Arboreal larder-hoarding in the tropical Indian giant squirrel *Ratufa indica*[1]

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Abstract: Squirrels, especially those in temperate regions, hoard seeds in terrestrial scatterhoards or larders. Arboreal seed storage is rare. Here we show for the first time that the tropical Indian giant squirrel (*Ratufa indica*) larder hoards seeds in arboreal nests, a behaviour not previously described. Seeds of 6 tree and liana species in an Indian cloud forest were hoarded during the fruiting season. Seeds of 2 species were hoarded but never consumed when fresh probably because of secondary metabolites. Common species with hard seed coats were most frequently hoarded. Squirrels exhibited variation in hoarding behaviour in different areas of the study site. Squirrels that were at risk of nest robbing resulting from competition for nesting sites did not hoard seeds.
Keywords: *Gnetum ula*, lianas, *Mangifera indica*, nest robbing, secondary metabolite manipulation, squirrel–plant interaction.

Résumé : Les écureuils, particulièrement ceux des régions tempérées, font des provisions de graines dans des caches terrestres soit éparpillées ou dans un garde-manger. Les caches dans les arbres sont rares. Nous démontrons ici pour la première fois que l'écureuil géant de l'Inde (*Ratufa indica*) cache ses provisions de graines dans des nids dans les arbres, un comportement qui n'avait pas été décrit précédemment. Les graines de 6 espèces d'arbres et de lianes dans une forêt nepheliphile de l'Inde ont été cachées durant la saison de fructification. Les graines de 2 espèces ont été cachées mais jamais consommées fraîches probablement à cause de métabolites secondaires. Les espèces communes de graines possédant une envelope dure étaient les plus fréquemment cachées. Le comportement d'approvisionnement des écureuils variait entre les différents secteurs du site d'étude. Les écureuilss qui étaient à risque de se faire voler leur nid à cause de la compétition pour les sites de nidification n'y cachaient pas de graines.
Mots-clés : *Gnetum ula*, interactions plante-écureuil, lianes, *Mangifera indica*, manipulations des métabolites secondaires, vol de nid.

Nomenclature: Corbett & Hill, 1992; Mali & Borges, 2003.

Introduction

Food hoarding is a response to unpredictable and seasonal resources (Vander Wall, 1990). Hoarding strategies may relate to food spatial distribution, pilferage, perishability, handling time, nutrients, infestation, and size (Vander Wall, 1990; Steele, Wauters & Larsen, 2005). Seed hoarding by squirrels is well known in temperate regions (Steele & Koprowski, 2001), less known in the tropics, and not at all recorded from the Indian tropics, despite high squirrel diversity (Corbett & Hill, 1992). This could be due to a paucity of research in the tropics in general and Asia in particular (Corlett, 1998), where squirrel research is scarce (*e.g.*, Borges, 1992; Paschoal & Galetti, 1995). Temperate squirrels cache seeds in terrestrial larders or scatterhoards (Steele & Koprowski, 2001). Tropical squirrels also cache food on or near the ground in scatterhoards (Emmons, 1980; Yasuda, Miura & Hussein, 2000) or in tree wedges (Payne, 1979). We present evidence, for the first time to our knowledge, for seed hoarding within arboreal nest larders in tropical tree squirrels. We also found intraspecific variation in seed hoarding and relate this to nest robbing.

The Indian or Malabar giant squirrel (*Ratufa indica*) is a large (median mass 1.4 kg), strictly arboreal, solitary, obligate herbivore that builds 6 to 8 leaf nests within individual territories of which 2 or 3 nests are used simultaneously (Borges, 2007). The nests are globular, single-chambered, built of a twig framework, and lined by leafy sprays; they have a single lateral opening and are constructed in the sub-canopy of tall trees. Squirrels prefer fruit whenever available, but will eat leaves, bark, stem pith, and flowers during lean fruiting periods (Borges, 1992; 1998). Home ranges in squirrels vary in size from 0.7 to 1.2 ha (Borges, 1989; 2007) and although home ranges overlap, nests as well as nesting and neighbouring trees are usually exclusive domains. Territoriality can restrict access by individual squirrels to specific rare tree species (such as *Ficus*) as well as to specific fruiting individuals within commoner tree species (Borges, 1993; 1998).

Methods

As part of a larger study on the foraging ecology of *R. indica*, we observed 11 focal squirrels from dawn to

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dusk (2883 observation hours) within a 22-ha intensive study area within which over 5000 trees were mapped. The study was conducted within the seasonal cloud forest of Bhimashankar Wildlife Sanctuary, Indian Western Ghats (900 m asl, monsoonal precipitation 3000 mm), a low diversity semi-evergreen forest dominated by *Mangifera indica* (Anacardiaceae), *Memecylon umbellatum* (Melastomataceae), and *Olea dioica* (Oleaceae), which account for 64% of tree relative dominance (Mali & Borges, 2003). Fruiting is highly seasonal (March–June), preceding the fruit-scarce monsoon season (Borges, 1993).

A part of the study area, which we refer to as the Bombay Road, was close to an abandoned road project for which a 20-m-wide strip of forest was clear-felled for 5 km, causing canopy discontinuity. The clearing was subsequently colonized by weedy invasive species. The forests adjoining the Bombay Road consist of naturally stunted, sparsely distributed trees on rocky slopes. The other part of the study area, which we refer to as the Bhima Valley, was relatively undisturbed, and consisted of riverine forest with tall trees, good canopy connectivity, and mature lianas. We estimated squirrel densities in both these areas using a combination of nest counts and direct sightings of individually identifiable animals. The sizes of individual home ranges of focal squirrels were estimated using mapped locations of trees. During focal animal sampling, we also collected data on interactions between squirrels, including aggressive encounters at food sources or nests. During this sampling, 2 squirrels were observed caching *M. indica* seeds within their nests and later retrieving them for consumption after the fruiting season was over. Since hoarding had never been recorded in this squirrel at this or other sites (Borges, 1989; 1992; 1998), we investigated 31 squirrel nests immediately after the fruiting season with the assistance of local tree climbers. Access was dangerous since nests occur near termini of canopy branches. Only active nests were investigated to exclude seed storage by other animals that use abandoned squirrel nests. We provide wet seed masses of hoarded and non-hoarded species (to include tree species up to nearly 90% relative dominance values at the site) for comparison.

Results

Ratufa indica almost always consumed seeds within source tree crowns, and observations of carrying seeds to another tree for immediate consumption or for hoarding were rare. Hoarded seeds were found scattered in the leafy nest material of the investigated nests within the single nest chamber. Only 8 of the 31 investigated nests contained seeds (mean ± SD seeds: 30.9 ± 9.9, n = 8, Table I). A total of 247 seeds of 6 species (3 tree, 2 liana, and 1 unidentified species) were recovered, and at least one seed of all hoarded species was found in each of the 8 nests (Table I). The gymnosperm liana *Gnetum ula* (Gnetaceae) and wild mango *M. indica* were most abundant in larders. Mango seeds had the highest wet mass per seed among hoarded species (Table II).

When all the nests belonging to 2 squirrels were investigated (4 in one territory and 6 in the other), only the nest in current use contained hoarded seeds. There was considerable variation in hoarding between locations within the study site; no hoarded seeds were found in nests (n = 20) in the Bombay Road area, while 8 of the 11 nests investigated in the Bhima Valley contained seeds (χ^2 = 19.61, df = 1, P < 0.0001).

Squirrel density in the Bombay Road area was higher (3.3 squirrels·ha^{-1}) compared to that in the Bhima Valley (0.8 squirrels·ha^{-1}), apparently owing to the habitat disturbance in the Bombay Road area. Aggressive encounters per squirrel were significantly higher in the Bombay Road area

TABLE I. Species composition of nest larders.

	Mean ± SD (Range) (n = 8 nests)	Total seeds	% of total seeds
Gnetum ula	11.9 ± 8.8 (2–26)	95	38.5
Mangifera indica	8.5 ± 4.8 (1–16)	68	27.5
Syzygium cumini	3.3 ± 1.7 (1–6)	26	10.5
Embelia ribes	3.1 ± 1.6 (1–5)	25	10.1
Olea dioica	2.6 ± 2.1 (2–6)	21	8.5
Unknown species	1.5 ± 1.5 (2–4)	12	4.9

TABLE II. Characteristics of hoarded and non-hoarded species in Bhimashankar.

Species	Family	Wet seed mass		Fruit size class[a]	Eaten when fresh/Hoarded	Hard seed coat	Relative dominance[c]
		Mean (g) ± SD	n				
Mangifera indica	Anacardiaceae	14.9 ± 9.0	22	L	Y/Y[b]	Y[b]	34.3
Memecylon umbellatum	Melastomataceae	–	–	S	Y/N	Y	15.5
Olea dioica	Oleaceae	0.3 ± 0.03	12	S	N/Y	Y	14.3
Xantolis tomentosa	Sapotaceae	0.6 ± 0.1	20	S	Y/N	N	6.9
Syzygium cumini	Myrtaceae	0.5 ± 0.1	20	S	N/Y	Y	6.5
Syzygium gardneri	Myrtaceae	0.5 ± 0.1	10	S	N/N	Y	2.5
Garcinia talbotii	Clusiaceae	7.7 ± 0.6	10	M	Y/N	N	2.1
Amoora lawii	Meliaceae	0.6 ± 0.2	20	S	Y/N	N	1.8
Diospyros sylvatica	Ebenaceae	1.0 ± 0.3	20	S	Y/N	N	1.5
Ficus nervosa	Moraceae	–	–	S	Y/N	N	1.4
Cassine glauca	Celastraceae	–	–	S	N/N	N	1.3
Litsea stocksii	Lauraceae	0.4 ± 0.04	20	S	Y/N	N	1
Gnetum ula (liana)	Gnetaceae	3.0 ± 0.5	12	S	Y/Y	Y	–
Embelia ribes (liana)	Myrsinaceae	–	–	S	Y/Y	Y	–

[a] Fruit size class: L = large (> 50 g), M = medium (10–49 g), S = small (< 10 g); For entire table: – = not available;

[b] Y = yes, N = no;

[c] Data from Mali & Borges, 2003.

compared to those in the Bhima Valley (35.0 ± 5.1 SD, n = 6 in Bombay Road; 11.4 ± 3.3 SD, n = 5 in Bhima Valley; Mann-Whitney $U = 0$, $P < 0.01$). Moreover, nest robbing, in which squirrels attempted to usurp another's nest, was observed only in the Bombay Road area (33 instances of nest-related aggression, which included cases where intruders were chased out of nests that did not belong to them).

Discussion

Diets of the Indian giant squirrel can consist of only bark and leaves during fruit scarcity, but squirrels prefer fruits, especially seeds, when they are available (Borges, 1992). Food is usually consumed within the source tree crown itself (Borges, 2007), as is the case with the pale giant squirrel *Ratufa affinis* and the pied giant squirrel *R. bicolor* in southeast Asia (Becker, Leighton & Payne, 1985). Hoarded seeds, *e.g., M. indica* and *G. ula*, were frequently consumed during regular feeding bouts (Borges, 1998). The unusual exceptions were *O. dioica* and *S. cumini*, the seeds of which were hoarded although they are never consumed when fresh. Squirrels consume the fresh fruit pulp of these 2 species in abundance, but they drop the seeds to the forest floor (Borges, 1989). Squirrels avoid fresh *O. dioica* seeds presumably because of their secondary metabolite content, which includes saponins (Borges, 1992; Mali & Borges, 2003). Moreover, squirrels consume soil after feeding on fresh *O. dioica* fruit pulp (R. M. Borges, unpubl. data), perhaps to neutralize the effect of these secondary metabolites. The seeds of *O. dioica* are also intensely bitter (Kirtikar & Basu, 1935), which suggested the presence of alkaloids, but they failed alkaloid confirmatory tests (Mali & Borges, 2003). The bitterness of *O. dioica* seeds may be because of secoiridoid glycosides, which are responsible for bitter taste and herbivore seed defence of their cultivated relative, the olive *Olea europaea* (Kubo, Matsumoto & Takase, 1985). Iridoids are also known to be predominant in the Oleaceae (Jensen, Franzyk & Wallander, 2002). Whether extended storage decreases the toxicity of *O. dioica* seeds is not known, although the toxicity of plants can decline during storage because of release of degradative enzymes on drying (Danninger *et al.,* 1983). For example, lagomorphs such as pikas reduce the phenolic content of harvested vegetation by extended storage (Dearing, 1997). Moreover, secoiridoid glycosides in *O. europaea* degrade on storage (Lavelli, Fregapane & Salvador, 2006), which suggests the possibility of storage-enhanced toxicity decline also in *O. dioica*. Assuming that storage reduces toxicity in these seeds, it is worth noting that *O. dioica* seeds, like those of *O. europaea*, have high lipid contents (23.1% dry mass; R. M. Borges, S. Mali & H. Somanathan, unpubl. data) and may also, therefore, be preferred for long-term hoarding as in the giant white-tailed rat *Uromys caudimaculatus*, which preferentially hoards seeds with high lipid contents (Finkelstein & Grubb, 2002). Squirrels may avoid consuming the fresh seeds of *S. cumini* since fresh tissues (*e.g.,* bark, fruit pulp, seeds) of this species are known hypoglycaemic (*i.e.,* they lower blood glucose levels) or anti-diabetic agents in traditional Asian medicine (Rafiullah *et al.,* 2006), the efficacy of which has been experimentally demonstrated in laboratory mice and rats (Rafiullah *et al.,* 2006; Villaseñor & Lamadrid, 2006). Since *S. cumini* seeds lower blood glucose levels in laboratory rodents, inducing hypoglycaemia, it is possible that this property is also exhibited in other rodents such as the giant squirrel, which may therefore hoard these seeds in order to consume them only when their hypoglycaemic activity has decayed. It must be noted, however, that there are no available data on the putative decay of the hypoglycaemic activity of *S. cumini* seeds with storage.

Squirrels consumed fresh seeds of 17 plant species, of which *M. indica, G. ula*, and *Garcinia talbotii* (Clusiaceae) ranked the highest in seed mass consumption (Borges, 1989). *Garcinia* seeds, although large, were not hoarded, probably because they are highly perishable since they lack a hard seed coat (Table II). In general, species hoarded by *R. indica* had hard seed coats, while most non-hoarded species had soft seed coats. The single exception was *Syzygium gardneri*, which was available only in low numbers (Table II). Hoarded and non-hoarded seeds did not differ in energy, total non-structural carbohydrate, lipid, or condensed tannin, total phenolic, and acid detergent fibre (ADF) contents (Mann-Whitney U-tests, $n_{\text{hoarded}} = 6$, $n_{\text{non-hoarded}} = 12$, $P > 0.05$; phytochemical data from Mali & Borges, 2003), thus indicating that nutrient or secondary metabolite content *per se* apparently did not influence hoarding decisions. However, amongst hoarded species, *M. indica* and *G. ula* have the largest seeds (Table II); *M. indica* is also the most common tree and *G. ula* the most common liana, and thus the seeds of these species may be preferred for hoarding because of lower transportation costs (other tropical rodents are known to favour seeds of the most abundant tree species for hoarding: Brewer, 2001). Furthermore, the 3 hoarded tree species (*M. indica*, *O. dioica*, *S. cumini*) constituted 55% of tree relative dominance values in this low-diversity forest, in which just 12 tree species account for nearly 90% of tree dominance (Table II), presenting a highly skewed frequency distribution. This squirrel–plant interaction is, therefore, similar to that in temperate regions, where within low-diversity forests, common species with low perishability or hard seed coats are hoarded (Steele & Koprowski, 2001).

Seed loss due to pilferage is potentially higher in undefended larders than in scatterhoards (Vander Wall & Jenkins, 2003). Despite their conspicuousness, nest larders are the safest hoarding sites for this arboreal, territorial squirrel because (1) nests are aggressively defended, (2) seed losses due to fungal attack and germination are minimal since nests are clean and dry, and (3) seed retrieval in this case requires neither spatial memory for specific seed hoards nor seed-related sensory cues. Only nests in current usage contained hoarded seeds, suggesting that squirrels do not hoard more than they can effectively defend. Moreover, we never observed these completely arboreal squirrels caching seeds on the ground, where they could not be defended from pilferers. In any case, caching seeds on the ground could result in heavy damage due to fungal attack in this high rainfall site, whereas by being stored in clean, currently used nests, larders are protected from spoilage.

Why didn't squirrels in the Bombay Road area hoard seeds? Squirrels in the disturbed Bombay Road area were more aggressive than those in the Bhima Valley, and were also the only squirrels that exhibited nest-robbing behaviour, in which they attempted to use another squirrel's nest. This difference in squirrel behaviour between the 2 locations was possibly due to increased competition for nesting sites due to higher squirrel densities and smaller home ranges in the Bombay Road area. Because nest ownership was not reliable in the Bombay Road area, seed hoarding would confer a lower benefit on squirrels in this area compared to those in the Bhima Valley.

Bhimashankar is also the only site where we have seen squirrels carrying seeds to nests or retrieving hoarded seeds from nests, and thus the only site where hoarding has been observed to occur. This could be because it is a seasonal cloud forest that experiences dense monsoon clouds that do not lift for 4 months after the fruiting season is over (Borges, 1989). Squirrels cannot travel easily through the canopy during cloud cover, when visibility is close to zero and rain is incessant. Therefore, the conditions are similar to snow-bound conditions in temperate regions during which squirrels rely exclusively on hoarded seeds (Steele & Koprowski, 2001). However, temperate squirrels cannot survive the lean winter season without access to stored seeds (Steele & Koprowski, 2001), while survival of giant squirrels in the cloud months is possible because lean seasons are much less extreme. Although intraspecific variation in hoarding strategies has been reported (Hurly & Robertson, 1990), this is the first study to show that squirrels exhibit variation in hoarding behaviour based on the likelihood of larder loss due to uncertain nest ownership. This variation in hoarding behaviour is also possible because during fruiting seasons giant squirrels feed almost exclusively on fruit (Borges, 1998), building up reserves to maintain themselves during lean fruiting periods; giant squirrels are also buffered by their large size and caecal digestion, and can thus consume leaves and bark extensively during lean fruiting seasons (Borges, 1992). Still, seed larders can supplement the low diet quality of lean fruiting seasons and are likely to have long-term fitness consequences for individuals that hoard. Arboreal hoarding by giant squirrels has only negative fitness consequences for plants since unlike terrestrial hoarding, where some unrecovered seeds may germinate (Theimer, 2005), in this case the potential for germination and establishment is completely absent.

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