process especially for large-seeded acorns because at least part of the cotyledons (ca. 60%) are still edible even after young seedlings emerge (Fox 1982). Therefore, germinating acorns are still worthy of being hoarded when their embryos are removed, which preserves remaining nutrients for as long as at least 6 months (Steele et al. 2001; Xiao et al. 2009). Moreover, dormant acorns would germinate at some point after hoarding and require additional management to efficiently exploit while stored in caches (Steele et al. 2001; Xiao et al. 2009).

In this study, we clearly show that positive frequency-dependent selection, mediated through behavioral preferences by scatter-hoarding squirrels, has the potential to enhance acorn dispersal and subsequent survival and establishment of the 2 WO species. We found that this dispersal/survival advantage to common phenotypes can markedly influence initial establishment of WO species, accounting for as much as 40.5% and 21.4% (r^2 from Spearman correlation coefficient, Figure 4) of the observed dispersal success in QAA and QSB, respectively. In this study, the observed variation in acorn germination among different parent plants in the 2 WO species indicates variable frequencies of both germination phenotypes during the fruiting season. Using the relationship we

found between germination frequency and dispersal success, we can predict the equilibrium germination frequencies expected in nature. Based on the relative dispersal success, the predicted optimal frequency of germinating phenotype was similar for the 2 WO species here, 72.5% for QAA and 72.8% for QSB, respectively (Figure 4). According to our germination experiment, the average accumulative germination rate (mean \pm 1 SE) after 5 weeks was $39.4 \pm 2.8\%$ (range: 31–47%) for QAA and $52.8 \pm 3.8\%$ (range: 44–64%) for QSB (Figure 2), which is much lower than the predicted frequency for either QAA or QSB. Our results, however, provide sound support for the prediction that a reliable proportion of acorns are dispersed unharmed prior to germination (see Fox 1982).

Our results suggest that the selection on germination phenotypes does not favor a single dormant phenotype either within or among prey species during the dispersal seasons. It is not entirely clear why selection by tree squirrels did not result in the fixation of either the nondormant or dormant phenotype in WO species during dispersal seasons. Our results suggest that there are opposing selective pressures that help prevent the fixation of a single germination phenotype but maintain both phenotypes in WO species possibly at the equilibrium frequencies observed here. Given that 2 germination phenotypes can occur at the same time in a given population, it seems likely that nondormancy and dormancy each may have its advantages and disadvantages (Fox 1982). The nondormant phenotype may have the advantage of escaping postdispersal predation through rapid germination for those acorns dispersed with embryos intact (Fox 1982), but the dormant phenotype also has some distinct advantages to enhance seed dispersal and escape from seed predation (including embryo removal) by tree squirrels. For example, dormant acorns have a lower probability of having their embryos removed by tree squirrels (Steele et al. 2001; Xiao Z, unpublished data; this study) and are more likely to be hoarded and dispersed farther (Fox 1982; Steele et al. 2007; Xiao Z, unpublished data; this study). In addition, dormant acorns also enjoy a longer dispersal period because the dispersal of viable acorns would end after germination (Fox 1982; Xiao Z, personal observation).

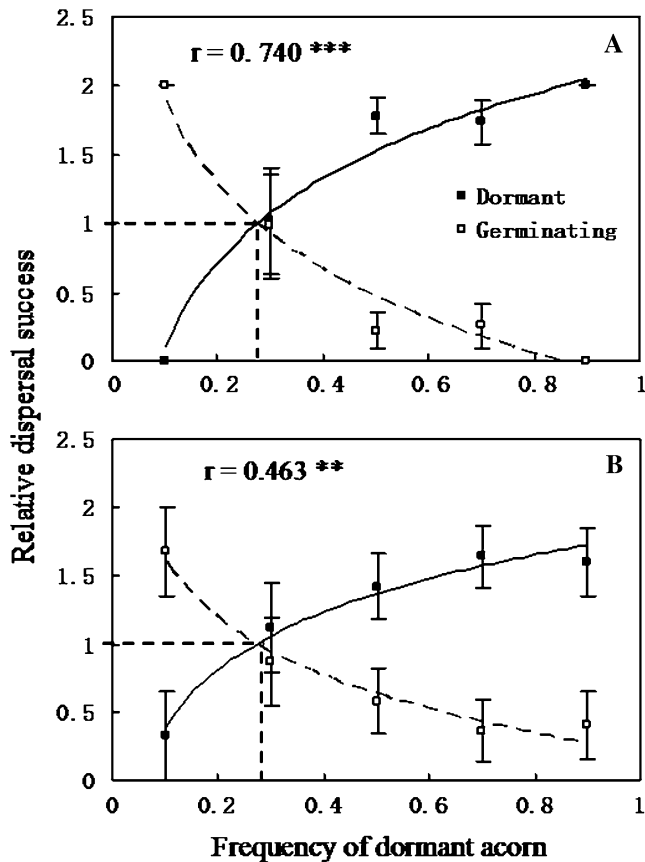


Figure 4
Relative dispersal success of each germination phenotype as a function of its relative frequency in (A) QAA and (B) QSB. Statistics were calculated by using all values. r is the Spearman correlation coefficient. $**P < 0.01$; $***P < 0.001$. The slopes given are the fitted regression lines: (A) $y = 0.88 \ln(x) + 2.14$ (dormant phenotype) or $y = -0.88 \ln(x) - 0.14$ (germinating phenotype); and (B) $y = 0.61 \ln(x) + 1.79$ (dormant phenotype) or $y = -0.61 \ln(x) + 0.21$ (germinating phenotype). The intersection between the fitted regression lines gives the value of predicted dormant/germinating frequency at equilibrium. Data displayed are means \pm SE.

According to this study, positive frequency-dependent selection may be an adaptive mechanism for escaping acorn-embryo removal by tree squirrels and promoting acorn dispersal and subsequent establishment in both nondormant WO species and dormant RO/QG species. Here, we observed that the dormant phenotype had a dispersal/survival advantage over germinating acorns in the 2 WO species. A high proportion (over 70%) of acorns from the latter phenotype was hoarded with embryos removed by tree squirrels (Figures 3 and 4). Dispersal/survival advantage to common phenotypes indicates that acorn dispersal is favored either when most acorns do not germinate (e.g., most of fruiting season) or when most acorns have germinated (e.g., the end of fruiting season). Evidence also shows that tree squirrels prefer to hoard more dormant acorns over nondormant acorns either within or among oak species though other covarying acorn traits such as tannin level, fat content, and handling time (or acorn size) could confound such preferences (Hadj-Chikh et al. 1996; Smallwood et al. 2001; Steele, Smallwood, et al. 2001, 2006; see also Xiao et al. 2008; Chang et al. 2009). If a reliable proportion of viable acorns can be dispersed prior to germination, rapid germination would further help WO acorns escape from postdispersal predation, assuming that each germina-

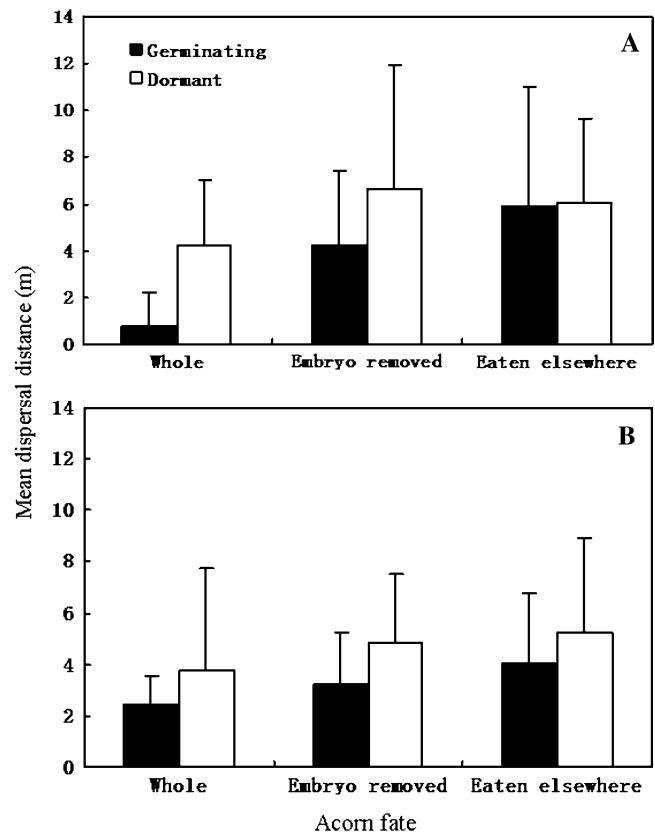


Figure 5
Mean dispersal distance (mean \pm 1 standard error of the mean) between germinating and dormant acorns after being removed from sources with 3 fate categories (whole, hoarded with embryos intact; embryo removed, hoarded with embryos removed; and eaten elsewhere, eaten somewhere from the sources). (A) QAA; (B) QSB.

tion phenotype has the same probability of recovery by the hoarder or another seed consumer (Fox 1982). Within communities, seed germination or dormancy varies considerably either within or among species (e.g., Vázquez-Yanes and Orozco-Segovia 1993; Rees 1996). For example, nondormant WO species often coexist with dormant RO species in North America or QG species in Asia. If the dispersal/survival advantage to the dormant phenotype is guaranteed through positive frequency-dependent or frequency-independent selection by tree squirrels, it may be easily understood why acorns from RO species or QG species remain dormant during dispersal seasons.

In summary, this study is the first to demonstrate that behavioral preferences of scatter-hoarding animals could cause frequency-dependent selection in the wild, and such selection in turn could have fundamental impacts on prey populations, including the evolution of related phenotypic traits. Our results further suggest convergent evolution of acorn-embryo removal behavior in tree squirrels across different continents and that this behavior is an adaptive response to nondormancy in WO species. Positive frequency-dependent selection by tree squirrels provides a new mechanism for improving our understanding of how nondormant WO species adapt to behavioral preferences of tree squirrels and such coadaptation may be a result of a "coevolutionary arms race" (see Dawkins and Krebs 1979) and benefit both oaks and tree squirrels. Moreover, frequency-dependent selection by tree squirrels may also provide new insights into the coexistence of sympatric seed species with contrasting or similar seed phenotypes (e.g., seed

germination/dormancy here), for example, WO and RO or QG species coexisting in many forests worldwide. Our results suggest that variation in seed traits, on which selection acts through behavioral preferences by seed predators/dispersers, can have a substantial impact on plant demography and vegetation diversity. Further efforts are required to test the generality of this mechanism.

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