

Short communications

Evidence for secondary seed dispersal by rodents in Panama

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Summary. The data presented show that *Virola nobilis* (Myristicaceae), a bird/mammal-dispersed tree species in Panama, may also be dispersed by a terrestrial rodent, the agouti (*Dasyprocta punctata*). Using a thread-marking method, we observed that agoutis scatterhoarded *V. nobilis* seeds that they found both singly or in clumps. Seed removal and seed burial rates were strongly affected by features of forest habitats, such as *V. nobilis* tree richness (rich vs poor) and/or forest age (old vs young), but not by seed dispersal treatment (scattered vs clumped). Predation (mostly post-dispersal) of unburied seeds by weevils was independent of habitat and dispersal treatment. Seeds artificially buried in a *Virola*-rich area were more likely to escape predation and become established than unburied seeds under natural conditions. The food reward for agoutis is in the germinating seedlings. The seed dispersal syndrome of *V. nobilis* involves long- and short-distance dispersers which both appear important for tree recruitment.

Key words: Tropical ecology – Panama – Seed dispersal – Rodents – *Virola nobilis*

Seed dispersal, a crucial phase of plant regeneration, has been traditionally defined as seed movement from the parent (Pijl 1972; Howe and Smallwood 1982) but the fate of the disseminated seeds is often unknown (Janzen 1983; Estrada and Coates-Estrada 1986; Chapman 1989). In Panama, the agouti (*Dasyprocta punctata*), a 3–5 kg caviomorph rodent (Smythe 1978), harvests and consumes seeds of a wide range of plant species (Smythe et al. 1982), but its role as reliable primary and/or secondary seed disperser (Smythe 1970; Janzen 1983) has remained controversial (see Larson and Howe 1987). Larson and Howe (1987) argued that “agoutis should not be assumed to be important secondary dispersal agents

or seed predators of plants known to be bat, bird, or monkey-dispersed...” However, seed burial allows seeds to escape consumption by terrestrial seed-eaters, such as beetles and mammals, prevents desiccation and accelerates germination, and promotes seedling establishment (Sork 1985; Smythe 1989; Forget 1990, 1991a). Therefore, secondary seed dispersal by scatterhoarding rodents (see Vander Wall 1990) could be important for the survival of some large-seeded species, and should be taken into account when describing the seed dispersal syndrome of neotropical forest trees dispersed by other means (Forget 1988). In this study, we report that agouti may be significant in secondary seed dispersal in *Virola nobilis* A.C. Smith (Myristicaceae) [(Duke 1962), formerly *V. surinamensis* (in Croat 1978)]. Indeed, agouti bury *V. nobilis* seeds that may have been primarily dispersed by birds and arboreal mammals (Howe and Vande Kerckhove 1980, 1981); these seeds are less likely to germinate and become established if they are not buried.

In June–July 1990 we studied the fates of *V. nobilis* seeds ($2.95 \pm \text{SE } 0.05$ g, $1.9\text{--}2.2 \times 1.5\text{--}1.7$ cm, $n=30$ seeds). Because forest habitat may influence seed removal and seed fate (e.g. Boucher 1981; Sork 1987), we created an artificial seed shadow ($n=800$ seeds) that covered different forest habitats with contrasting *V. nobilis* tree densities (rich vs poor) and contrasting ages (old vs young) near R.C. Shannon Trail on Barro Colorado Island (BCI), Panama (Leigh et al. 1982). The *Virola*-rich habitat (areas 1 and 2) consisted of two 250-m transects (two sections of 125 m for the second transect) crossing an old forest (Foster and Brokaw 1982) where *V. nobilis* is frequent (see also Howe 1990). Five and six trees grew within 30 m of each transect, respectively. The *Virola*-poor habitat consisted of two 1-ha plots at a young (area 3) and a naturally disturbed (area 4) forest (Foster and Brokaw 1982; pers. obs.) delimited by a network of five parallel transects 100 m long and 25 m apart. One *V. nobilis* tree occurred 10–15 m outside each plot.

At four fruiting trees located near each study area, we collected freshly fallen seeds, and removed both the aril and the thin layer covering the seed. We took samples of

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100 freshly-fallen seeds from each tree to measure the proportion containing insect larvae (pre-dispersal predation).

In order to assess the importance of primary seed dispersal, we placed scattered and clumped seeds (Howe 1989) along transects in each habitat in early June. We determined the fates of removed seeds by attaching a 60-cm thread to each seed, which were used to locate seeds (Forget 1990). To see if marking affected removal rate, we duplicated each treatment using unmarked seeds. The features of the seed dispersal experiment are as follow: Scattered treatment – 50 paired seeds (unmarked and marked) were placed 1 m apart every 5 m in areas 1 and 2, and every 10 m in areas 3 and 4; Clumped treatment – 10 paired groups of 5 seeds (unmarked and marked) were placed at every 25 m interval in areas 1 and 2, and randomly distributed in areas 3 and 4. Each spot was marked with a wire flag 50 cm in height. Unmarked seeds were placed in a superficial depression in the ground, made with the thumb, near a wooden stake. We searched for removed seeds and threads within 5 m of each origin. By dissecting the remaining seeds after 6 weeks (seeds germinate in 2–5 weeks under artificial conditions, Howe et al. 1985), we estimated total infestation by insects.

In late June, i.e. approximately the period of peak fruiting in *V. nobilis* (Howe and Vande Kerckhove 1981), we simulated scatterhoarding by burying paired seeds 1 m apart at 5 m intervals ($n=200$ seeds) in the *Viola*-rich area. Germination was monitored every 2–3 days. For comparison with the study of Howe et al. (1985), we determined the survivorship of germinated (buried) seeds after 8 and 12 weeks.

Only 2.25% of seeds ($n=400$) were infested before dispersal by birds or mammals. The marking method had no overall effect on seed removal ($\chi^2=1.33$, $df=1$, $P=0.249$) (Table 1). Seed removal was strongly affected by habitat ($\chi^2=158.65$, $df=3$, $P<0.001$) but not by dispersal treatment ($\chi^2=0.006$, $df=1$, $P=0.939$) (Table 1). Many of the seeds that were removed by terrestrial animals, especially in the *Viola*-poor habitats, were buried (Table 1). This is probably due for a large part to agouti, which with acouchies (*Myoprocta* spp.) in amazonian forests (see Emmons and Feer 1990), are the only vertebrates actually known to bury (not just cache under the litter, see Forget 1991b) large seeds in the ground (Morris 1962; Smythe 1970, 1978; Dubost 1988; Forget 1990). The group of “lost” seeds may include some seeds that were buried farther than 5 m (e.g. 7 m in one instance). Because agouti rarely consume fresh seeds (Smythe et al. 1982; Larson and Howe 1987; pers. obs.), the observed low levels of destruction and some loss of fresh seeds may be correlated with the low population of spiny rats (*Proechimys semispinosus*) on BCI (Glanz 1982; pers. obs.), which eat and larderhoard *Viola* seeds (see Fleming 1974; Guillotin 1982).

All unremoved marked seeds ($n=114$) were infested, probably because the threaded hole facilitated infestation by larvae. Because of this artefact we could not account for the survival of naturally buried seeds which, in many instances, appeared to be infested before dispersal by

Table 1. Seed removal rate and fate (%) of marked *V. nobilis* seeds within 6 weeks near R.C. Shannon trail in June–July 1990 on Barro Colorado Island, Panama, by forest habitat and dispersal treatment (sc: scattered seeds; cl: clumped seeds). 50 seeds were provided for each treatment at each area. Neither the marking method nor the dispersal treatment affected seed removal (all $P>0.05$). Seed removal was strongly affected by forest habitats ($P<0.001$)

Habitat	<i>Viola</i> -rich		<i>Viola</i> -poor	
	1	2	3	4
Areas				
Treatment	sc	cl	sc	cl
Unmarked seeds				
Removed	48	46	58	48
Marked seeds				
Removed	34	26	72	78
Buried	14	8	40	42
Gnawed	2	10	2	8
Lost	18	8	30	28

Table 2. Percentage (number) of unremoved unmarked seeds infested or not after 6 weeks at *Viola*-rich (areas 1 and 2) and *Viola*-poor (areas 3 and 4) habitat depending on dispersal treatment. Infestation depends neither on habitat ($P>0.05$) nor on dispersal treatment ($P>0.05$)

Habitat	<i>Viola</i> -rich		<i>Viola</i> -poor	
	% infested	total n	% infested	total n
Scattered	87.2	47	87.5	16
Clumped	90.6	53	76.9	13

rodents, and thus rotted and died in the caches. In general, under natural conditions at the study areas, we never encountered unburied seeds that had successfully germinated and become established; all were insect-infested and rotten. Occasionally, we observed germinating seedlings that arose from naturally agouti-dispersed seeds, i.e. from seeds cached and buried at the bases of rotting logs, palms or tree trunks.

Of seeds that were artificially buried ($n=200$), 58.5% germinated ($n=117$) and pushed up from under the ground surface within 8 weeks, and none after that period. In contrast, none of the remaining unmarked seeds ($n=129$) germinated, 87.6% of them being infested within 6 weeks (Table 2). Infestation was not significantly associated with either habitat (Mantel-Haenszel $\chi^2=0.784$, $P=0.376$) or with dispersal treatment (Mantel-Haenszel $\chi^2=0.001$, $P=0.978$) (Table 2). By 6 weeks, remaining insect-free seeds may be less likely to establish, since *Viola* spp. seeds are recalcitrant and rapidly lose their ability to germinate (F. Corbineau, CNRS, Meudon, pers. comm. in Forget 1988).

Only 2% of the artificially buried seeds survived 12 weeks (4 live seedlings from 200 buried seeds). This percentage is consistent with those of Howe (1986a) and Howe et al. (1985) which are based on survival of transplanted seedlings, therefore escaping early post-dispersal seed predation. The high mortality was due to various

factors that affect both buried seeds and germinated seeds: rotting due to pre-dispersal predation; removal by agoutis for eventual seed predation or re-burial elsewhere when ungerminated; predation by weevils when germinating seeds emerges from under the ground; and post-establishment predation by mammals, especially agoutis which consume the hypocotyles of the germinated seeds and established seedlings (pers. obs.; see also Howe et al. 1985 and Howe 1990).

Though the morphology of *V. nobilis* fruits is undeniably adapted for consumption by long-distance dispersers (Janson 1983; Howe 1986b), short-distance dispersers such as agouti also appear to be involved in the dispersal syndrome of *V. nobilis* seeds. Exclusive seed dispersal by bird and arboreal mammals might not ensure effective recruitment of the tree, and seed burial by rodents might enhance the chance of escape from various seed- and seedling-eating organisms. By facilitating germination of buried seeds and food storage in the hypocotyle before emergence, a well-established root system may, indeed, efficiently defend seedlings from drought stress and allow leaf renewal after defoliation (see Howe 1990; pers. obs.).

The observed range of seed removal and seed burial rates could be due to differences in both the levels of predator satiation and overall food availability at each area, which may correlate with the age (old vs young) of each forest habitat. At least, spatial distribution of *V. nobilis* recruitment might also depend on agouti foraging behavior in those habitats where other animals are the primary seed dispersers (Schupp et al. 1989). Therefore, secondary seed dispersal and seed burying by rodents could be as important as primary seed dispersal for the regeneration of *V. nobilis*. The same could be true for many other large-seeded neotropical forest species whose seeds suffer disproportionate mortality by insects and mammals, especially rodents.

Actually, it is unknown whether the same phenomenon occurs in other *Virola* spp. in other neotropical forests. For example, because agouti (*D. leporina*) also bury *V. michelii* seeds (Forget and Dubost, pers. obs.), it is possible in French Guiana. However, in view of the seedling shadows which often form under some parent trees (Forget 1991a), it is not known whether its occurrence would be as important as in Panama.

The recruitment pattern of *V. nobilis* may have been selected to take advantage of the scatterhoarding behavior of rodents. Therefore, presence or absence of agoutis in a given forest could ultimately have profound consequences on the regeneration of *V. nobilis*, since buried seeds are more likely to become established under natural conditions than unburied seeds. This study suggests that future researches on regeneration of large-seeded species should focus more often on the natural history and the ecological implications of the scatterhoarding and foraging behavior of the agoutis (*Dasyprocta* spp.), as well as that of the acouchies (*Myoprocta* spp.), for tree recruitment and tree diversity in neotropical forests.

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