

# Using seed-tagging methods for assessing post-dispersal seed fate in rodent-dispersed trees

Zhishu Xiao<sup>a</sup>, Patrick A. Jansen<sup>b</sup>, Zhibin Zhang<sup>a,\*</sup>

<sup>a</sup>State Key Laboratory of Integrated Management of Pest Insects and Rodents in Agriculture, Institute of Zoology, Chinese Academy of Sciences, Beisihuanxilu 25, Haidian District, Beijing 100080, China

<sup>b</sup>Community and Conservation Ecology group, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands

Received 25 March 2005; received in revised form 21 October 2005; accepted 24 October 2005

## Abstract

Seed tagging is widely used for tracking seeds during dispersal by seed-caching animals. No studies, however, have fully examined the effects of seed tagging on post-dispersal seed fate. We studied how two seed tagging techniques – thread-marking and wire tin-tagging – affected seed fate by placing tagged and untagged seeds in simulated seed sources and caches and comparing removal rates and fates, and by comparing seedling establishment between tagged and untagged seeds. Tagging had little effect on whether seeds were eaten or dispersed, though both marking methods significantly delayed seed removal by rodents. Both marking methods proved effective for retrieving removed seeds and their fates, but because rodents bit off thread not wire, wire tin-tagging yielded a much higher recovery rate and more accurate estimation of seed fate. We found little difference in dispersal distance between the tagging methods. Piercing of the cotyledons negatively affected seedling emergence in one of two seed species tested. Wire tin tags are a suitable alternative for tracking seeds where seed-caching rodents tend to cut or detach thread marks and yield results comparable to thread-marking. However, both seed tagging methods may underestimate seed dispersal and survival due to delayed removal and damage of the cotyledons by piercing.

© 2005 Elsevier B.V. All rights reserved.

**Keywords:** Thread-marking; Wire tin-tagging; Seed-caching rodents; Seed dispersal; Seed fate

## 1. Introduction

Determining the ultimate fate of individual seeds is an important aspect of studies on seed dispersal by animals, required to fully understand the role of seed-dispersing animals in forest dynamics, the ecological and evolutionary consequences of seed dispersal, and the coevolutionary interactions between these animals and plants. However, following the movements and fates of dispersed seeds has proven a major obstacle (Levey and Sargent, 2000; Wang and Smith, 2002). A wide range of marking techniques have been developed for tracking seeds, especially those dispersed by seed-caching rodents (reviewed by Forget and Wenny, 2005).

Which seed-marking method is used varies greatly among continents or vegetation types (Forget and Wenny, 2005). Radioisotope methods, in which seeds are given radioactive

particles on their surface and are relocated after dispersal using a Geiger counter, are the most-used method in Europe (e.g. Jensen, 1985; Jensen and Nielsen, 1986) and Northern America (e.g. Lawrence and Rediske, 1959, 1962; Abbott, 1961; Abbott and Quink, 1970; Vander Wall, 1992, 1993, 1994; Vander Wall and Joyner, 1998). Thread-marking methods, in which a piece of thread or wire (sometimes with flagging tape or a tag at the end) is attached to the seeds, allowing retrieval of cached seeds by marks protruding from the soil, are used in the majority of studies in Southern America (e.g. Hallwachs, 1986; Forget, 1990, 1991, 1992; Forget and Milleron, 1991; Wenny, 1999, 2000a, 2000b; Brewer and Rejmánek, 1999; Brewer, 2001; Jansen et al., 2002, 2004; Chauvet et al., 2004), Australia (e.g. Theimer, 2001, 2003; Dennis, 2003), and Asia (e.g. Yasuda et al., 1991, 2000; Wang and Ma, 1999; Zhang and Wang, 2001; Hoshizaki and Hulme, 2002; Li and Zhang, 2003; Xiao et al., 2004a, 2004b, 2005). The methodological bias complicates the comparison of results across the world because the differential effects of seed-marking techniques on seed handling by animals are largely unknown.

\* Corresponding author. Tel.: +86 10 62556418; fax: +86 10 62565689.  
E-mail address: [zhangzb@ioz.ac.cn](mailto:zhangzb@ioz.ac.cn) (Z. Zhang).

Radioisotopes are not apparent to man or animals, and isotope-labeling is therefore believed to not affect the removal and further handling of seeds by animals (Forget and Wenny, 2005). However, radioisotope methods are relatively expensive because they require specific detection equipment (Xiao and Zhang, 2003; Forget and Wenny, 2005). Moreover, radioisotopes are heavily regulated, and some countries prohibit use in the field for environmental reasons (e.g. Iida, 1996; Sone and Kohno, 1996). Thread-marking methods, in contrast, are cheap, simple, and versatile (Xiao and Zhang, 2003; Forget and Wenny, 2005). No study, however, has fully examined how the often-conspicuous thread marks affect seed removal and seed handling by animals, and how passage of thread through the seed affects seed survival and germination (but see Wenny, 2000b). Most thread-marking studies assume that the marking has little or negligible effect on seed fate or animal behavior (Forget and Wenny, 2005, but see Wenny, 2000b). A second problem is that thread marks are often bitten off by rodents, which seems to preclude the use of thread-marking where animals frequently cut or detach thread marks, e.g. the northern temperate zone.

We studied the effects of tags on seed handling by rodents and on germination for two seed-tagging methods: thread-marking, the most used technique, and wire tin-tagging, a relatively new method in which a tin tag is attached to the seed with a short metal wire that rodents cannot easily cut (Zhang and Wang, 2001; Li and Zhang, 2003; Xiao et al., 2004a, 2004b, 2005; Zhang et al., 2005). Wire tin-tagging may be suitable for use in both the northern temperate zone and the rest of the world, which would facilitate comparison, but has not yet been tested against other methods.

## 2. Materials and methods

Fieldwork was conducted in the Banruosi Experimental Forest (elevation 700–1000 m, 31°4' N, 103°43' E) in Dujiangyan City, Sichuan Province, Southwest 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 range 800–1000 and a mean annual relative humidity of more than 80%. Common tree species include *Castanopsis fargesii*, *Quercus variabilis*, *Q. serrata*, *Pinus massoniana*, *Acer catalpifolium*, *Lithocarpus harlandii*, *Phoebe zhenman*, *Cyclobalanopsis glauca*, and *Camellia oleifera*.

Experiments were carried out with seeds of *C. oleifera* and *Q. variabilis*. Both species produce large seeds (mean seed mass, 0.9 and 2.42 g, respectively) in September–November and are dispersed by seed-caching rodents, especially Edward's long-tailed rat (*Leopoldamys edwardsi*) (Xiao, 2003; Xiao et al., 2003, 2004b; Zhang et al., 2005). Fresh seeds were collected from the ground or from parent plants. Three hundred fresh, sound seeds were randomly selected for each seed species, and assigned to one of the following three treatments: (1) thread-marking, 100 cm of white fishing thread (diameter, 0.3 mm) with a numbered white plastic tag (5 × 2 cm) at the end (cf. Jansen et al., 2002, 2004); (2) wire tin-tagging, 10 cm

of thin stainless-steel wire (diameter, 0.2 mm) with a coded tin tag (4 × 1 cm; cut from soda cans) at the end (cf. Xiao et al., 2004a, 2004b, 2005); and (3) control, seeds unlabelled. Both wire and thread were attached to seeds by drilling a 0.5-mm diameter hole through the cotyledons.

For each species, we established 10 artificial seed sources (ca. 1 m<sup>2</sup>) with 10–15 m interspacing along a transect on 5 October 2004. At each seed station, we placed 10 seeds for each treatment. We then monitored seed removal, first daily, 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. Seeds at seed stations were categorized as remaining, eaten, removed, or mark cut (only for marked seeds), while removed seeds were categorized as cached (i.e. buried in the surface soil or covered with leaf litter), eaten (marks and seed fragments found), mark cut (cut off marks found, seed fate unknown), or missing (not retrieved). 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). At 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 randomly searched. When a cached seed was excavated and subsequently found recached, we measured the distance to its original seed source as well as its previous cache.

To estimate how seed tags and the marking of caches themselves affected cache survival, we set up three transects, each with 50 artificial caches containing a single *C. oleifera* seed in the autumn (from mid-October to early December) of 2003. We applied three treatments: (1) seed wire tin-tagged and cache marked with a bamboo stick (15 × 1.5 cm) placed at 10 cm distance; (2) seed tin-tagged but cache unmarked; and (3) seed and cache both unmarked ( $n = 50$ ). All seeds were buried 1–3 cm deep in the soil to mimic caching by rodents, with 1-m interspacing between seeds.

Seeds were pierced for attaching tags by drilling a 0.5-mm diameter hole through the cotyledons. We studied to what extent this influenced seed germination or seedling emergence by planting 50 wire tin-tagged seeds and 50 unmarked seeds for both *C. oleifera* and *Q. variabilis* in sand at 1–3 cm depth in November 2003, and recording how many had emerged after 8 months.

Cox regression was used to compare the time to removal from seed stations and from caches between seed-marking treatments. A Wilcoxon test was used to test for differences in the proportion of seeds removed from seed stations. Student's *t*-test was used to test for differences in dispersal distance. Chi-square tests were used for all other comparisons.

## 3. Results

### 3.1. Seed removal

Seed removal rates differed significantly among the three seed-tagging treatments, both for *C. oleifera* (Wald = 49.872,

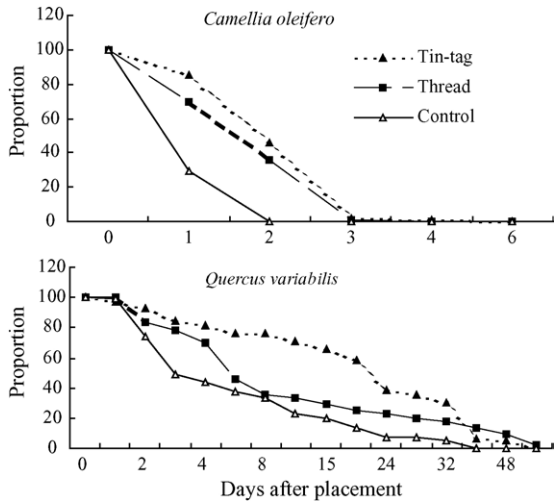


Fig. 1. Removal of *Camellia oleifera* and *Q. variabilis* seeds from seed stations for three seed-tagging treatments: thread-marking (thread), wire tin-tagging (wire), and unlabelled (control).

d.f. = 2,  $P < 0.001$ ) and *Q. variabilis* (Wald = 32.633, d.f. = 2,  $P < 0.001$ ). Unmarked seeds were removed faster than marked seeds, and thread-marked seeds were in turn removed faster than tin-tagged seeds (Fig. 1). Despite these differences, all seeds had been harvested from the seed stations after several days for *C. oleifera* or after about 2 months for *Q. variabilis* (except for two thread-marked seeds). Besides the eaten seeds at seed stations, many thread-marked seeds had the thread bitten-off before seed removal (34 and 69%, for *Camellia* and *Quercus*, respectively), while all tin-tagged seeds had been removed with their tag intact.

3.2. Recovery rate

Not counting the seeds that lost their tag, the proportion of seeds that we retrieved upon removal from seed stations was

significantly higher for thread-marked than for tin-tagged seeds in *Q. variabilis* (76% versus 54%;  $\chi^2 = 3.9$ , d.f. = 1,  $P = 0.047$ ) but not in *C. oleifera* (92% versus 86%;  $\chi^2 = 1.7$ , d.f. = 1,  $P = 0.196$ ). We found the thread marks easier to retrieve than the wire tin tags, probably because the plastic tags were more conspicuous than the tin tags. The proportion of seeds that we retrieved upon excavation from the caches, however, was significantly higher for wire-tagged seeds than for thread-marked ones, in both *C. oleifera* (51% versus 30%, respectively,  $\chi^2 = 4.3$ , d.f. = 1,  $P = 0.038$ ) and *Q. variabilis* (38% versus 7%, respectively,  $\chi^2 = 4.9$ , d.f. = 1,  $P = 0.027$ ). Moreover, the proportion recovered was significantly higher after seed removal from seed stations than from caches for both species and marking methods except for tin tags in *Q. variabilis*. If we include the seeds that lost their tag, the proportion retrieved was two or more times higher for wire tin-tagged seeds (70 and 48%) than for thread-marked seeds (38 and 16%) (Fig. 2).

3.3. Post-dispersal seed fate

In both *C. oleifera* and *Q. variabilis*, rodents cached and recached the marked seeds up to three times. The proportions found that cached and recached were greater for wire tin-tagged seeds than for thread-marked seeds (Fig. 2). The two methods differed significantly in recorded seed fate, both after removal from seed stations ( $\chi^2 = 15.1$ , d.f. = 2,  $P = 0.001$ ) and upon recovery from caches ( $\chi^2 = 8.9$ , d.f. = 2,  $P = 0.012$ ) in *C. oleifera*, and upon recovery from caches in *Q. variabilis* ( $\chi^2 = 7.186$ , d.f. = 2,  $P = 0.028$ ) (Fig. 2).

3.4. Post-dispersal survival

After 2 months, the proportion of seeds still present in known caches was much higher for wire tin-tagged seeds (16%) than for thread-marked seeds (2%). The difference was due to the high proportion (>80%) of the thread-marked seeds that

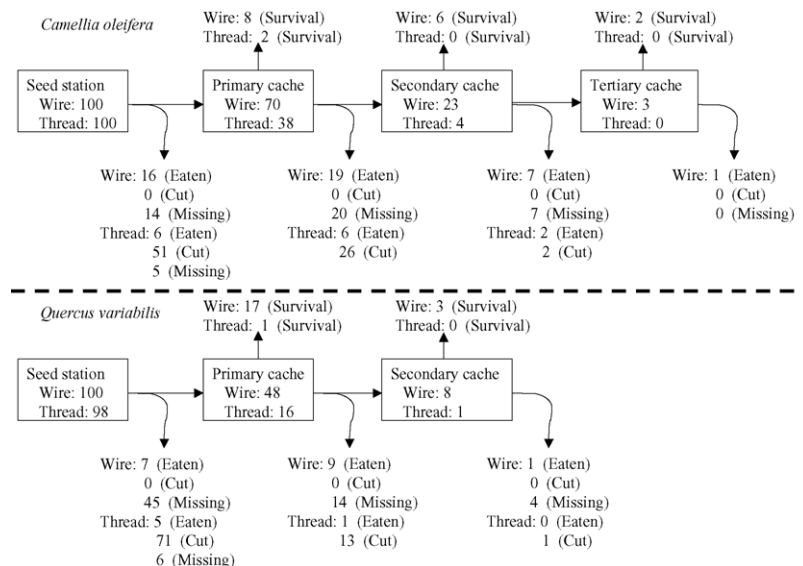


Fig. 2. Fate pathways of *Camellia oleifera* and *Q. variabilis* seeds placed at experimental seed stations, for two seed tagging methods: thread-marking (thread) and wire tin-tagging (wire). Two thread-marked *Q. variabilis* seeds, remaining at one seed station, are not included in this figure.

Table 1  
Dispersal distances for thread-marked and wire tin-tagged seeds

Fate category	Treatment	<i>C. oleifera</i>			<i>Q. variabilis</i>		
		Mean $\pm$ S.D.	Maximum	<i>n</i>	Mean $\pm$ S.D.	Maximum	<i>n</i>
After removal							
Cached	Thread-marked	4.2 $\pm$ 6.8	28.5	38	4.7 $\pm$ 3.5	15.5	16
	Wire tin-tagged	7.6 $\pm$ 10.5	45.2	70	5.6 $\pm$ 9.5	42.5	48
Eaten	Thread-marked	26.0 $\pm$ 18.2	52.3	6	2.8	2.8	1
	Wire tin-tagged	7.5 $\pm$ 5.5	19.7	15	4.5 $\pm$ 3.0	9.5	5
Cut	Thread-marked	8.8 $\pm$ 8.0	28.4	17	5.6 $\pm$ 4.4	8.7	2
	Wire tin-tagged	–	–	–	–	–	–
After excavation from caches							
Recached	Thread-marked	26.6 $\pm$ 14.6	48.5	4	4.2	4.2	1
	Wire tin-tagged	10.0 $\pm$ 9.5	39.5	23	13.3 $\pm$ 13.2	40.7	8
Eaten	Thread-marked	14.6 $\pm$ 9.9	24.5	3	–	–	–
	Wire tin-tagged	10.6 $\pm$ 4.3	17.8	5	6.3 $\pm$ 2.2	7.8	2
Cut	Thread-marked	21.7 $\pm$ 23.8	38.5	2	–	–	–
	Wire tin-tagged	–	–	–	–	–	–

Values are mean distances (*m*) to the source for seeds or tags retrieved after removal from seed stations and for seed or tags retrieved after excavation from caches.

lost their thread marks (Fig. 2). The ultimate seed fate recorded differed between treatments (thread,  $22.34 \pm 22.24$  d; wire,  $32.17 \pm 21.77$  d) significantly in *C. oleifera* ( $\chi^2 = 20.0$ , d.f. = 2,  $P < 0.001$ ) and marginally significantly in *Q. variabilis* (thread,  $21.44 \pm 18.59$  d; wire,  $36.17 \pm 15.69$  d;  $\chi^2 = 5.5$ , d.f. = 2,  $P = 0.063$ ) (Fig. 2). The lifetime of caches (including all secondary and tertiary caches) was independent of the marking method in both *C. oleifera* (Wald = 1.2, d.f. = 1,  $P = 0.266$ ) and *Q. variabilis* (Wald = 0.9, d.f. = 1,  $P = 0.333$ ).

### 3.5. Dispersal distance

Greater initial cache distances were recorded for tin-tagged seeds than for thread-marked seeds in *C. oleifera* ( $t = 3.47$ , d.f. = 106,  $P = 0.001$ ), but not in *Q. variabilis* ( $t = -0.62$ , d.f. = 62,  $P = 0.539$ ; Table 1). Secondary dispersal of seeds excavated from caches further increased dispersal distance: the maximum dispersal distance found was greater for wire tin-tagged seeds than for thread-marked seeds (*C. oleifera*, 45.2 m versus 28.2 m, respectively; *Q. variabilis*, 42.5 m versus 15.5 m, respectively, Table 1). The numbers of secondary caches that we found were too small to test for differences in secondary dispersal distance (Table 1).

### 3.6. Cache survival

The proportion of seeds recovered from artificial caches did not differ ( $\chi^2 = 2.024$ , d.f. = 2,  $P = 0.363$ ) among the three treatments (10, 14, and 20%, respectively). This suggests that tin tags and bamboo sticks had no effect on cache survival.

### 3.7. Germination

Seedling emergence at 8 months after sowing was significantly less frequent among marked (pierced) seeds than among unmarked seeds in *C. oleifera* (26% versus 76%;  $\chi^2 = 25.0$ , d.f. = 1,  $P < 0.001$ ) but not in *Q. variabilis* (92%

versus 86%;  $\chi^2 = 0.9$ , d.f. = 1,  $P = 0.338$ ). This indicates that piercing the seeds can (but need not) negatively affect the ability of seeds to germinate and establish.

## 4. Discussion

Both the tagging methods proved effective for tracking the fates of individual seeds upon their removal by seed-caching rodents. Fate pathways were similar to those found using radioisotope methods (Vander Wall and Joyner, 1998; Vander Wall, 2002, 2003), which are believed not to affect animal behavior (Forget and Wenny, 2005). Some tagged seeds were handled, moved, and cached more than two times, which has been found in many rodent-dispersing species worldwide (Xiao et al., 2004c; and references therein). This suggests that both tagging methods are adequate for following seed movements by seed-caching animals. We found no effect of tin tags or even the more conspicuous bamboo sticks on the recovery rate of cached seeds in our study system. Similar work conducted by Forget and Milleron (1991) also indicated that thread-marking had little effect on seed removal of *Virola nobilis* (Myristicaceae) in Barro Colorado Island, Panama. Markers are known to provide cues for cache pilferage by diurnal rodents (e.g. Jacobs and Liman, 1991; Vander Wall, 1991, 2003), but do not appear to do so for the nocturnal ones in our study site.

Our results suggest that wire tin tags are a good alternative to the now widely used thread methods for estimating post-dispersal seed fate and seed shadows. Wire tin tags yield comparable results, but are resistant to rodents removing tags. A general problem with all seed tagging methods is that all the removed seeds cannot be relocated. Both tagging methods allow establishing large samples of the marked seeds, which may make up for the ones missing due to tag loss. Tin tagging, however, yields greater sample sizes and more accurate estimation of seed fate with fewer assumptions, because no tags are lost. Wire tin-tagging also seems superior to thread-marking in estimating post-dispersal seed fate, such as higher



seed re/caching, higher recovery rate or lower seed missing or cutting, longer lifetime at caching sites, and longer dispersal distances.

However, our results also indicate that both seed tagging methods have some limitations in estimating post-dispersal seed fate. Although all marked seeds were removed from our seed stations, tagged seeds were not removed as fast as the untagged ones. This indicates that rodents notice the tags and prefer untagged seeds. Slower removal of tagged seeds implies longer exposure to seed predators, pathogens and weather, which can negatively influence seed condition and the likelihood to be removed at all. Seed removal and survival estimates from tagged seeds may thus be underestimated. Generally, piercing physically damages the cotyledons or endosperm in many seed species, which may facilitate attack of seeds by fungi and insects (Jansen et al., 2004; Z.-S. Xiao, personal observation) or increase dehydration (Xiao and Zhang, 2003; Forget and Wenny, 2005). Thus, the piercing of seeds to attach the tags may reduce seedling emergence and survival. This implies that studies tracking tagged seeds until emergence may ultimately underestimate germination and seedling establishment from caches (Forget and Wenny, 2005). It is not difficult to imagine how longer exposure of seeds and effects of piercing together result in an underestimation of performance of rodents as seed dispersers. Seed drilling, however, need not affect all the species. In our study, it reduced seedling emergence of one species but had little effect on another. That piercing may affect seed viability, and behavior should be taken into account in studies involving seed tracking over longer periods, e.g. until seedling establishment. Glueing the thread to the seed coat (cf. Wenny, 1999) may be a good alternative for piercing, but only if rodents do not detach or cut the thread (Forget and Wenny, 2005). Otherwise, radioisotopes may be the only suitable method for tracking seeds of even large-seeded plant species.

## Acknowledgements

We thank the Subalpine Mountain Plant Garden of west China, CAS, and the Forest Bureau of Dujiangyan City of Sichuan Province, for support. Funds were provided by National Natural Science Foundation of China (30430130 and 30500072), key program of Ministry of Science and Technology (G2000046802) and CAS Innovative Research International Partnership Project (CXTDS2005-4). P.A.J. was supported by the Netherlands Foundation for the Advancement of Tropical Research (grant W84-584).

## References

Abbott, H.G., 1961. White pine seed consumption by small mammals. *J. For.* 59, 197–201.

Abbott, H.G., Quink, T.F., 1970. Ecology of eastern white pine seed caches made by small forest mammals. *Ecology* 51, 271–278.

Brewer, S.W., 2001. Predation and dispersal of large and small seeds of a tropical palm. *Oikos* 92, 245–255.

Brewer, S.W., Rejmánek, M., 1999. Small rodents as significant dispersers of tree seeds in a neotropical forest. *J. Veg. Sci.* 10, 165–174.

Chauvet, S., Feer, F., Forget, P.-M., 2004. Seed fates of two Sapotaceae species in a Guianan rain forest in the context of escape and satiation hypotheses. *J. Trop. Ecol.* 20, 1–9.

Chen, C., 2000. The Dujiangyan region—pivot sector of assemblage, differentiation and maintenance of biodiversity in northern part of Hengduan mountain. *Acta Ecol. Sin.* 20, 28–34 (in Chinese with English abstract).

Dennis, A., 2003. Scatter-hoarding by musky rat-kangaroos, *Hypsiprymnodon moschatus*, a tropical rain-forest marsupial from Australia: implications for seed dispersal. *J. Trop. Ecol.* 19, 619–627.

Forget, P.M., 1990. Seed-dispersal of *Vouacapoua americana* (Caesalpiniaceae) by caviomorph rodents in French Guiana. *J. Trop. Ecol.* 6, 459–468.

Forget, P.M., 1991. Scatterhoarding of *Astrocarum paramaca* by *Proechimys* in French Guiana comparison with *Myoprocta exilis*. *Trop. Ecol.* 32, 155–167.

Forget, P.M., 1992. Seed removal and seed fate in *Gustavia superba* (Lecythidaceae). *Biotropica* 24, 408–414.

Forget, P.M., Milleron, T., 1991. Evidence for secondary seed dispersal by rodents in Panama. *Oecologia* 87, 596–599.

Forget, P.M., Wenny, D., 2005. How to elucidate seed fate? A review of methods used to study seed removal and secondary seed dispersal. In: Forget, P.M., Lambert, J., Hulme, P.E., Vander Wall, S.B. (Eds.), *Seed Fate: Seed Predation, Seed Dispersal and Seedling Establishment*. CABI, Publishing, Wallingford, pp. 379–393.

Hallwachs, W., 1986. Agoutis (*Dasyprocta punctata*): the inheritors of quapinol (*Hymenaea courbaril*: Leguminosae). In: Estrada, A., Fleming, T.H. (Eds.), *Frugivores and Seed Dispersal*. Junk, Dordrecht, pp. 285–304.

Hoshizaki, K., Hulme, P.E., 2002. Mast seeding and predator-mediated indirect interactions in a forest community: evidence from post-dispersal fate of rodent-generated caches. In: Levey, D., Silva, W.R., Galetti, M. (Eds.), *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CABI, Publishing, Wallingford, pp. 227–239.

Iida, S., 1996. Quantitative analysis of acorn transportation by rodents using magnetic locator. *Vegetatio* 124, 39–43.

Jacobs, L.F., Liman, E.R., 1991. Grey squirrels remember the locations of buried nuts. *Anim. Behav.* 41, 103–110.

Jansen, P.A., Bartholomeus, M., Bongers, F., Elzinga, J.A., Den Ouden, J., Van Wieren, S.E., 2002. The role of seed size in dispersal by a scatter-hoarding rodent. In: Levey, D., Silva, W.R., Galetti, M. (Eds.), *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CABI, Publishing, Wallingford, pp. 209–225.

Jansen, P.A., Hemerik, L., Bongers, F., 2004. Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. *Ecol. Mon.* 74, 569–589.

Jensen, T.S., 1985. Seed-predator interactions of European beech (*Fagus sylvatica* L.) and forest rodents, *Clethrionomys glareolus* and *Apodemus flavicollis*. *Oikos* 44, 149–156.

Jensen, T.S., Nielsen, O.F., 1986. Rodents as seed dispersers in a heather-oak wood succession. *Oecologia* 70, 214–221.

Lawrence, W., Rediske, J.H., 1959. Radiotracer technique for determining the fate of broadcast Douglas-fir seed. *Soc. Am. For. Proc.* 99–101.

Lawrence, W., Rediske, J.H., 1962. Fates of sown Douglas-fir seed. *For. Sci.* 8, 210–218.

Levey, D.J., Sargent, S., 2000. A simple method for tracking vertebrate-dispersed seeds. *Ecology* 81, 267–274.

Li, H.-J., Zhang, Z.-B., 2003. Effect of rodents on acorn dispersal and survival of the Liaodong oak (*Quercus liaotungensis* Koidz.) *Forest Ecol. Manag.* 176, 387–396.

Sone, K., Kohno, A., 1996. Application of radiotelemetry to the survey of acorn dispersal by *Apodemus* mice. *Ecol. Res.* 11, 187–192.

Theimer, T.C., 2001. Seed scatter-hoarding by white-tailed rats: consequences for seedling recruitment by an Australian rain forest tree. *J. Trop. Ecol.* 17, 177–189.

Theimer, T.C., 2003. Intraspecific variation in seed size affects scatter hoarding behavior of an Australian tropical rain-forest rodent. *J. Trop. Ecol.* 19, 95–98.

Vander Wall, S.B., 1991. Mechanisms of cache recovery in yellow chipmunks. *Anim. Behav.* 41, 851–863.

- Vander Wall, S.B., 1992. The role of animals in dispersing a “wind-dispersed” pines. *Ecology* 73, 614–621.
- Vander Wall, S.B., 1993. Cache site selection by chipmunks (*Tamias* spp.) and its influence on the effectiveness of seed dispersal in Jeffrey pine (*Pinus jeffreyi*) *Oecologia* 96, 246–252.
- Vander Wall, S.B., 1994. Seed fate pathways of antelope bitterbrush: dispersal by seed-caching yellow pine chipmunks. *Ecology* 75, 1911–1926.
- Vander Wall, S.B., Joyner, J.W., 1998. Recaching of Jeffrey pine (*Pinus jeffreyi*) seeds by yellow pine chipmunks (*Tamias amoenus*): potential effects on plant reproductive success. *Can. J. Zool.* 76, 154–162.
- Vander Wall, S.B., 2002. Masting in animal-dispersed pines facilitates seed dispersal. *Ecology* 83, 3508–3516.
- Vander Wall, S.B., 2003. Effects of seed size of wind-dispersed pines (*Pinus*) on secondary seed dispersal and the caching behavior of rodents. *Oikos* 100, 25–34.
- Wang, B.C., Smith, T.B., 2002. Closing the seed dispersal loop. *Trends Ecol. Evol.* 17, 379–385.
- Wang, W., Ma, K.-P., 1999. Predation and dispersal of *Quercus liaotungensis* acorns by Chinese rock squirrel and Eurasian jay. *Acta Bot. Sin.* 41, 1142–1144 (in Chinese).
- Wenny, D.G., 1999. Two-stage dispersal of *Guarea glabra* and *G. kunthiana* (Meliaceae) in Monteverde, Costa Rica. *J. Trop. Ecol.* 15, 481–496.
- Wenny, D.G., 2000a. Seed dispersal of a high quality fruit by specialized frugivores: high quality dispersal? *Biotropica* 32, 327–337.
- Wenny, D.G., 2000b. Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. *Ecol. Mon.* 70, 331–351.
- Xiao, Z.-S., 2003. Effects of small mammals on tree seed fates and forest regeneration in Dujiangyan Region, China. PhD thesis, Institute of Zoology, Chinese Academy of Sciences, Beijing, China (in Chinese with English abstract).
- Xiao, Z.-S., Zhang, Z.-B., 2003. How to trace seeds and fruits dispersed by frugivorous animals: a review. *Biodiv. Sci.* 11, 248–255 (in Chinese with English summary).
- Xiao, Z.-S., Zhang, Z.-B., Wang, Y.-S., 2003. Observations on tree seed selection and caching by Edward’s long-tailed rat (*Leopoldamys edwardsi*). *Acta Theriol. Sin.* 23, 208–213 (in Chinese with English summary).
- Xiao, Z.-S., Zhang, Z.-B., Wang, Y.-S., 2004a. Dispersal and germination of big and small nuts of *Quercus serrata* in subtropical evergreen broadleaved forest. *Forest Ecol. Manag.* 195, 141–150.
- Xiao, Z.-S., Zhang, Z.-B., Wang, Y.-S., 2004b. Impacts of scatter-hoarding rodents on restoration of oil tea *Camellia oleifera* in a fragmented forest. *Forest Ecol. Manag.* 196, 405–412.
- Xiao, Z.-S., Zhang, Z.-B., Lu, J.-Q., Cheng, J.-R., 2004c. Repeated caching of plant seeds by small rodents. *Chin. J. Zool.* 39, 94–99 (in Chinese with English summary).
- Xiao, Z.-S., Zhang, Z.-B., Wang, Y.-S., 2005. The effects of seed abundance on seed predation and dispersal by rodents in *Castanopsis fargesii* (Fagaceae). *Plant Ecol.* 177, 249–257.
- Yasuda, M., Miura, S., Hussein, N.A., 2000. Evidence for hoarding behaviour in terrestrial rodents in Pasoh forest reserve, a Malaysian lowland rain forest. *J. Trop. For. Sci.* 12, 164–173.
- Yasuda, M., Nagagoshi, N., Takahashi, F.R., 1991. Examination of the spool-and-line method as a quantitative technique to investigate seed dispersal by rodents. *Jpn. J. Ecol.* 41, 257–262.
- Zhang, Z.-B., Wang, F.-S., 2001. Effect of rodents on seed dispersal and survival of wild apricot (*Prunus armeniaca*). *Acta Ecol. Sin.* 21, 839–845.
- Zhang, Z.-B., Xiao, Z.-S., Li, H.-J., 2005. Impact of small rodents on tree seeds in temperate and subtropical forests, China. In: Forget, P.M., Lambert, J., Hulme, P.E., Vander Wall, S.B. (Eds.), *Seed Fate: Seed Predation, Seed Dispersal and Seedling Establishment*. CABI, Publishing, Wallingford, pp. 269–282.