

SHORT COMMUNICATION

**The fruits the agouti ate: *Hymenaea courbaril*
seed fate when its disperser is absent**

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The neotropical canopy tree *Hymenaea courbaril* L. (Caesalpiniaceae) has long been hypothesized to depend on mammals for the dispersal of its seeds. Hallwachs (1986) suggested that agouti (*Dasyprocta* spp., Rodentia) inherited the role of disperser of *H. courbaril* seeds from large Pleistocene mammals (Janzen & Martin 1982). She further postulated that agouti are currently the only effective disperser of *H. courbaril* seeds, and predicted that they are now so critical for the regeneration of this tree that in the absence of *Dasyprocta*, *H. courbaril* would go extinct in areas where its other seed predators are present (Hallwachs 1986).

Not only does this prediction have important conservation ramifications but similar predictions have been made about other neotropical tree species (Forget 1994, Leigh *et al.* 1993, Smythe 1989). However, these predictions have yet to be critically tested at sites with and without agouti. In this communication we test Hallwachs' (1986) prediction on islands in Lago Guri, a 4300-km² hydroelectric impoundment in east-central Venezuela. When inundation of Lago Guri was completed in 1986, scores of forested land-bridge islands were

created. Many of these islands are now too small to support agouti, but some small islands do currently support adult *H. courbaril* trees.

Fruiting *H. courbaril* trees produce 100 to 500 indehiscent, hard, 10–20-cm-long pods (Janzen 1975), each of which contains up to seven seeds ($n = 20$ pods). Paca (*Agouti paca*), peccaries (*Pecari* spp.) tapir (*Tapirus* spp.) and horses (*Equus caballus*) can open *H. courbaril* pods, but all are seed predators and are unlikely to be efficient dispersers (Hallwachs 1986). Capuchin monkeys (*Cebus* spp.) break open pods and disperse seeds (Oliveira *et al.* 1995). However, any seeds dispersed by capuchins (and for that matter, paca, tapir and horses) usually remain on the soil surface, available to other seed predators such as small- (Hallwachs 1986) and medium-sized rodents (Adler 1995). In contrast, caviomorph rodents of the genus *Dasyprocta* (and in Amazonia, the genus *Myoprocta* [P-M. Forget *pers. comm.*]) bury scatter-hoarded pods and seeds below the soil surface where they are relatively safe from predation. Moreover, *Dasyprocta* spp. disperse *H. courbaril* pods up to at least 225 m (Hallwachs 1986). Agouti clearly influence *H. courbaril* recruitment, but are they as critical for regeneration as Hallwachs (1986) proposes?

In July–August 1995 and July 1996, the peak of the rainy season in Lago Guri, we assessed *H. courbaril* seed fate in the presence and absence of agouti. We ran experiments on the 350-ha island of Danto Machado (7°21'N, 62°52'W) and 11 other islands (1–20 ha) within a radius of 15 km. We also used one island (11 ha) and two mainland sites 30 km north of the Danto Machado cluster. Lago Guri is situated at a savanna–forest interface although all of our sites were located in semi-deciduous tropical forest (Huber 1986). *H. courbaril* is a common canopy tree in the region and is a preferred timber species.

The terrestrial seed-eating mammal community at each site during our experiments is given in Table 1. Determination of presence or absence of agouti on the landmasses was not straightforward, because agouti are shy and elusive animals, easily overlooked in a cursory survey. A team of four observers surveyed each of 12 islands (small, medium and large) and a mainland control site in 1994. Each site was searched by the team for an hour on three occasions,

Table 1. Terrestrial seed-eating mammal community at sites in and around Lago Guri, Venezuela in 1995/96.

	DM, M	Pan	Cor	Lom Búm	Col, Igu, Pal, Per, Roc, Tri	Mie
Small rodent spp.	x	x	x	x	x	
<i>Dasyprocta agouti</i>	x	x	x	x		
<i>Agouti paca</i>	x	x	x			
<i>Tapirus terrestris</i>	x	x				
<i>Pecari tajacu</i>	x					

Source: Terborgh *et al.* (1997a,b) and personal observations. Landmasses: Búm = Búmeran (0.9 ha); Col = Colon (0.6 ha); Cor = Corral (12.3 ha); DM = Danto Machado (± 350 ha); Igu = Iguana (1.4 ha); Lom = Lomo (12.0 ha); M = mainland (our mainland site is ± 30 km from that of Terborgh *et al.* (1997a,b)); Mie = Miedo (0.7 ha); Pal = Palizada (1.8 ha); Pan = Panorama (11.1 ha); Per = Perimetro (1.7 ha); Roc = Rocas (0.6 ha); Tri = Triángulo (2.3 ha). We observed agouti on another island, Redonda (= Red) (± 10 ha), in 1996.

twice diurnally and once nocturnally. The results, based on visual detections, are reported in Terborgh *et al.* (1997a,b). Numerous additional visits were made to most of the sites in connection with the research reported here, and J.T. and others have visited many of the sites in subsequent years (1997, 1998).

In most cases, the results of the surveys undertaken in 1994 have been confirmed by subsequent experience involving both direct (visual records) and indirect evidence (described below). However, indirect evidence obtained at three sites is in conflict with the results of the visual surveys. Agouti have not been seen on Lomo, a 12-ha island, despite numerous visits by investigators over a 5-y period. Nevertheless, on Lomo, pods are systematically removed from beneath fruiting *H. courbaril* trees. The ground under 32 and 36 adult trees on Lomo was searched in 1997 and 1998, respectively, and only scattered pods were found. A search of the leaf litter on Lomo in 1998 revealed empty pods opened in the characteristic manner of agouti, in which a broad longitudinal slit is gnawed along one side of the pod. Thus, there is compelling indirect evidence that agouti occur on Lomo despite the lack of visual evidence.

In contrast, an observer reported seeing an agouti on the islands of Iguana (1.4 ha) and Triangulo (2.3 ha) in 1994, but subsequent searches and all available indirect evidence indicates the absence of agouti on these islands. Despite many hours of observation we have not recorded agouti on Iguana or Triangulo since 1994. Moreover, fresh crops of pods were produced by five adult *H. courbaril* trees on Iguana in 1996, 1997 and 1998, and unopened pods littered the ground under each adult tree in all of those years. In 1998, J.T. noticed that <10 % of the pods had been gnawed open at one end, but these pods remained *in situ* under the parent tree. Neither the small-diameter opening nor the habit of leaving opened pods under the parent tree is characteristic of agouti, so the holes were presumably made by another species of rodent, most likely *Rhipidomys* which is known to be common on the island.

Combining direct and indirect evidence, we conclude that during the period of our experiments agouti were present on Lomo even if unseen, and absent on Iguana and Triangulo, even if once seen there. Thus, for the purpose of our analysis, the mainland sites and six islands support agouti, while seven islands do not. Our experiments tested a number of predictions that follow from the hypothesis that agouti are a critical species for *H. courbaril* regeneration.

Prediction: Where agouti are present pods will be removed; where agouti are absent, more pods will remain in situ. We placed four pods on the forest floor at each of 12 sites in July 1995. Two pods at each site were protected from mammalian seed predators by 1-m high wirecloth cages, which were securely staked to the ground. Similar cages were used to exclude mammals by Asquith *et al.* (1997). Five sites had agouti present (Búm, DM, Pan, Red, Lom—see Table 1 for island names); seven did not support agouti (Col, Igu, Mie, Pal, Per, Roc, Tri). By July 1996 all pods remained in the cages. Two of 14 pods disappeared from

outside the cages where there were no agouti, while all ten disappeared from outside the cages where agouti were present (Fisher's exact test $P < 0.001$).

Prediction: Where agouti are present seeds will be removed; where agouti are absent, more seeds will remain in situ. We placed 20 seeds on the forest floor at each of the above 12 sites in July 1995. Ten seeds were protected from mammals by wirecloth cages and 10 were open to mammals. Five sites had agouti present; seven did not support agouti. After 2 mo, where there were no agouti, almost equal numbers of seeds remained inside (31 of 70) and outside (28 of 70) the cages. At agouti-free sites, the number of seeds remaining *in situ* was independent of whether mammals were excluded or not: seed loss at these sites was a function of invertebrate seed predation and rotting rather than vertebrate seed removal. In contrast, at sites with agouti, 31 of 50 seeds remained in the cages, while only 4 of 50 seeds remained outside the cages (Fisher's exact test $P < 0.001$).

Prediction: Where agouti are present some seeds will be buried; where agouti are absent no seeds will be buried. During the first week of July 1996, we placed 16 seeds on the forest floor at each of 14 sites. Seven sites had agouti present (Búm, Cor, DM, Lom, M, Pan, Red); seven sites did not support agouti (Col, Igu, Mie, Pal, Per, Roc, Tri). Each seed was threaded with a 40-cm length of monofilament line (Forget 1994), to which a 4-cm piece of pink-glo flagging tape was attached. Each thread had a unique number. We attempted relocation of the seeds within a 7-m radius of each experimental site. After 1-wk no seeds (of 112) had been buried at the sites where agouti were absent, whereas a total of 19 seeds (of 112) had been buried at three (Cor, M, Pan) of the seven sites where agouti were present. At one of these three sites none of the other larger, seed-eating mammals was present. Two weeks from the outset, seven of these buried seeds had been recovered and eaten, leaving 12 seeds buried. This distribution of seed burial—all 12 were at the sites where agouti are present—has a binomial probability of $P < 0.001$.

Prediction: H. courbaril germination success is improved if the pod is buried. In July 1995 we put out 56 pods in wirecloth cages, with four pods at each of 14 different sites. A total of 28 pods was buried flush with the soil surface to mimic burial by agouti (Hallwachs 1986), and 28 were left on the soil surface. After 1 y, no seedlings had emerged from any of the unburied pods, whereas seedlings had emerged from six buried pods. The binomial probability of this occurring by chance is $P = 0.03$.

Prediction: H. courbaril germination success is improved if seeds are buried. We put out 448 seeds in wire cages, with 32 seeds at each of 14 sites, in July 1995. Two hundred and twenty-four seeds were buried 0.5 cm below the surface of the soil to mimic burial by agouti and 224 were left on the soil surface. After 1 y, 23 buried seeds and 10 unburied seeds had developed into seedlings (paired *t*-test, $P = 0.04$).

Prediction: Where agouti are absent, many pods will lie under H. courbaril trees

Table 2. Number of intact pods (on four 10-m \times 1-m transects) and seedlings < 30 cm height (within a 10-m radius of the bole) under focal *Hymenaea courbaril* trees.

Site	Agouti presence	Number of intact pods	Number of seedlings
Lomo	Yes	0	31
Mainland	Yes	13	23
Redonda	Yes	2	31
Danto Machado	Yes	1	3
Perimetro	No	>150	2
Iguana	No	>150	0
Palizada	No	0	2

unopened and few seedlings will be present; where agouti are present, few fresh pods will remain intact, but many seedlings will be present. At four sites with, and three sites without, agouti we counted intact pods under one randomly chosen adult *H. courbaril* tree. Pods were counted on four 1-m wide transects radiating 10-m out from the tree bole. Seedlings < 30 cm in height were censused within a 10-m radius of the tree. All sites were censused in July 1995 except for the island of Palizada, which was censused in July 1996. As predicted, the mainland site, Lomo, and Redonda, each of which support agouti, had few intact pods and numerous *H. courbaril* seedlings (Table 2). The islands of Perimetro and Iguana, which do not support agouti, had many unopened pods and very few seedlings. However, two other sites did not follow the predicted pattern. We expected Danto Machado, which supports agouti, to have many *H. courbaril* seedlings, but it did not. We also expected to find many unopened pods on Palizada, but there were none.

These results show that the presence of agouti increases the probability that a *H. courbaril* seed will successfully establish. At sites with only small rodents present, neither seeds nor pods were removed by mammals from outside the cages. With agouti present, and also when other medium-size mammals were present, seed and pod removal was significant. In Costa Rica some of these removed pods are buried hundreds of metres away by agouti (Hallwachs 1986); our data indicate that individual seeds are also removed and buried by agouti, up to 6 m away from where they were placed.

Inside the mammal-proof cages, pod burial significantly increased one-year germination rates, as did the burial of individual seeds. As all of these seeds were protected from mammals, burial appears to afford not only protection from mammalian seed predators, but also from other agents of mortality such as invertebrate seed predators or desiccation. Unfortunately, from these data we cannot assess the advantage a seed gains from being removed from a pod by a mammal, as we do not know how many viable seeds were in each pod at the start of the experiment. Although *H. courbaril* seeds do occasionally germinate inside the pod and push it open, these young seedlings are usually deformed; most do not appear to establish a root system adequate to survive the dry season (Janzen 1983).

Five of the seven sites confirmed our prediction relating the presence of agouti and *H. courbaril* recruitment. Further, results from the two other sites did not damage the prediction; the low numbers of intact pods and recruits on Palizada and Danto Machado respectively may simply indicate that the *H. courbaril* trees on these islands have not produced fruit in recent years. Alternatively, agouti may maintain an intermittent presence on some Guri islands. Inter-island channels can be reduced and even disappear during the dry season when water levels are low. This may permit agouti and other mammals to occasionally visit sites and consume seeds and fruits which would otherwise be unavailable, thus complicating simple patterns of mammal presence and tree regeneration.

H. courbaril has continued to reproduce since the loss of its putative Pleistocene disperser (Hallwachs 1986, Janzen & Martin 1982), and it is possible that limited regeneration may occur in the absence of agouti. If agouti and all other large mammal species are eradicated from a forest, as has occurred at Los Tuxtlas in Mexico (Dirzo & Miranda 1991), *H. courbaril* pods will probably lie on the forest floor unopened. Although a few of the undispersed seeds within the pods may germinate, they will do so close to their parent tree, and their deformed root system will probably not be sufficient for survival (Janzen 1983). After 1–2 y pods rot and can easily be opened by small rodents. If any seeds have survived, they may then be collected and scatter-hoarded by spiny rats (*Proechimys* spp.). However, it is unlikely that this dispersal mechanism could be as efficient as the agouti–*H. courbaril* interaction.

Agouti clearly enhance the probability of recruitment and may be necessary for the long-term survival of *H. courbaril*. Moreover, changes in mammal community composition, including the loss of agouti, appear to have played an important role in the reduction of forest diversity on islands in Lago Gatun, Panamá (Asquith *et al.* 1997, Leigh *et al.* 1993). Agouti appear to be a critical part of some tree species' regeneration ecology, such that the loss of the rodent may ultimately precipitate the local extinction of the tree. It is of special concern that a number of such tree species, such as *Hymenaea courbaril* and *Dipteryx panamensis* (Forget 1993), are the dominants in old-growth neotropical forests.

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