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Nut predation and dispersal of Harland Tanoak *Lithocarpus harlandii* by scatter-hoarding rodents

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ABSTRACT

Plants that use the propagule to co-opt animals as dispersal agents must balance the costs of seed predation with the benefits of dispersal. Successful post-dispersal germination is a key metric that reflects these costs and benefits. By tracking individual nuts with coded tin-tags over 3 years (2000–2003), this study quantified nut predation and dispersal of harland tanoak (*Lithocarpus harlandii*) by seed-caching rodents in a subtropical evergreen broadleaved forest in the Duiangyan Region of Sichuan Province, Southwest China. We found that tanoak seedlings established from rodent-generated caches in the primary stands over a 12-month post-dispersal period. Our results indicate that seed-caching rodents are effective dispersers of tanoak nuts, but dispersal effectiveness varies among years and stands, probably due to mast seeding of harland tanoak or community-level seed availability according to the predator satiation hypothesis. Some nut traits in tanoak species, e.g. large seed size, hard nut husk, lower tannin and mast seeding, are important characteristics for seed dispersal by scatter-hoarding rodents, compared with oak species with higher tannin content.

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1. Introduction

Many studies have examined interactions between scatter-hoarding rodents and nut-bearing plants (e.g. Price and Jenkins, 1986; Vander Wall, 1990, 2001; Jansen and Forget, 2001; Smallwood et al., 2001). Plants that use the propagule to co-opt animals as dispersal agents must balance the costs of seed predation with the benefits of dispersal. Successful post-dispersal germination is a key metric that reflects these costs and benefits (Price and Jenkins, 1986). But, it is not well understood how nut-bearing plants evolved to balance seed predation and seed dispersal via scatter-hoarding animals.

Much attention has been paid to the dispersal biologies of the oaks (*Quercus*, Fagaceae) (e.g. Miyaki and Kikuzawa, 1988;

Steele et al., 1993, 2001; Smallwood et al., 2001; Shimada, 2001; Li and Zhang, 2003; Gómez, 2004; Xiao et al., 2004a), which are common or dominant tree species in many temperate and tropical forests (Vander Wall, 1990, 2001). However, the tanoaks (*Lithocarpus* Blume) in the same family as oaks, are less well studied. Tanoaks produce large nuts (e.g. nuts of harland tanoak *Lithocarpus harlandii* found to be up to 7 g in this study), which may also be potentially dispersed by scatter-hoarding rodents (Vander Wall, 1990, 2001; Corlett, 1998). Many tanoak species have a harder seed husk and lower tannin content than acorns from oaks (Xiao et al., 2003; Z-S Xiao, unpublished data). Differences in physical and chemical nut traits play a vital role in determining seed predation, dispersal and seedling establishment for both tanoak species and oak species. Edward's long-tailed rats (*Leopoldamys edwardsii*) scatter-hoard the nuts of harland tanoak (*L. harlandii*) in a subtropical evergreen broadleaved forest in the Duiangyan Region of Sichuan Province, China (Xiao et

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al., 2003). So far, however, no field evidence indicates whether seed dispersal by seed-caching rodents can lead to successful seed dispersal and seedling establishment for the tanoaks.

We used harland tanoak (*L. harlandii*) to quantify nut predation and dispersal by seed-caching rodents in two stands by tracking individual nuts with coded tin-tags over 3 years (2000–2003), in a subtropical evergreen broadleaved forest in the Dujiangyan Region of Sichuan Province, China. Here, we address two questions: 1) Are seed-caching rodents effective dispersal agents for the tanoak species? 2) Which nut traits of tanoak species are adaptive to seed dispersal by scatter-hoarding rodents, compared with oak species (including the white oak and black oak groups)?

2. Study site and study species

The study was carried out from October 2000 to November 2003 in the Banruosi Experimental Forest (altitude 700–1000 m, 31°4'N, 103°43'E) in the Dujiangyan City of Sichuan Province, China. The site lies in the middle of the subtropical zone, with a mean annual temperature of 15.2 °C, and an annual precipitation of 1200–1800 mm (Chen, 2000). The weather is often cloudy and foggy, with annual hours of sunlight typically in the 800–1000 h range and a mean annual relative humidity of more than 80%.

The experimental forest can be sorted into three kinds of stands according to variation in stand age and vegetation structure: primary stands (80–90 years), secondary stands (< 50 years) and shrublands (< 10 years). We conducted this study in one primary and one secondary stand. Detailed descriptions of these stands have been presented by Xiao et al. (2004a, 2004b, 2005a, 2005b); Zhang et al. (2005). Most fruiting trees (DBH > 15 cm) of harland tanoak are restricted to a very narrow area (< 0.5 ha.) in the primary stand near a temple named Banruosi, while no or few individual trees of harland tanoak occur in secondary stands (probably due to logging). The seed rain period of harland tanoak coincides with those of other nut-bearing tree species (e.g. *Quercus variabilis*, *Q. serrata*, *Castanopsis fargesii* and *Camellia oleifera*), with little difference in peak time (Xiao, 2003; Z-S Xiao, personal observation). Total seed abundance was higher in primary stands (i.e. seed-rich stands) than in secondary stands (seed-poor stands) according to tree abundance and their fruiting conditions (Xiao et al., 2001, 2004a, 2005a; Zhang et al., 2005).

The genus *Lithocarpus* Blume contains about 300 species and subspecies, mainly distributed in Asia, especially in southeast and south Asia (Chun and Huang, 1998). There are 137 species and subspecies recorded in China (Chun and Huang, 1998). The tanoaks have been an important element of forests since the Miocene and presently grow in diverse mixed species communities throughout their range (see Cannon and Manos, 2003 and references therein). Nearly all tanoak species are canopy trees in tropical and subtropical evergreen broadleaved forests (Chun and Huang, 1998). There are at least two tanoak species in the subtropical evergreen broadleaved forest in the Dujiangyan region: harland tanoak (*L. harlandii*) (*Catalog for Plants of Dujiangyan City of China*. Conservation Experimental Center of Wild Plants of West-China

and Forest Bureau of Dujiangyan City, 1991) and another unidentified species (*Lithocarpus* sp.). Harland tanoak nuts mature from next mid-October to November after flowering in May to June. Fully fruiting trees of harland tanoak can produce several thousand nuts, especially in masting years. Both occasional fruiting of individual trees (2000, 2001 and 2003) and synchronous masting of the whole population (2002) of harland tanoak have been observed in the study site during the past 4 years (Z-S Xiao, personal observation). Harland tanoak is one of the largest nuts in the study site with fresh mass of 4.56 ± 1.22 g (mean \pm 1 S.D., range 2.2–7.0 g, $n = 40$). The nut husk of harland tanoak is harder than that of co-occurring oak species (*Q. variabilis* and *Q. serrata*). The tannin content (1.34% of nut dry mass) of harland tanoak nuts is much lower than that of *Q. variabilis* (11.68%) and *Q. serrata* (10.62%), but nutrient reserves (protein, fat and starch) and caloric value of these species are similar (Xiao et al., 2003).

Eleven nocturnal rodent species occurred in the study site: chestnut rat (*Niviventer fulvescens*), Edward's long-tailed rat (*L. edwardsi*), Bower's rat (*Berylmys bowersi*), white-bellied rat (*N. confucianus*), Himalayan rat (*Rattus nitidus*), Norway rat (*R. norvegicus*), Sichuan field mouse (*Apodemus latronum*), Chevrier's field mouse (*A. chevrieri*), South China field mouse (*A. draco*), striped field mouse (*A. agrarius*) and harvest mouse (*Micromys minutus*), among which chestnut rat, Edward's long-tailed rat, Bower's rat and white-bellied rat, are dominant species (Xiao et al., 2002; Z-S Xiao and Z-B Zhang, unpublished data). The rodent species and abundance are similar in both primary and secondary stands (Xiao et al., 2002; Xiao, 2003). Of the captured rodents, chestnut rat, Edward's long-tailed rat, Bower's rat, white-bellied rat, Himalayan rat and Norway rat are known to consume harland tanoak nuts, but other smaller rodent species (e.g. *Apodemus* and *Micromys*) may not, due to the difficulty of opening the hard husk (Xiao and Zhang, 2004). At present, Edward's long-tailed rat, the largest of the rodents (weight, 200–500 g), is the only known rodent species to potentially disperse harland tanoak nuts by scatter-hoarding them in soil (Xiao et al., 2003; Xiao, 2003). Edward's long-tailed rat needs about 777.78 ± 200.34 s ($n = 6$) to consume one tanoak nut, which is a longer handling time than for other nut species (e.g. *Q. variabilis*, 204.97 ± 168.74 s, $N = 3$; *Q. serrata*, 81.60 ± 43.91 s, $N = 6$) (Xiao et al., 2003). In the study site, no birds or other mammals (except humans) can open the hard nut husks of harland tanoak (Z-S Xiao, personal observation).

3. Methods

After harland tanoak nuts ripened, we collected fresh nuts from the ground under the parent plant, and used water flotation to distinguish between sound and insect-damaged/empty nuts. Then we randomly selected 400 fresh, sound nuts each year, and labeled them using slightly modified methods reported by Zhang and Wang (2001); Li and Zhang (2003). A tiny hole, 0.5 mm in diameter, was drilled through the husk near the germinal disc of each nut, without damaging the cotyledon and the embryo. A tin tag (4 cm \times 1 cm, < 0.1 g) was tied through the hole in each nut using an 8 cm

thin steel thread. Each tag was numbered using a fine point metal-pen engraving tool to make each nut individually identifiable. When rodents buried the nuts in the soil, the tin tags were often left on the surface, making them easy to visually relocate. Tagging has a negligible effect on seed removal and caching by rodents (Zhang and Wang, 2001; Z-S Xiao, P. A. Jansen and Z-B Zhang, unpublished manuscript). In order to see whether seed abundance (e.g. mast seeding or community-level seed availability) affects nut predation, caching and dispersal of harland tanoak, we selected two stands as the experimental sites (a secondary stand: area, 2.5 ha, aspect, 20–40°, direction, northwest; a primary stand: area, 2 ha., aspect, 35–70°, direction, east). In each stand, 20 plots were established as experimental seed stations, spaced 10 m apart along a transect line. In November of each year (from 2000 to 2002), we placed 10 tagged nuts at each seed station. We then initially monitored seed removal daily, and later at increasing intervals. During each visit, we also searched the area along the transect with equal effort (2–4 h for two people each visit) to retrieve removed seeds and record their fate. Each time we checked all seed stations as well as cache sites located in previous visits. The monitoring schedule was similar for each year on days 1, 2, 3, 4, 6, 8, 12, 16, 24, 32, 48, 160–170 (next April), and 365–370 (next November) after seed release. Post-dispersal seed fates can be sorted into three categories: 1) cached (including buried intact in the soil and deposited intact on the surface with leaf litter), 2) eaten leaving only tin-tags and seed fragments, and 3) missing with their true fates unknown (Xiao et al., 2004a, 2004b, 2005a, 2005b). For retrieved tags and seeds, we recorded their numbers and measured the distance to their source. Cached seeds were carefully reburied, attempting to minimize cache disturbance, and their locations marked using a numbered bamboo stick (15 × 1.5 cm). These sticks might give rodents some cues for pilfering, but we found that

they had no effect on cache survival by establishing artificial caches (Z-S Xiao, P.A. Jansen and Z-B Zhang, unpublished manuscript). During subsequent visits, we also checked the caches located in previous visits until those were recovered by rodents. If a marked cache was removed, the area around the cache was searched. When a cached seed was excavated and subsequently found re-cached or eaten elsewhere, we measured the distance to its original seed source as well as to its previous cache.

Cox regression was used to compare the time to removal from seed stations or from caches between stands or among years. Two-way ANOVA was used to test the difference in dispersal distances of the primary caches or the eaten nuts from seed stations among years and stands. Two-way ANOVA was also used to test the difference in dispersal distances from seed stations of primary caches and secondary caches or eaten nuts (by pooling all the 3-year data in each stand) between stands. Dispersal distances were log₁₀-transformed to meet normality if necessary.

4. Results

4.1. Nut harvest

Based on regular surveys and nut debris analysis, rodents consumed and removed all the tagged nuts after placement at seed stations. Except for two nuts eaten at seed stations in each stand, all other tagged nuts were removed and potentially dispersed or eaten (Table 1). The proportion of nut final removal at seed stations was very similar (nearly 100%) among years ($F = 1.241$, $df = 2$, $P = 0.293$), stands ($F = 0.859$, $df = 1$, $P = 0.356$) and the year–stand interaction ($F_{2, 114} = 0.286$, $P = 0.751$) (Fig. 1). Nut lifetime at seed stations was generally short, but longer in 2002 (masting year) than in

Table 1 – Fates (seed number and %) of the tagged nuts of harland tanoak *L. harlandii* after placement at experimental seed stations

Fates	Primary stand				Secondary stand			
	2000 (%)	2001 (%)	2002 (%)	Sum (%)	2000 (%)	2001 (%)	2002 (%)	Sum (%)
<i>Fates from seed stations</i>								
Eaten in situ	0 (0)	2 (1.0)	0 (0)	2 (0.3)	0 (0)	0 (0)	2 (1.0)	2 (0.3)
Removed and eaten	26 (13.0)	24 (12.0)	7 (3.5)	57 (9.5)	8 (4.0)	12 (6.0)	18 (9.0)	38 (6.3)
Removed and cached	27 (13.5)	70 (35.0)	82 (41.0)	179 (29.8)	43 (21.5)	10 (5.0)	16 (8.0)	69 (11.5)
Removed and missing	147 (73.5)	104 (52.0)	111 (55.5)	362 (60.4)	149 (74.5)	178 (89.0)	164 (82.0)	491 (81.9)
Sum (%)	200 (100)	200 (100)	200 (100)	600 (100)	200 (100)	200 (100)	200 (100)	600 (100)
<i>Fates from primary caches</i> ^a								
Survived	3 (1.5)	2 (1.0)	7 (3.5)	12 (2.0)	2 (1.0)	1 (0.5)	0 (0)	3 (0.5)
Recached ^c	3 (1.5)	10 (5.0)	6 (3.0)	19 (3.2)	2 (1.0)	1 (0.5)	3 (1.5)	6 (1.0)
Eaten	1 (0.5)	14 (7.0)	3 (1.5)	18 (3.0)	3 (1.5)	1 (0.5)	0 (0)	4 (0.7)
Missing	20 (10.0)	44 (22.0)	66 (33.0)	130 (21.6)	36 (18.0)	7 (3.5)	13 (6.5)	56 (9.3)
Sum (%)	27 (13.5)	70 (35.0)	82 (41.0)	179 (29.8)	43 (21.5)	10 (5.0)	16 (8.0)	69 (11.5)
<i>Ultimate seed fates</i> ^b								
<i>Seedlings</i> ^d								
Eaten	1 (0.5) ^e	0 (0)	3 (1.5) ^e	4 (0.7)	0 (0)	0 (0)	0 (0)	0 (0)
Missing	28 (14.0)	45 (22.5)	10 (5.0)	81 (13.5)	11 (5.5)	13 (6.5)	20 (10.0)	44 (7.3)
Sum (%)	171 (85.5)	155 (77.5)	187 (93.5)	515 (85.8)	189 (94.5)	187 (93.5)	178 (89.0)	554 (92.7)
Sum (%)	200 (100)	200 (100)	200 (100)	600 (100)	200 (100)	200 (100)	200 (100)	600 (100)

^a The survey date was in next spring (i.e. late April).

^b Ultimate seed fates meant that the fates of seeds are determined at the end of annual survey in November.

^c “Recached” means the nut in the primary caches was removed and cached in a new place.

^d The survey date was in next November.

^e One cached nut didn’t emerge as a seedling due to fungal infestation when examined in November of 2001 and 2003, respectively (see detail in text).

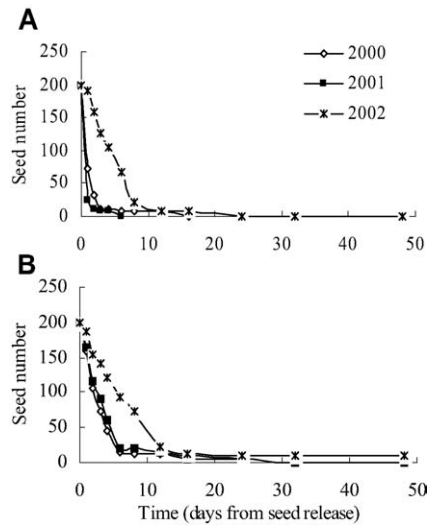


Fig. 1 – Nut harvest of harland tanoak *L. harlandii* after placement at seed stations at primary (a) and secondary (b) stands.

the other 2 years (2000 and 2001) in both stands (Fig. 2a). Nut lifetime at seed stations was shorter in the primary stand than in the secondary stand in each year (Figs. 1,2a). Differences in nut lifetimes were highly significant among years (Wald = 212.181, df = 2, $P < 0.001$) and between stands (Wald = 125.825, df = 1, $P < 0.001$).

4.2. Seed fates

During the 3-year survey, we relocated less than 50% of the tagged nuts (primary stand: 26.5–47.5%; secondary stand, 10.5–25.5%) after they were removed from seed stations. Of the tagged nuts relocated, most were scatter-hoarded in the surface soil: 50.94–92.13% (the highest in 2002) in the primary stand; 45.45–84.31% (the highest in 2000) in the secondary stand, while the rest were eaten (Table 1). Some of the ca-

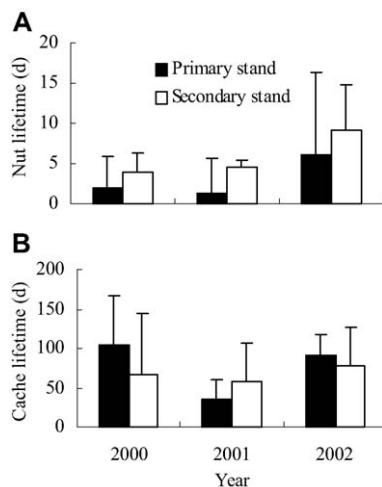


Fig. 2 – Nut lifetime (days) of harland tanoak *L. harlandii* at seed stations (a) and at primary cache sites (b).

ched nuts in primary cache sites were recovered and moved into new cache sites (i.e. secondary cache sites) (Table 1). We relocated 272 caches (not including two mixed big caches, see below) in two stands: 247 primary caches (primary stand: 27 in 2000, 70 in 2001 and 81 in 2002; secondary stand: 43 in 2000, 10 in 2001 and 16 in 2002) and 25 secondary caches (primary stand: three in 2000, 10 in 2001 and six in 2002; secondary stand: two in 2000, one in 2001 and three in 2002). The total number of caches (including primary and secondary caches) was higher (72.4%) in the primary stand.

Except for one 2-nut cache in the primary stand (2002), all other caches contained only one tagged nut in both stands. However, we found two mixed caches: one cache contained one tagged tanoak nut, two *Q. variabilis* acorns and one *C. oleifera* nut in a rock cave (covered with leaf litter) in the primary stand (2001); and the other cache (in an underground burrow at least 80 cm deep) contained at least two tagged tanoak nuts, five *Q. variabilis* acorns (but four of them were eaten) and one *Q. serrata* acorn (also eaten) in the secondary stand (2002). This suggests that some local rodents larder-hoard nuts in underground burrows or elsewhere.

Over a 12-month period after seed placement, more than 78% of the tagged nuts disappeared and their ultimate seed fates are unknown (Table 1). Three possible outcomes for these missing nuts include: 1) Some nuts may be transported into underground burrows or nests, rock caves and dense shrubs (for larder-hoarding), where we could not find them (some direct evidence was listed above); 2) Some nuts may be transported outside the surveyed area because some seeds were cached or eaten more than 90 m from seed stations; 3) Some nuts may survive to emerge as a seedling, but they were not examined in this study.

4.3. Dispersal distances

Both in the primary and in the secondary stands, over 80% of the caches and the eaten nuts were distributed within 20 m of seed stations (Table 2), but some tagged nuts were dispersed over 35 m from seed stations (Fig. 3). In the primary stand, maximum dispersal distances of the caches and the eaten nuts were 91.5 and 91.8 m, respectively. In the secondary stand, maximum dispersal distances of the caches and the eaten nuts were 52.8 and 52.0 m, respectively. Mean dispersal distances were very similar between the primary caches and the eaten nuts from seed stations over 3 years in either stand, but dispersal distances increased when the tagged nuts were moved from primary cache sites to secondary cache sites or eaten sites in either stand (Table 2). In 2000, dispersal distances of the primary caches or the eaten nuts were longer in the secondary stand than in the primary stand, but the reverse was true in 2001 and 2002. For the primary caches, dispersal distances were significantly different among years ($F = 12.241$, df = 2, $P < 0.001$), but not among stands ($F = 0.536$, df = 1, $P = 0.465$) or the year-stand interaction ($F = 2.664$, df = 2, $P = 0.072$). For the eaten nuts from seed stations, dispersal distances were similar among years ($F = 0.487$, df = 2, $P = 0.616$), stands ($F = 2.926$, df = 1, $P = 0.091$) or their interaction ($F = 2.363$, df = 2, $P = 0.100$).

Since only several secondary caches were found in both stands each year, the data of these secondary caches were

Table 2 – Mean dispersal distances (mean ± 1 S.D. m) of the dispersed nuts or nut fragments of harland tanoak *L. harlandii* relocated in different dispersal stages

Seed fates	Primary stand			Secondary stand		
	2000	2001	2002	2000	2001	2002
<i>After seed stations</i>						
Burial	11.1 ± 18.0 (27)	19.4 ± 19.6 (70)	7.3 ± 10.0 (82)	13.3 ± 12.9 (43)	12.5 ± 5.8 (10)	6.4 ± 10.0 (16)
Eaten	10.1 ± 6.6 (26)	22.7 ± 28.1 (24)	12.7 ± 11.3 (7)	14.3 ± 16.0 (8)	6.2 ± 2.6 (12)	7.9 ± 11.2 (18)
Total	10.6 ± 13.5 (53)	20.2 ± 22.0 (94)	7.7 ± 10.1 (89)	13.5 ± 12.3 (51)	8.9 ± 5.2 (21)	7.2 ± 10.5 (34)
<i>After primary caches</i>						
Burial	30.0 ± 41.6 (3)	21.6 ± 20.3 (10)	13.6 ± 9.0 (6)	10.0 ± 4.2 (2)	17.4 (1)	14.6 ± 15.8 (3)
Eaten	14.5 (1)	28.2 ± 26.3 (12)	27.5 ± 1.5 (2)	23.1 ± 12.9 (2)	17.3 (1)	–
Total	26.1 ± 34.9 (4)	25.1 ± 23.3 (22)	17.1 ± 9.9 (8)	16.6 ± 10.9 (4)	17.4 ± 0.1 (2)	14.6 ± 15.8 (3)
<i>After secondary caches</i>						
Eaten	9.90 (1)	26.7 ± 34.6 (3)	–	–	–	–

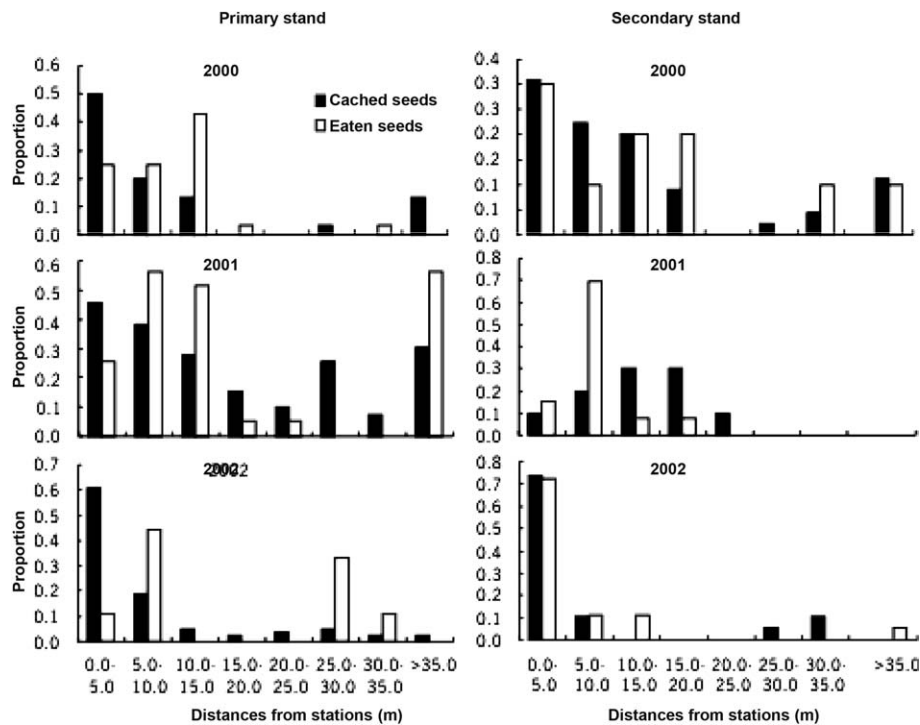


Fig. 3 – Frequency distributions of the dispersal distances (m) of primary caches (i.e. the cached nuts) and seed tags with seed fragments (i.e. the eaten nuts) of harland tanoak *L. harlandii* (based on the data until the following April).

pooled for analysis. In both stands, dispersal distances of the tagged nuts increased when they were moved from primary cache sites to secondary cache sites or eaten sites (i.e. secondary caching or recaching) (Table 3). For secondary caches (by pooling data from all 3 years), the dispersal distances to seed stations were significantly longer than those of primary caches ($F = 6.658$, $df = 1$, $P = 0.013$), but there were no differences between stands ($F = 2.685$, $df = 1$, $P = 0.108$) and the year-stand interaction ($F = 0.730$, $df = 1$, $P = 0.397$). For nuts retrieved and eaten from primary caches, the dispersal dis-

tances to seed stations were not different between stands ($F = 0.338$, $df = 1$, $P = 0.566$), dispersal order ($F = 1.708$, $df = 1$, $P = 0.202$) or their interaction ($F = 0.093$, $df = 1$, $P = 0.763$) (Table 3).

4.4. Cache survival and seedling establishment

Cache/nut lifetime for primary caches was slightly longer in the primary stand than in the secondary stand (Wald = 0.682, $df = 1$, $P = 0.409$), but significantly different among years

Table 3 – Dispersal distances (m) from seed stations to primary caches or secondary caches or nut fragments of harland tanoak *L. harlandii* by pooling all the 3-year data

Seed states	Primary caches			Secondary caches or eaten nuts		
	Mean	S.D.	N	Mean	SD	N
<i>Primary stand</i>						
Cached	17.3	24.3	20	21.9	21.8	20
Eaten ^a	10.1	9.0	4	20.8	20.6	8
<i>Secondary stand</i>						
Cached	6.7	12.2	5	12.8	11.6	5
Eaten ^a	16.0	11.7	10	22.6	20.4	10

^a “Eaten” means that the nuts in primary caches were recovered and moved into new sites to be eaten rather than to be cached (i.e. secondary caches).

(Wald = 21.138, df = 2, $P < 0.001$) (Fig. 2b). Only a tiny proportion of the caches survived to the next spring (late April) in both stands (primary stand: 10.0% (3) in 2000, 2.5% (2) in 2001 and 8.0% (7) in 2002; secondary stand: 4.4% (2) in 2000, 10.0% (1) in 2001 and 0% (0) in 2002) (Table 1). In the primary stand, four cached nuts survived over 12 months—one from 2000 and three from 2002. Of these caches, both from 2002 successfully produced a seedling but fungal pathogens killed the other two nuts from the other two caches (Table 1). No caches survived until the next November over 3 years in the secondary stand (Table 1).

5. Discussion

5.1. Nut predation and dispersal by seed-caching rodents

Our results indicate that seed-caching rodents are effective dispersal agents for harland tanoak. The following aspects should be included to understand dispersal effectiveness of tanoak species by seed-caching rodents: 1) high nut harvest rate, as shown by short nut lifetime (1 or 2 weeks) at seed stations, high proportion of nut removal (over 99%) and very low nut consumption in situ, indicating a lower probability of seed predation by non-seed-caching species; 2) high cache/dispersal proportion, (over 50% of the relocated nuts were cached in both stands); 3) high proportion of one-nut caches (over 99%), indicating lower sibling competition and more potential sites for seedling establishment. In addition, dispersal distances of harland tanoak, including distribution frequency, mean and maximum distances, were longer than those of the other four fagaceous species (e.g. *Q. variabilis*, *Q. serrata*, *C. fargesii* and *C. glauca*) in the study site (e.g. Xiao et al., 2005b), indicating potential dispersal/colonization ability. Moreover, secondary caching is more common for harland tanoak, compared with the other four fagaceous species (Xiao et al., 2005b; Z-S Xiao, unpublished data). Though only two seedlings (0.17% of 1200 tagged nuts) were found establishing from the rodent-generated caches, our results may underestimate dispersal effectiveness (i.e. seedling establishment) of harland tanoak by seed-caching rodents in this study since a large proportion of the tagged nuts disappeared and their ultimate fates were unknown. However, harland ta-

noak can produce adequate offspring to replace itself even when its nuts have only a 0.17% probability of seedling establishment rate after being dispersed, because they can produce thousands of nuts when they are fully mature in a given year, especially in masting years (Z-S Xiao, personal observation).

Our results also indicate that dispersal effectiveness of harland tanoak varied among years and stands. This may result from mast seeding of harland tanoak or community-level seed availability. The variation between primary and secondary stands mainly involves vegetation structure and tree composition, subsequently including the abundance of the fruiting trees and seed production, while the annual variation mainly involves seed production (e.g. mast seeding) and community dynamics of seed-eating rodents (Xiao et al., 2004a, 2004b, 2005a; Zhang et al., 2005). For example, mast seeding of harland tanoak occurred in 2002 (Z-S Xiao, personal observation), therefore nut dispersal should be greater (Smith and Reichman, 1984) and cache survival and seedling establishment should be higher in the following year according to the predator satiation hypothesis (Janzen, 1970, 1971; Silvertown, 1980). This matched our field investigation very well. Vander Wall (2002); Jansen et al. (2004) also indicated that mast seeding enhances cache survival and seedling establishment. Community-level seed availability (including *Q. variabilis*, *Q. serrata*, *C. fargesii* and *C. oleifera*) was also higher in the primary stand than in the secondary stand (Xiao, 2003; see also Zhang et al., 2005), which may further increase cache survival and seedling establishment of harland tanoak.

5.2. Nut traits adaptive to rodent dispersal in relation to oak species

In general, a whole nut should include two functional traits to facilitate seed dispersal by seed-eating animals:

- 1) attractive traits, e.g. seed mass and nutrient material;
- 2) defensive traits, e.g. secondary compounds and seed coat (see Zhang et al., 2005).

The trade-off between these dual traits may drive the evolutionary responses (i.e. seed predation and seed dispersal) for both nut-bearing plants and seed-caching animals. For both tanoak species and oak species, attractive traits are very similar, including seed mass (commonly large), nutrient material and mast seeding (Table 4). Commonly, both tanoak and oak species have large seed mass with a greater nutritional value (Table 4), thus scatter-hoarding animals prefer these high-value nuts. According to the optimal cache spacing models, large seeds are cached further than small ones (Stapanian and Smith, 1978; Clarkson et al., 1986). Moreover, large seeds are more likely to be cached than small ones (e.g. Forget et al., 1998; Jansen et al., 2002, 2004; Vander Wall, 2003). Additionally, large seed size also facilitates secondary caching, which can further increase cache spacing (Jansen et al., 2002, 2004; Vander Wall, 2003; Xiao et al., 2004a; Z-S Xiao, unpublished data). We also note that large seed size also results in better provisioning for germination and seedling establishment (e.g. Gómez, 2004), which may compensate for reduced ability to produce propagules. On the other hand, mast seeding in both tanoak and oak species is very com-

Table 4 – Comparison of dispersal traits between tanoak species (i.e. harland tanoak) and oak species (including white oak group and black oak group)

Seed traits and dispersal agents	Harland tanoak	Oak species ^a	
		White oak group	Black oak group
Dry mass (g)	3.14	0.40–4.66	2.12–4.21
Protein (%)	5.8	3.9–7.4	3.7–10.3
Fat (%)	0.9	4.1–11.5	8.1–26.7
Starch (%)	38	56–79	78–89
Caloric value (kJ/g)	17.1	17.4–18.7	19.0–21.8
Mast seeding	Yes	Yes	Yes
Nut husk	Hard	Soft	Soft
Tannin content (%)	1.34 (low)	0.6–5.6 (medium)	5.7–11.3 (High)
Dispersal agents	Rodents ^b and human ^c	Rodents and birds	Rodents and birds

^a The data of oak species (only including white oak group and black oak group) were derived from Vander Wall (2001).

^b Rodent species may include only those with medial to large body size, e.g. chestnut rats, Edward's long-tailed rats, Bower's rats, white-bellied rats, Himalayan rats and Norway rats in the study site, but only Edward's long-tailed rats are scatter-hoarders (Xiao et al., 2003; J-R Cheng, Z-S Xiao and Z-B Zhang, unpublished data).

^c The dispersal agents of tanoak species (and some oak species as well) should include human. Because tanoak and oak species can serve as human food, timbering or just a toy for local people (Z-S Xiao, personal observation), and potential dispersal (including long-distance dispersal) may have occurred through human-mediated methods.

mon (Sork, 1993; Koenig et al., 1994; Chun and Huang, 1998; Z-S Xiao, personal observation). An important advantage of mast seeding may be that it satiates insect and vertebrate seed predators (Janzen, 1970, 1971; Silvertown, 1980; Kelly, 1994; Crawley and Long, 1995), but it may attract more seed dispersers (e.g. scatter-hoarding animals) (Vander Wall, 2002). During the 3-year survey, synchronous mast seeding of harland tanoak occurred in 2002. In 2002, nearly all the fruiting tanoak individuals produced thousands of nuts, which potentially increases nut survival and seedling establishment (Z-S Xiao, field observation for seedlings in November of 2003).

However, defensive traits differ. Many tanoak species (e.g. harland tanoak) have a hard nut husk, which potentially increases seed handling time for seed-eating animals (mean, 777.78 s for Edward's long-tailed rats, Xiao et al., 2003), and thus increases the seed-eaters risk of predation (Jacobs, 1992; Hadj-Chikh et al., 1996). Therefore, seed-caching rodents may increase caching but reduce instant consumption (e.g. *P. armeniaca* in Zhang and Wang, 2001; Li, 2002; see also Zhang et al., 2005). In addition, seeds with a hard seed husk can be stored for a long time (Jansen and Forget, 2001; Z-S Xiao, personal observation), and thus storing a large quantity of these seeds may relieve food shortage of hoarding animals in winter and spring. Seeds with a hard husk could also reduce potential seed-eaters, which have not evolved the ability to open these nuts. In contrast, oak species, e.g. white oak and black oak groups, have a higher tannin content, which can reduce acorn consumption and digestive efficiency of acorn predators, including seed-caching animals (Steele et al., 1993; Smallwood et al., 2001; Vander Wall, 2001). In addition,

a very low fat level (0.92%) was found in harland tanoak nuts in relation to oak species (4.1–26.7%). It is possible that high fat level in oak species may potentially increase food value to attract potential seed-caching animals for dispersal, as it does in oil tea (*C. oleifera*) nuts with 51.9% of fat content in our study site (Xiao et al., 2004b). But, nuts of oak species in the study site, i.e. *Q. variabilis* and *Q. serrata*, were found to have a lower cache probability in contrast to those of harland tanoak (Xiao, 2003; Xiao et al., 2004a), though some other studies indicate that black oak species with high tannin and fat content have a higher probability of storability over white oak species with low tannin and fat content (e.g. Steele et al., 1993; Smallwood et al., 2001). It is possible that high tannin level in oak species might counteract potential impacts of high fat level, and this warrants further study.

For animal seed dispersers (e.g. rodents and birds), adaptive responses to attractive traits and defensive traits include the capacity to load (e.g. large seed size), detoxify seeds (e.g. tannin or other secondary compounds) or open hard seed husks. Therefore, many rodent species and jays can use acorns as food (Vander Wall, 1990, 2001; Den Ouden et al., 2005), while only rodents with medium to large body size (e.g. Edward's long-tailed rats) can effectively use tanoak nuts with hard husks. No birds could open tanoak nuts in the study site. In addition, the dispersal agents of tanoak species (and some oak species) should include humans. Because some tanoak species can serve as human food, timbering or just a toy for local people (Z-S Xiao, personal observation), potential dispersal (including long-distance dispersal) may have occurred through human-mediated methods in recent times. This possibility needs to be studied further.

In conclusion, we found evidence for nut dispersal and subsequent seedling establishment of tanoak species (i.e. harland tanoak) by seed-caching rodents, indicating that seed-caching rodents are effective seed dispersers for tanoak species. Though previous studies assumed that the tanoak species possess no obvious features to facilitate dispersal (Ng, 1991), our results suggest that some nut traits in tanoak species, e.g. large seed size, nut husk, tannin content and mast seeding, seem responsible for seed dispersal through scatter-hoarding animals. However, examination of the combined effects of abiotic factors, establishment requirement, nut predators and dispersers on the design of tanoak nuts is needed to better understand the evolutionary trade-off of dispersal traits in tanoak species, and phylogenetic relationships with other genera in the family Fagaceae.

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