Long-term seed survival and dispersal dynamics in a rodent-dispersed tree: testing the predator satiation hypothesis and the predator dispersal hypothesis

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Summary

1. Mast seeding in animal-dispersed plants has previously been accounted for by two main hypotheses: the predator satiation hypothesis (that it increases seed survival and establishment before dispersal) and the predator dispersal hypothesis (that it increases seed dispersal or dispersal distance). However, neither hypothesis has been rigorously tested with simultaneous data on seed production, seed predation and seed dispersal by vertebrate seed predators.

2. We studied oil tea *Camellia oleifera* (Theaceae) seed production for eight years (2002–2009) in a subtropical forest in south-west China, and investigated how annual seed and rodent abundance determined per capita seed availability for rodent seed predators and seed dispersers and how seed and rodent abundance were related to seed dispersal and seed survival via scatter-hoarding. We predicted the patterns of seed dispersal and survival to test the two hypotheses about mast seeding. Edward's long-tailed rat *Leopoldamys edwardsi* acted as the principal seed disperser of oil tea seeds because of scatter-hoarding, while other sympatric rodent species acted only as seed predators.

3. We first provided a reasonable method to estimate per capita seed availability based on annual seed abundance and annual metabolic rodent abundance (corrected for metabolic-scaling body mass of each rodent species). We found that annual seed abundance, annual metabolic rodent abundance and per capita seed availability all had some significant effects on different estimators of seed fates (including dispersal distances) across each stage from seedfall to seedling establishment. Both annual seed abundance and per capita seed availability were positively correlated with pre-dispersal seed survival, but negatively correlated with scatter-hoarding (and recaching), seed survival after dispersal and dispersal distances. However, annual metabolic rodent abundance had a positive effect on scatter-hoarding, but had a negative effect on the time to cache recovery.

4. *Synthesis.* Since greater seed production was associated with improvement in pre-dispersal survival of oil tea seeds but a reduction in dispersal (including secondary dispersal and dispersal distance), our long-term study indicates that, compared with the predator dispersal hypothesis, the predator satiation hypothesis provides a better mechanism predicting seed dispersal and seed survival in animal-dispersed plants by integrating seed abundance and animal abundance.

Key-words: abundance, dispersal/survival trade-off, Edward's long-tailed rat *Leopoldamys edwardsi*, mast seeding, predator satiation, scatter-hoarding, seed dispersal

Introduction

Mast seeding, which occurs in many perennial plant species, is the intermittent production of large seed crops by a plant population (Kelly 1994). A number of hypotheses have been proposed to explain mast seeding (reviews in Kelly 1994;

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Kelly & Sork 2002). For many animal-dispersed species such as nut-bearing plants, the most widely supported hypothesis for mast seeding is the predator satiation hypothesis. This hypothesis predicts that mast seeding is an adaptation for enhancing pre-dispersal seed survival by reducing seed losses from seed predators because predators become satiated with increased productivity during mast years (Janzen 1971; Silvertown 1980; Ims 1990; Sork 1993; Kelly 1994; Kelly &

Sork 2002). However, for many species of nut-bearing plants, scatter-hoarding vertebrate granivores (mainly rodents and birds) are the only vectors of seed dispersal. Recently, some studies have examined a second hypothesis about mast seeding, the predator dispersal hypothesis (Vander Wall 2002; Jansen, Bongers & Hemerik 2004; Li & Zhang 2007). This hypothesis has two key predictions: large seed crops may enhance per capita seed dispersal rates or dispersal distances may be greater during mast years compared with those during non-mast years (Smith, Hamrick & Kramer 1990; Kelly & Sork 2002). Although these two hypotheses are not mutually exclusive, there is currently little evidence supporting the predator dispersal hypothesis (Kelly & Sork 2002; but see Vander Wall 2002). Rigorous testing of either hypothesis, however, is still limited by the lack of knowledge regarding how mast seeding interacts with seed predator and disperser abundance to determine patterns of seed dispersal and seedling establishment.

In general, seedling recruitment depends on how many seeds and seedlings survive at sites close to parent plants (i.e. survival of non-dispersed seeds) and away from parent plants (i.e. survival of dispersed seeds; Janzen 1970; Connell 1971). The primary factors affecting this process are annual seed production and seed demands by animal seed predators and seed dispersers. Thus, per capita seed availability (related to satiation levels of seed predators and seed dispersers) may not only be related to annual seed production, but also to annual abundance of seed predators and seed dispersers. Kelly & Sork (2002) suggest that when testing the predator satiation hypothesis, it is essential to quantify how seed predation, seed dispersal and seed survival are related to per capita seed availability, which is determined by annual seed production and annual abundance of seed predators and seed dispersers. To our knowledge, however, few studies have quantified how per capita seed availability varies and the effect that it has on seed fates (but see Klinger & Rejmánek 2009, 2010).

We tracked the fate of oil tea *Camellia oleifera* (Theaceae) seeds during 2002–2009 in a subtropical evergreen broad-leaf forest in south-west China, and investigated seed dispersal and seed survival dynamics across each stage from seedfall to seedling establishment by integrating seed abundance and rodent abundance. In this study, we first provided a reasonable method to estimate per capita seed availability (PCSA) based on annual seed abundance and annual metabolic rodent abundance (corrected for metabolic-scaling body mass of each rodent species). Seed production of oil tea varies considerably in both cultivated and natural populations over time and space (Zhang 2008; Z. S. Xiao, pers. obs.). Based on previous studies, we found that oil tea seeds are predominantly dispersed by the scatter-hoarding rodent, Edward's long-tailed rat (*Leopoldamys edwardsi;* Fig. 1c), though this rodent also consumed and killed oil tea seeds as did other rodent species that acted only as seed predators (Xiao, Zhang & Wang 2003; Chang & Zhang 2011). Then, we tested the following two key predictions: (i) pre-dispersal seed survival should be increased with increasing seed availability if the predator satiation hypothesis holds, and (ii) seed dispersal rates or

Fig. 1. Oil tea *Camellia oleifera* and its key seed disperser. (a) oil tea flowers; (b) oil tea fruits; (c) key seed disperser, scatter-hoarding Edward's long-tailed rat (*Leopoldamys edwardsi*); and (d) seedlings established from rodent-made caches.

dispersal distances via scatter-hoarding should be increased with increasing seed availability if the predator dispersal hypothesis holds. Finally, we discuss the evolution of mast seeding in predator-dispersed plants based on both the predator satiation hypothesis and the predator dispersal hypothesis.

Materials and methods

STUDY SITE AND SPECIES

Field work was carried out in the Banruosi Experimental Forest (700–1000 m, 31°4′ N,103°43′ E) in Dujiangyan City of Sichuan Province, south-west China. Climatically, 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. The weather is often cloudy and foggy, with 800–1000 mean annual hours of sunshine and mean annual relative humidity $\geq$ 80%. Vegetation at the study site is subtropical evergreen broad-leaf forest and common tree species include *Castanopsis fargesii, Quercus variabilis, Q. serrata, Lithocarpus harlandii, Cyclobalanopsis glauca, Pinus massoniana, Acer catalpifolium, Phoebe zhennan* and *Camellia oleifera.* The forest at the study site is a mosaic of isolated and fragmented small stands (0.5–15 ha) caused by agricultural development with the result that populations of many otherwise common tree species are rare or locally extinct.

Oil tea (*C. oleifera*) is a small broad-leaved, evergreen tree that is widespread in many subtropical forests of south and south-west China. It is also cultivated commercially in large areas across southern China for the cooking oil that is extracted from its seeds (Zhang 2008). Oil tea seeds have a high fat content (> 50%). In addition, oil tea seeds contain low tannins (0.24%), but high levels of saponins (ca. 8.56%; Xiao, Zhang & Wang 2003; Zhang 2008). Oil tea was once common in the subtropical broad-leaved evergreen forests (altitude 700–1500 m) at the study site, but populations now exist mainly in some old-growth (here *Camellia*-rich) stands (5–10 ha) and secondary stands (1–8 ha) (Z. S. Xiao, pers. obs.). Oil tea is pollinated

by insects such as bees, butterflies and flies, and its flowering period coincides with its fruit-ripening period, that is, from September to December (Fig. 1a). After ripening, oil tea fruits typically dehisce on the tree and the seeds inside the fruits fall to the ground under or close to parent plants (Fig. 1b), although intact fruits also sometimes fall to the ground. Oil tea fruits are capsules, and each fruit contains 1 and 10 seeds (seed weight, mean $\pm$ SD, 0.9 $\pm$ 0.3 g, $n = 40$). Seed crops of oil tea vary considerably among years within natural populations.

At the study site, there are at least 10 sympatric rodent species: Edward's long-tailed rats (*L. edwardsi*), chestnut rats (*Niviventer fulvescens*), Chinese white-bellied rats (*N. confucianus*), Sichuan field mice (*Apodemus latronum*), Chevrier's field mice (*A. chevrieri*), South China field mice (*A. draco*), striped field mice (*A. agrarius*), Norway rats (*Rattus norvegicus*), Himalayan rats (*R. nitidus*) and harvest mice (*Micromys minutus*) (Xiao *et al.* 2002; Z. S. Xiao, unpubl. data). No diurnal rodents were found at the study site. In our previous research, we have tested the differences in hoarding of oil tea seeds among seven of the most common rodent species (see Chang & Zhang 2011; Z. S. Xiao, unpubl. data): *L. edwardsi*, *N. fulvescens*, *N. confucianus*, *A. latronum*, *A. chevrieri*, *A. draco* and *R. nitidus*. We found that *L. edwardsi* scatter-hoarded far more oil tea seeds than any other rodent species. Very few individuals from the six other rodent species scatter-hoarded any seeds, although several individuals of the two *Niviventer* species did hoard some seeds in underground nests (Xiao, Zhang & Wang 2003; Zhang *et al.* 2008; Chang & Zhang 2011). Thus, rodent species at the study site can be divided into two main functional groups for oil tea seeds: *L. edwardsi* acts as the key seed disperser and the other rodent species function primarily as seed predators.

QUANTIFYING RODENT ABUNDANCE AND SEED AVAILABILITY

We measured oil tea seed crops by collecting all mature fruits from 60 fruiting plants in an isolated *Camellia*-rich stand (*c.* 8 ha; ca. 1000 individuals/ha with DBH > 2 cm in this stand, Z. S. Xiao, unpubl. data) from 2002 to 2009 during autumn when oil tea seeds are dispersed. In addition, other nut-bearing trees such as *C. fargesii*, *Q. variabilis*, *Q. serrata* and *L. harlandii* also occurred in this *Camellia*-rich stand, and they also produced variable seed crops each year, which were also consumed by rodents (Xiao, Zhang & Wang 2005; Z. S. Xiao, unpubl. data). Meanwhile, we estimated the relative abundance of rodent seed predators and seed dispersers using 20 or 40 live traps for three successive nights each year (September or October) in the same stand used to quantify oil tea seed production. The procedures quantifying annual seed production of oil tea and annual rodent abundance are presented in Appendix S1 in the Supporting Information. We conservatively estimated the population of rodent seed predators and seed dispersers using the minimum number alive (MNA) per 100 trap-nights (see similar analysis in Hoshizaki & Hulme 2002).

In this study, we estimated per capita seed availability (PCSA) based on the following two parameters, that is, annual seed production (estimated by average crop size per plant each year, ACS) and annual metabolic rodent abundance (the sum of metabolic-scaling body mass from each rodent species each year, AMRA). Since more than one rodent species predate on seeds at the study site, and these rodent species vary greatly in body mass (from 26 g for *A. draco* to 281 g for *L. edwardsi*), our measure of PCSA took these variations into account by means of metabolic rates. Regardless of food habitats and foraging behaviour, food intake is proportional to body mass

($BM^{0.75}$) for many mammals (see Clauss *et al.* 2007, and references therein). Therefore, PCSA is a function of ACS and AMRA as follows:

$$PCSA = ACS/AMRA$$

where

$$AMRA = \sum_{i=1}^{k} N_i BM_i^{0.75}$$

k = the number of rodent species;

N_i = the population size (here MNA) of a given rodent species in a given year i;

$BM_i^{0.75}$ = the average metabolic-scaling body mass (based on our survey) of rodent species i.

QUANTIFYING YEAR-TO-YEAR SEED FATES

Each year (2002–2009), we randomly selected 400–800 sound oil tea seeds (800 seeds in 2002, 500 seeds in 2003 and 400 seeds in each of the rest other years; 3700 seeds in total) to track their fates from autumn to the following spring (late April) in the same stand used to quantify oil tea seed crops and rodent abundance. We labelled the seeds with a numbered tag attached by a thin stainless steel wire 10 cm long (cf. Xiao, Jansen & Zhang 2006b). This method involves piercing the seed, which damages the cotyledons and thus may reduce seed germination, but this damage is no more intense than that produced by the commonly used method of thread-marking (Xiao, Jansen & Zhang 2006b). Our seed-tagging method allowed us to follow the exact fate and spatial pattern of caches over time until the seeds germinate and emerge as seedlings (e.g. Xiao, Zhang & Wang 2004, 2005; Li & Zhang 2007; see Fig. 1d).

The tagged seeds were placed on the ground at 1 of 10 (2003–2009) or 20 (2002) seed stations in early or mid-October each year. Seed stations were located 10–15 m apart along a single transect in the stand, and each was one square metre located directly under or near an oil tea plant. We placed 40 (2002 and 2004–2009) or 50 (2003) seeds at each seed station. The fate of the tagged seeds was monitored weekly or biweekly during the first seven weeks after seed placement. During each visit, we searched the area around each seed station (radius: 25 m) to record the fate of each tagged seed. Seeds found at the source were categorized as remaining, eaten (seed fragments with dental marks found) or removed. Removed seeds were further categorized as cached (i.e. buried in the surface soil or covered with leaf litter), eaten or missing (not found). We recorded the tag number of each recovered seed and measured the distance to their seed station. Cache sites were marked using one numbered bamboo chopstick (10–15 × 1.5 cm). We rechecked the caches periodically in subsequent visits until all cached seeds were recovered by animals. If a marked cache was removed, the area around the cache was also searched. When a cached seed was excavated and subsequently found recached, we measured the distance to its previous cache and to its original seed station. In the following spring (late April), we also surveyed all seed stations and all previous cache sites to determine whether seeds survived or germinated.

DATA ANALYSIS

Based on the seed fate data, we calculated the following variables through different subsequent stages from source to establishment sites: (i) the proportion of non-dispersed and uneaten seeds at the source (i.e. pre-dispersal seed survival), (ii) the proportion of seeds

removed at each seed source by the following spring, (iii) the proportion of seeds cached after removal (primary caches), (iv) the proportion of seeds recached from the primary cache into a secondary cache and (v) the proportion of seeds finally surviving for all cached seeds from the primary and secondary caches the following spring (i.e. post-dispersal seed survival). Parameters (ii), (iii) and (iv) were considered as seed dispersal rates by scatter-hoarding because these parameters showed the proportion of seeds being moved from the source to other sites with the potential for seed germination or seedling establishment. The seed fate data were proportional data, thus we ran two kinds of generalized linear mixed models with a binomial error (Package lme4 in R) for the seed fate data: one model with ACS and AMRA as fixed factors and year as a random factor, and the other model with RSA as a fixed factor and year as a random factor. In the analysis, ACS, AMRA and PCRA were log10-transformed.

The time to removal from the source and that to recovery from primary caches by animals were censored at seven weeks after seed placement and at the end of the seed fate experiment the following spring, respectively. The Cox regression model was used to test the difference in seed survival at the source or at primary caches among years. Linear mixed models were used to test the effects of ACS + AMRA or PCRA (as fixed factors) with year as a random factor on the following variables (Package nlme in R): (i) mean time (weeks) to removal from the source each year, (ii) mean time (weeks) to recovery from primary caches each year and (iii) mean distance (m) for either primary caches or all surviving caches during the following spring. The time to removal from the source, the time to recovery from primary caches and all distances were log10-transformed to meet assumptions of the statistical models.

Linear mixed models and generalized linear mixed models were carried out in the R program (version 2.8.1, R Development Core Team 2008), and other statistical analyses were conducted using SPSS for windows (version 10.0, SPSS, Chicago, Illinois, USA).

Results

### RODENT ABUNDANCE AND SEED AVAILABILITY

The combined rap success for all rodent species also varied greatly among years: the highest (18.33%) in 2002 and the lowest (0.83%) in 2006. During the eight-year survey, MNA for Edward's long-tailed rat was much lower (except in 2006) than that for the other rodent species combined ($Z = 2.225$, $P = 0.026$, Mann–Whitney U-test): there were two peaks (2002 and 2007) for Edward's long-tailed rat, but three peaks (2002, 2005 and 2007) for the other rodents (Fig. 2a). Similar to trap success, AMRA showed large variation among years with three peaks (2002, 2005 and 2007; Fig. 2a).

The average crop size (ACS) per plant ($N = 60$) varied significantly across the 8 years ($X^2 = 114.4$, d.f. = 7, $P < 0.001$): the highest (180.5 ± 25.7 (SD) seeds per plant) was in 2007 and the lowest (27.4 ± 4.5 seeds per plant) in 2003 with a coefficient of variation of 125.8% for yearly seed production (95% confidence limits, 77.0–159.8%; Fig. 2b). The CV values of oil tea seed production are similar to those from other predator-dispersed plants (mean 167%, Kelly & Sork 2002). PCSA was much higher in the two years of the highest seed production (2007 and 2008) and lower in most other years (i.e. 2002–2005), but the years 2006 and 2009

were an exception with higher PCSA values, which were as high as or even higher than those in the high seeds years due to lower AMRA but higher ACS (Fig. 2b; Table S1).

SEED SURVIVAL AND SEED DISPERSAL

During the first seven weeks after seed placement, seed removal rate varied greatly among years ($X^2 = 2671.6$, d.f. = 7, $P \ll 0.001$; Figs 3a and S1). The time to seed removal from the source (censored at seven weeks) was positively related to either ACS ($t = 4.771$, $P = 0.005$, Fig. S3) or PCRA ($t = 3.606$, $P = 0.011$, Figs S2 and S3), but was marginally negatively related to AMRA ($t = 2.409$, $P = 0.061$; Table S2). Each year, most (62–96%) of the seeds were removed from the source with the rest eaten *in situ*, but some seeds (0–22%) still remained at the source (Fig. 3c). The proportion of seeds finally removed from the source in the following spring did not correlate with ACS ($z = 1.647$, $P = 0.100$), AMRA ($z = 0.137$, $P = 0.891$) or PCRA ($z = 0.927$, $P = 0.354$; Table 1). In addition, the proportion of seeds surviving at the source during the following spring was positively correlated with either ACS ($z = 2.763$, $P = 0.006$) or PCRA ($z = 2.109$, $P = 0.035$; Figs 4c,d), but
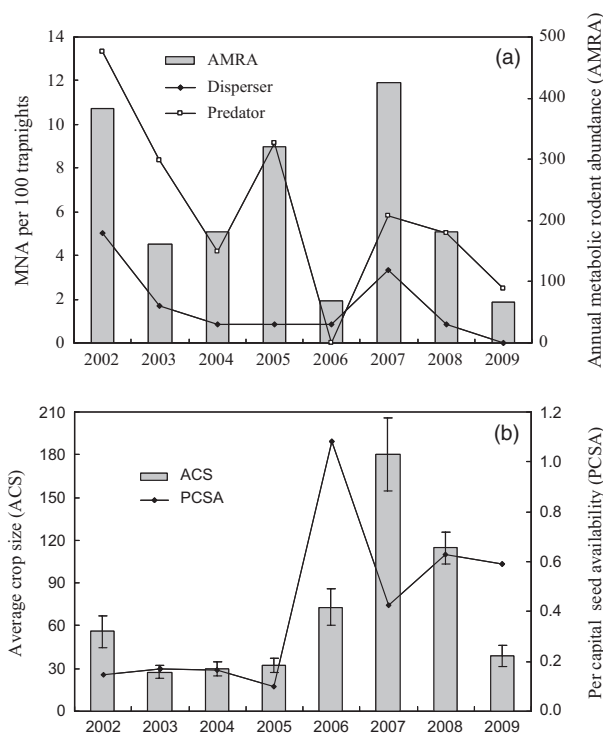
Fig. 2. Annual changes in rodent abundance and oil tea seed crops. (a) annual metabolic rodent abundance (AMRA, the sum of metabolic-scaling body mass from each rodent species each year), and minimum number alive (MNA) per 100 trap-nights for seed dispersers (*Leopoldamys edwardsi*) and seed predators (other rodent species); and (b) oil tea seed crops: ACS, average crop size per plant, mean ± SD; and PCSA, per capita seed availability, ACS divided by AMRA.

marginally negatively correlated with AMRA ($z = 1.839$, $P = 0.066$; Table 1).

We located most (62.9–93.6%) of the seeds removed by rodents each year, but the relocation rate was significantly different among the eight years ($X^2 = 57.10$, d.f. = 7, $P < 0.001$, Pearson's chi-squared test). The specific fates of 2000 removed seeds (78.6%) were determined. Some of the seeds removed were cached at primary caches (5.4–62.2% per year), and some of the seeds at primary caches (0–16.1%, $n = 64$ in total) were then moved and recached at secondary caches (Fig. 3b). Most (50–96% per year) of primary caches contained only 1 seed, 97% of secondary caches (only three of which contained two seeds) and all tertiary caches contained only one seed.

The proportion of seeds hoarded at primary caches each year was negatively correlated with both ACS ($z = 3.643$, $P = 0.0003$) and PCRA ($z = 3.215$, $P = 0.001$), but positively with AMRA ($z = 2.057$, $P = 0.040$; Table 1). The proportion
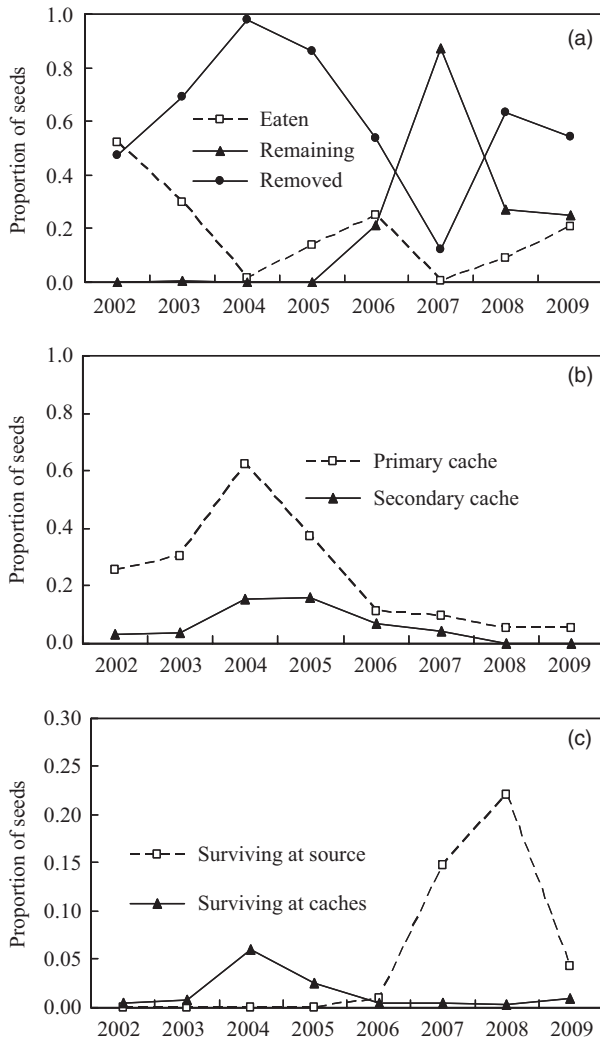
Fig. 3. Annual changes in seed fates across different dispersal stages: (a) fate (eaten, remaining, removed) at the source after 7-week placement; (b) fate after removal from source, including primary caches and secondary caches; (C) final fate (the following spring), including seeds surviving at the source and at caches.

of seeds hoarded into secondary caches showed a similar pattern, being negatively correlated with ACS ($z = 2.582$, $P = 0.010$) and PCRA ($z = 2.427$, $P = 0.015$), but not with AMRA ($z = 1.377$, $P = 0.168$; Figs 3b and 4a,b; Table 1). The time to recovery for primary caches varied significantly among years ($X^2 = 56.862$, d.f. = 7, $P < 0.001$; Fig. S2A). The mean time to recovery for primary caches was significantly correlated with ACS ($t = 2.635$, $P = 0.056$, Fig. S3C), AMRA ($t = 2.892$, $P = 0.045$) and their interactions ($t = 2.939$, $P = 0.042$; Table S2). However, the time to recovery for primary caches was not correlated with PCRA ($t = 0.950$, $P = 0.379$; Fig. S3D; Table S2).

During the next spring, a small part of the cached seeds (0.25–6.0% per year) survived and established as seedlings especially when PCRA was low (e.g. 2002–2005; Fig. 3c), but for all the surviving seeds at caches, most of them were from primary caches and only a few seeds were from secondary caches (2004, $n = 3$; 2005, $n = 1$) and tertiary caches (2005, $n = 1$). The proportion of seeds surviving at caches until the following spring was negatively correlated with ACS ($z = 2.546$, $P = 0.011$), but not with PCRA ($z = 1.835$, $P = 0.067$) or AMRA ($z = 0.668$, $P = 0.504$; Fig. 4c,d and Table 1).

SEED DISPERSAL DISTANCES

Dispersal distances for primary caches were negatively correlated with PCRA ($t = 2.695$, $P = 0.036$), but not with ACS ($t = 1.873$, $P = 0.120$) or AMRA ($t = 2.014$, $P = 0.100$; Figs 5 and 6a,b; Table 2). Dispersal distances for caches surviving until the following spring were not correlated with either ACS ($t = 0.954$, $P = 0.384$), AMRA ($t = 1.368$, $P = 0.230$) or PCRA ($t = 1.604$, $P = 0.160$; Fig. 5; Table 2).

Discussion

THE PREDATOR SATIATION HYPOTHESIS AND THE PREDATOR DISPERSAL HYPOTHESIS

Our results showed that annual seed abundance, annual metabolic rodent abundance and per capita seed availability all had some significant effects on different estimators of seed fates (including dispersal distances) across each stage from seedfall to seedling establishment. Both annual seed abundance and per capita seed availability were positively correlated with pre-dispersal seed survival (including the time to seed removal after placement during the first seven weeks), but negatively correlated with scatter-hoarding (and recaching), final survival of dispersed seeds at caching sites (including the time to cache recovery after scatter-hoarding) and dispersal distances. However, seed removal rate was not related to any of the above three abundance parameters. This indicates that seed removal rate alone is not a reliable predictor of seed dispersal. In addition, annual metabolic rodent abundance had a positive effect on scatter-hoarding but had a negative effect on the time to cache recovery. Therefore, our results provide strong support for the predator satiation hypothesis, but not for the predator dispersal hypothesis,

Table 1. Statistical results from generalized linear mixed models for seed fate data: one model with average crop size (ACS) and annual metabolic rodent abundance (AMRA) and year as a random factor (*Model A*), and the other model with per capita seed availability (PCSA) as a fixed factor and year as a random factor (*Model B*) (see details in text). Fixed factors in bold indicate significant differences ($P < 0.05$)

| Fixed factors	Proportion of seeds removed		Proportion of seeds hoarded at primary caches		Proportion of seeds hoarded at secondary caches		Proportion of seeds surviving at seed source		Proportion of seeds surviving at caches	
	Estimate ± SD	z (P)	Estimate ± SD	z (P)	Estimate ± SD	z (P)	Estimate ± SD	z (P)	Estimate ± SD	z (P)
Model A										
Intercept	4.318 ± 2.987	1.446 (0.148)	−0.152 ± 2.332	−0.065 (0.948)	−2.089 ± 4.77	−0.438 (0.661)	−13.554 ± 6.233	−2.175 (0.030)	−0.995 ± 2.886	−0.345 (0.730)
ACS	−2.030 ± 1.233	−1.647 (0.100)	**−3.466 ± 0.951**	**−3.643 (0.0003)**	**−4.973 ± 1.926**	**−2.582 (0.010)**	**12.389 ± 4.484**	**2.763 (0.006)**	**−3.076 ± 1.208**	**−2.546 (0.011)**
AMRA	0.162 ± 1.180	0.137 (0.891)	**1.887 ± 0.917**	**2.057 (0.040)**	2.425 ± 1.761	1.377 (0.168)	−6.301 ± 3.426	−1.839 (0.066)	0.713 ± 1.067	0.668 (0.504)
Model B										
Intercept	0.606 ± 0.654	0.927 (0.354)	**−3.282 ± 0.519**	**−6.328 (<0.001)**	**−7.187 ± 1.073**	**−6.700 (<0.001)**	−1.352 ± 1.763	−0.767 (0.443)	**−5.632 ± 0.659**	**−8.547 (<0.001)**
PCSA	−1.045 ± 1.046	−0.999 (0.318)	**−2.625 ± 0.816**	**−3.215 (0.001)**	**−3.684 ± 1.518**	**−2.427 (0.015)**	**9.999 ± 4.740**	**2.109 (0.035)**	−1.779 ± 0.969	−1.835 (0.067)

because of reduced seed dispersal (including secondary dispersal and dispersal distances) but improved pre-dispersal seed survival with increasing seed production.

A predator satiation strategy may be favoured in forests where one dominant species or group of related species predominate, since mast seeding is very common in such communities (Kelly & Sork 2002). Therefore, high survival of non-dispersed seeds during mast years may be a factor contributing to tree dominance in many natural forests where a small number of tree species have extremely high densities (Janzen 1976). Boucher (1981) showed that survival of *Quercus oleoides* acorns was high in the forest with high *Q. oleoides* density due to the satiation of mammal seed predators and acorn survival substantially increased when mammal populations were reduced. Seeds of dominant mangrove species suffered lower predation in monoculture stands than in mixed species stands in Australia (Smith 1987). Hart (1995) found similar results with higher survival of *Gilbertiodendron dewevrei* seeds in a single-dominant forest compared with survival in a mixed forest in Africa. In tropical Asia, reproductive synchrony among sympatric Dipterocarpaceae species increased seed escape from vertebrate predation and subsequently seedling establishment (Curran & Leighton 2000; Curran & Webb 2000). Our long-term study here shows that the survival of non-dispersed seeds of oil tea was higher in most of the years with high relative seed availability (2006–2009), but no seeds survived at the source in other years (2002–2005) with lower relative seed availability as well as in other stands without oil tea trees (Xiao, Zhang & Wang 2004).

However, other similar studies provide some evidence for the predator dispersal hypothesis. It had been shown that scatter-hoarding was enhanced and dispersal distances were greater during mast years compared with those during non-mast years (e.g. *Pinus* species, Vander Wall 2002; *Prunus armeniaca*, Li & Zhang 2007). After scatter-hoarding, seed survival and subsequent establishment were also higher in mast years, for example *Pinus* species (Vander Wall 2002) and *Carapa procera* (Jansen, Bongers & Hemerik 2004). None of these studies presented data on both seed abundance and rodent abundance to measure per capita seed availability for both seed predators and seed dispersers. If per capita seed availability experienced by rodent seed predators and seed dispersers in these studies is similar to that observed in our study, their results may be consistent with the predator satiation hypothesis, rather than the predator dispersal hypothesis.

THE EVOLUTION OF MAST SEEDING IN PREDATOR-DISPERSED PLANTS

Kelly & Sork (2002) suggest that seed dispersal by scatter-hoarders may be 'unaffected or worsened' by mast seeding. If mast seeding reduces seed dispersal but increases escape from pre-dispersal predation, there may be a trade-off between seed dispersal and seed survival to explain the evolution of masting behaviour in predator-dispersed plants (Kelly & Sork 2002). As Moore & Swihart (2007) suggested, the net benefits from mast seeding may depend on both the total per
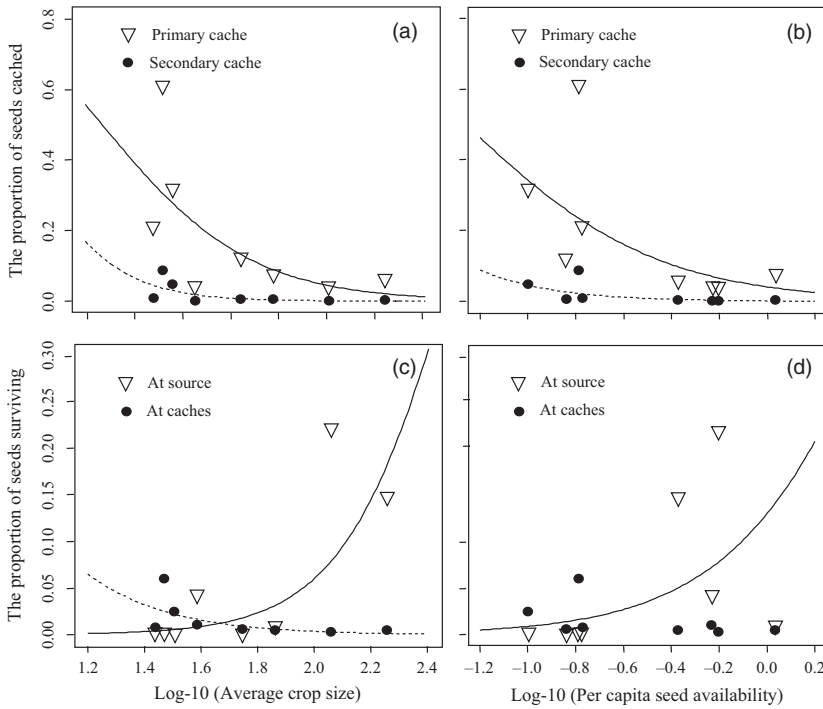
Fig. 4. Relationships between annual crop size (average crop size per plant, log-transformed, Panels a and c) or per capita seed availability (annual crop size divided by the sum of metabolic-scaling body mass from each rodent species each year, log-transformed, Panels b and d) and seed fates. The proportions of seeds hoarded at primary caches are indicated by the solid line (logistic regression line) and those at secondary caches are indicated by the dashed line (logistic regression) (Panels a and b). The proportions of seeds surviving at sources are shown by the solid line (logistic regression) and at caches by the dashed line (logistic regression) (Panels c and d).
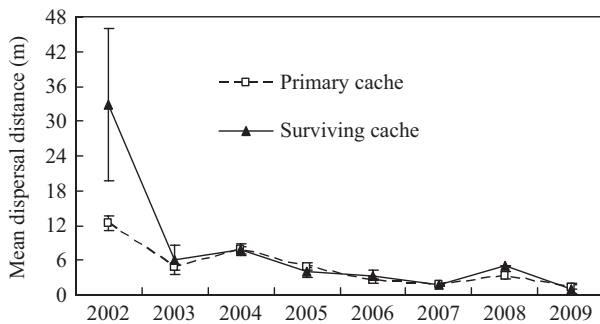

Fig. 5. Annual changes of the mean dispersal distance (m) of primary caches and surviving caches (the following spring).

Table 2. Statistical results from linear mixed models for dispersal distance of primary caches and the seeds surviving in caches: one model with average crop size (ACS) and annual metabolic rodent abundance (AMRA) and year as a random factor, and the other model with per capita seed availability (PCSA) as a fixed factor and year as a random factor (see details in text). Fixed factors in bold indicate significant differences ($P < 0.05$)

Fixed factors	Estimate $\pm$ SD	d.f.	t	P
Dispersal distance of primary caches				
Intercept	0.192 ± 0.829	5	0.232	0.826
ACS	-0.638 ± 0.341	5	-1.873	0.120
AMRA	0.661 ± 0.328	5	2.014	0.100
Intercept	0.240 ± 0.151	6	1.593	0.162
PCSA	$\mathbf{-0.647 \pm 0.240}$	**6**	$\mathbf{-2.695}$	**0.036**
Dispersal distance of the seeds surviving in caches				
Intercept	-0.098 ± 1.398	5	-0.070	0.947
ACS	-0.548 ± 0.574	5	-0.954	0.384
AMRA	0.757 ± 0.553	5	1.368	0.230
Intercept	0.319 ± 0.256	6	1.245	0.259
PCSA	-0.655 ± 0.408	6	-1.604	0.160

capita proportion of seeds surviving and the per capita proportion of seeds dispersed at longer distances, which is counterbalanced by mast seeding. Our long-term data from oil tea further support this finding; the per capita proportion (up to 6%) of seeds surviving at caches was higher when seed availability was lower (2002–2005), whereas the per capita proportion (up to 22% in 2007) of seeds surviving at source was higher when seed availability was higher (2006–2009; Figs 4 and 6). If the dispersal/survival trade-off exists in predator-dispersed plants, non-dispersed seeds near parent plants should also have the potential to establish and recruit as adults (e.g. Boucher 1981; Moore & Swihart 2007; but see Forget, Munoz & Leigh 1994; Forget, Kitajima & Foster 1999; Jansen, Bongers & Hemerik 2004). By simulating burial by rodent seed dispersers, our data showed that unburied oil tea seeds had a relatively high probability (41%) of surviving to two years of age, though buried seeds had twice the survival rate (81%) as unburied seeds (Z. S. Xiao, unpubl. data).

Vander Wall (2010) argued that there are three key points distinguishing the predator dispersal hypothesis from the predator satiation hypothesis when explaining the evolution of mast seeding. These include whether scatter-hoarding seed dispersers are satiated or not during mast events, whether burial by the animals affects seed germination or seedling establishment, and whether burial by the animals reduces predation or cache pilferage by other seed predators. However, none of these three points is closely associated with enhanced seed dispersal or dispersal distances during high-seed years (mast years) as the predator dispersal hypothesis predicts (Smith, Hamrick & Kramer 1990; Kelly & Sork 2002). Moreover,
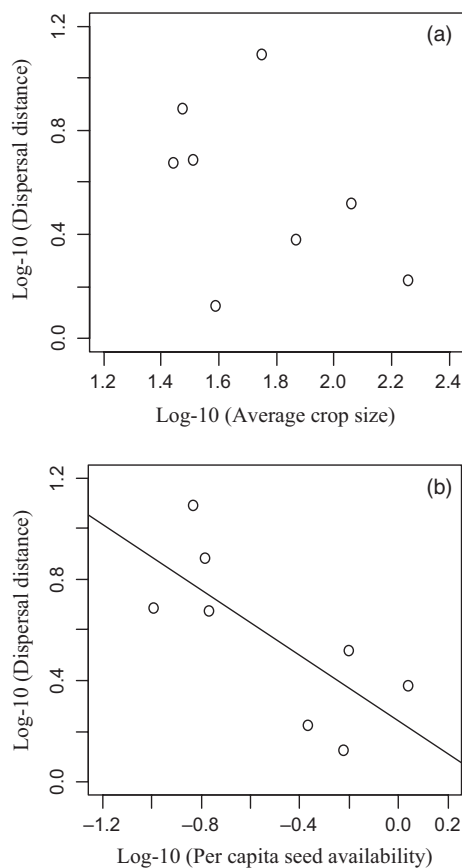
Fig. 6. Relationships between annual crop size (average crop size per plant, log-transformed, Panel a) or per capita seed availability (annual crop size divided by the sum of metabolic-scaling body mass from each rodent species each year, log-transformed, Panels b) and the mean dispersal distances (m, log-transformed) of primary caches.

our results do not provide evidence supporting Vander Wall's (2010) argument that 'the predator satiation hypothesis is not a complete explanation for masting in nut-bearing plants'. In fact, our findings challenge the predator dispersal hypothesis that the evolution of mast seeding is to improve seed dispersal (including dispersal distance) and subsequent seedling establishment. First, it is critical how we estimate per capita seed availability to test the predator dispersal hypothesis and the predator satiation hypothesis. In general, annual seed production may be positively related with per capita seed availability if animal populations remain stable over time and space, but rodent abundance can have a negative effect on per capita seed availability especially when rodents are very abundant considering the limited seed crops at a given time. Moreover, rodent abundance is also found to have a negative effect on pre-dispersal seed survival (DeMattia, Curran & Rathcke 2004) or post-dispersal seed survival (after hoarding, Sone & Kohno 1999). In this study, we found that annual metabolic rodent abundance was positively correlated with scatter-hoarding but negatively with the time to cache recovery. Thus, it is essential to measure both seed and rodent abundance at the same time. Secondly, we found that higher dispersal and subsequent survival of the hoarded seeds

(including longer dispersal distances) occurred during the years with lower seed availability (2002–2005), which is the reverse of the predictions made by the predator dispersal hypothesis. Thirdly, our study indicates that for oil tea and other animal-dispersed plants, there may be a trade-off between seed dispersal and seed survival, depending on per capita seed availability by seed predators and seed dispersers.

Conclusions

Our long-term study has demonstrated that, compared with the predator dispersal hypothesis, the predator satiation hypothesis provides a better mechanism for predicting seed dispersal and seed survival in animal-dispersed plants by integrating seed abundance and animal abundance. In addition to mast seeding, however, community-level seed abundance (i.e. seed crops from other plants) may have some impact on the population and behavioural responses of both seed predators and dispersers and subsequently on seed dispersal and survival dynamics in co-occurring plants (Hoshizaki & Hulme 2002; Xiao, Zhang & Wang 2005; Xiao *et al.* 2006a). Therefore, future studies are also needed to understand better how community-level seed abundance interacts with seed predators and seed dispersers to predict seed dispersal and seed survival in animal-dispersed plants. As first suggested by Kelly & Sork (2002), we further emphasize the importance of long-term studies that integrate annual seed production with population and behavioural responses of seed predators to predict their impacts on seed dispersal and seed survival through time and space, and thereby to further our understanding of the evolution of mast seeding in animal-dispersed plants.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Detailed methodology for annual census of both rodent and seed abundance.

Table S1. Statistical results comparing seed crop size per plant between all of the pairs of the 8 years of samples.

Table S2. Statistical results from linear mixed models for each dispersal parameter.

Figure S1. Survivorship curves for seeds remaining at the source after placement.

Figure S2. Annual changes of the mean time (weeks) to seed removal at source or seed recovery at primary caches.

Figure S3. Relationships between annual crop size or relative seed availability and the mean time to seed removal at source or the mean time to recovery for primary caches.