SHORT COMMUNICATIONS

Variation in Seedling Density and Seed Predation Indicators for the Emergent Tree *Dipteryx panamensis* in Continuous and Fragmented Rain Forest[1]

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ABSTRACT

Seedling density and the condition of stony endocarps of the tree *Dipteryx panamensis* were assessed in protected continuous forest and two forest fragments exposed to hunting and selective logging. Seedling density was higher in forest fragments than in continuous forest, while more whole endocarps and fewer chewed and half endocarps were found in fragments, indicating lower seed predation at fragment sites. These findings appear to contradict two earlier *D. panamensis* studies and we discuss methodological differences that could account for our disparate results. Hunting and fragmentation effects on mammal populations are suggested as a cause for the altered recruitment pattern in fragments.

RESUMEN

La densidad de las plantulas y la condición de los endocarpios de *Dipteryx panamensis* fueron determinadas en bosque intacto no perturbado y dos bosques fragmentados expuestos a caza y a tala selectiva. La densidad de las plantulas fue mayor en los fragmentos del bosque que en el bosque intacto. Mas endocarpios enteros y menos endocarpios masticados y medios fueron encontradas en los fragmentos, indicando menor depredación de las semillas en los fragmentos de bosque. Estos resultados contradicen dos estudios anteriores de *D. panamensis* y discutimos las diferencias metodológicas que pueden explicar nuestros resultados dispares. Se sugiere la presión de la caza como una causa para el ambiente alterado de reclutamiento en los fragmentos.

FOREST LOSS IN THE TROPICS EXCEEDS 15 MILLION HECTARES ANNU-ALLY (Whitmore 1997), leaving behind a mosaic of forest patches in a human-dominated matrix (Dale & Pearson 1997, Laurance & Bierregaard 1997). Many remnants on private land face continued pressure from hunting and resource extraction. It can be challenging to differentiate between strict fragmentation effects and the influence of ongoing human activities (Terborgh 1992), but forest fragments typically experience significant changes in their faunal communities (Peres 2001). Hunters often target known seed predators and seedling browsers, including forest ungulates and large-bodied rodents (Peres 2001). Hunting pressure has been implicated in altered rates of seed predation for tropical trees, either through direct loss of important frugivores and granivores (De Steven & Putz 1984, Wright *et al.* 2000, Wright & Duber 2001, Wyatt & Silman 2004), or through the ecological release of nontarget species (Guariguata *et al.* 2002). Spatial patterns of seed and seedling mortality are thought to influence the high diversity and spatial heterogeneity of tropical forest tree communities (Janzen 1970, Connell 1971). Changing these patterns and processes will probably change forest community characteristics and may exacerbate the long-term loss of species diversity in fragmented and disturbed tropical forest (Putz *et al.* 1990, Terborgh 1992, Wright & Duber 2001).

Dipteryx panamensis (Pittier) Record & Mell (Fabaceae; Papillionoideae) is a large canopy emergent tree occurring in lowland wet tropical forests of the Caribbean slope, from Colombia to Nicaragua (Flores 1992). Considered a keystone species for the timing and quantity of its fruit production, *D. panamensis* bears single-seeded drupes during the low-rainfall season when few other trees are in fruit (Frankie *et al.* 1974). The seeds are encased in a thick woody endocarp that can persist on the forest floor for 2 yr or more (T. Hanson, pers. obs.). Primary seed dispersal is by frugivorous bats and occasionally by primates or other mammals (Bonaccorso *et al.* 1980). Known seed predators include agoutis (*Dasyprocta punctata*), squirrels (*Sciurus* spp.), peccaries (*Tayassu* spp.) and the great green macaw (*Ara ambigua*; Bonaccorso *et al.* 1980, Flores 1992). Scatterhoarding by agoutis probably also contributes to seed dispersal (Bonaccorso *et al.* 1980, Forget 1993). The very high seed and seedling mortality near parent trees (Clark & Clark 1984, De Steven & Putz 1984) may promote wide spacing in natural populations (Bonaccorso *et al.* 1980, Clark & Clark 1984). Though reduced by harvest and forest clearing over much of its range, *D. panamensis*

persists in fragments and pastures and remains a conservation priority. It is listed as a CITES Appendix III species (UNEP-WCMC 2005) and was recently designated as vulnerable to extinction in an evaluation of Costa Rican plant species using IUCN Red List criteria (Estrada Chavarría *et al.* 2005). Understanding the effects of forest fragmentation on seed predation and seedling recruitment has important management and conservation implications.

This study addresses two questions: (1) Does the density of seedlings differ between continuous forest and medium-sized forest fragments? (2) Do the proportions of whole, half, and chewed endocarps vary between continuous forest and medium-sized fragments? Seeds and seedlings can experience different predation pressures when dispersed away from adult trees than when dispersed close to or beneath adults (Janzen 1970, Connell 1971). To assess both situations, our research questions are addressed at a distance >20 m from all potential parents, as well as directly below adult crowns. With the expectation that fragmented forests contain reduced populations of known *D. panamensis* seed predators, we predict higher seedling density and lower seed predation at forest fragment sites.

One continuous forest and two medium-sized fragments in northeastern Costa Rica served as the study sites for this project. La Selva Biological Station (1600 ha) adjoins Braulio Carrillo National Park, forming the largest intact forest in the region (described in detail in McDade *et al.* 1994). Pineda (40 ha) and Ladrillera 3 (52 ha) are privately held remnants surrounded by pastures and managed under sustainable forestry principles in partnership with the Fundación para el Desarrollo y Conservación de la Cordillera Volcánica Central (FUNDECOR), a local nongovernmental organization. The fragment sites and the focal area at La Selva are separated by a mean distance of 17.9 km, lying in primary wet tropical forest at elevations of 40–75 m, with annual rainfall of *ca* 4000 mm (measured at La Selva; McDade & Hartshorn 1994). Ladrillera 3 and Pineda maintain diverse canopies with populations of adult (>30 cm DBH) *D. panamensis* at 0.21/ha and 0.58/ha respectively, determined by extensive ground surveys and GPS mapping of all adult individuals at each site. Personal observations of hunting activity and conversations with landowners and local residents indicate that both fragments experience continuous hunting pressure. The focal study area at La Selva (*ca* 85 ha) is in unlogged continuous old-growth forest protected from hunting for at least the last 20–30 yr, with adult *D. panamensis* populations at 0.45/ha. Adult density and location data at La Selva are from an ongoing demographic study by Clark and Clark (*e.g.*, 1984; 1985; 1987).

To assess predation pressures away from adult trees, endocarps and seedlings were surveyed within 100 × 4 m transects placed at preselected start points and directions within the La Selva Grid System (described in Clark 1998) (N = 33) and along GPS-referenced transects in the fragments (Ladrillera 3, N = 16; Pineda, N = 12). These transects were spatially arranged for a systematic sample of each site and their numbers reflect the relative size and shape of sites. Transects passing within 20 m of the bole of an adult *D. panamensis* were discarded. All *D. panamensis* seedlings in the transects were measured at the base of the stem and classified as <5 mm or 5–10 mm in diameter, following size-classes established by Clark and Clark (1987). All *D. panamensis* endocarps were individually inspected and classified as either whole, half, or chewed. Whole endocarps included those with the dorsal and ventral sutures intact and no markings breaching the inner seed cavity; these were considered undamaged by predators. Chewed endocarps were empty and bore the piercing tooth marks of agoutis, squirrels or other animals; these were considered preyed upon. Half endocarps included those split along the sutures, which could occur through germination or natural drying, or through predation by peccaries or great green macaws. Their predation status is discussed below. Transects away from adult trees were carried out from January to March 2005 at La Selva, and in the fragments from February to April 2005.

To assess predation pressures near adult trees, *D. panamensis* seedling density and endocarp condition were similarly surveyed in a second set of transects located directly under the crowns of adult *D. panamensis* (La Selva, N = 10; Ladrillera 3, N = 4; Pineda, N = 3). These transects measured 20 × 4 m and were sited to radiate in randomly selected directions from the trunks of focal trees. Focal trees were chosen to reflect similar site conditions: closed-canopy interior forest on alluvial soils with moderate slope (<10%). All near-adult transects were completed in July 2005.

Limited sample size prevented separate analysis of seedling size-classes, so count data for both classes were combined and compared between La Selva and the two fragment sites using Wilcoxon signed rank tests. Count data for endocarp condition at La Selva and the fragments were compared using chi-square tests for Independence. Data from near-adult and away-from-adult sampling were analyzed separately. All analyses were performed with SAS software, version 9.1 (©2002-2003, SAS Institute Inc.).

Density of seedlings was significantly higher in the fragments than at La Selva near adult trees (Z = 3.6456, P = 0.003), and trended higher away from adults (Z = 1.8148, P = 0.0696) (Fig. 1). The number of half, whole and chewed endocarps differed between La Selva and the fragments near adults (χ^2 = 630.829, P < 0.0001) and away from adults (χ^2 = 56.491, P < 0.0001) (Fig. 2). In both cases chewed endocarps and half endocarps were more common at La Selva, while more whole endocarps were found at fragment sites. Though not analyzed separately, large seedlings (5–10 mm dia) were present in fragments both near adults (N = 21) and away from adults (N = 7), while none was encountered anywhere at La Selva. All trends between La Selva and the fragments were similar near and away from adult trees, suggesting causal factors that affect both settings.

Results of this study support the premise that forest fragmentation and human disturbance can strongly influence seed predation and seedling recruitment. Hunting pressure is particularly high in this landscape (T. Hanson, pers. obs.), and Guariguata *et al.* (2000, 2002) found a depauperate mammal fauna in other fragments nearby. They noted few or no signs of squirrels, agoutis, or peccaries: three of the most important *D. panamensis* seed consumers. The lower proportion of chewed endocarps and the increase in whole endocarps in the fragments met our expectations and suggest less seed predation in Pineda and Ladrillera 3 than at La Selva (Fig. 2). Half-endocarps can result from seed predation, but may also be the product of natural splitting during germination. Guariguata *et al.* (2002), however, found no difference between germination rates for surface-sown or buried *D. panamensis* seeds in nearby fragments and at La Selva, while De Steven and
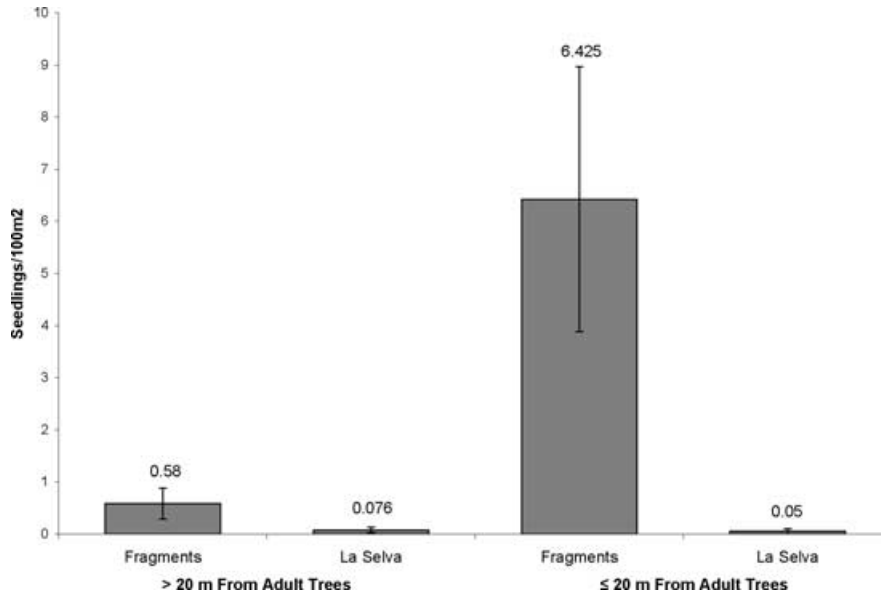
FIGURE 1.   Mean number of *D. panamensis* seedlings per 100 m² sampled away from adult trees (>20 m) and near adult trees (≤20 m) in forest fragments and at La Selva Biological Station, Costa Rica. Error bars indicate one SE; numbers indicate mean seedlings/100 m².

Putz (1984) found similar germination rates among surface-sown laboratory treatments and surface-sown and buried field treatments. Assuming similar germination patterns among our sites, the reduced number of half-endocarps in the fragment site may again indicate less seed predation, particularly by peccaries. Data from our seed predation indicators represent at least two fruiting periods, due to the long persistence of *D. panamensis* endocarps on the forest floor.

Altered mammal populations also offer an explanation for the higher densities of *D. panamensis* seedlings found at our fragment sites (Fig. 1). In a review of hunting effects on vertebrate and plant populations, Wright (2003) supported this view, noting that more seeds may survive to germination in defaunated sites, and that postgermination survival may benefit from reduced vertebrate herbivory on seedlings. Alternatively, among-site differences in seedling
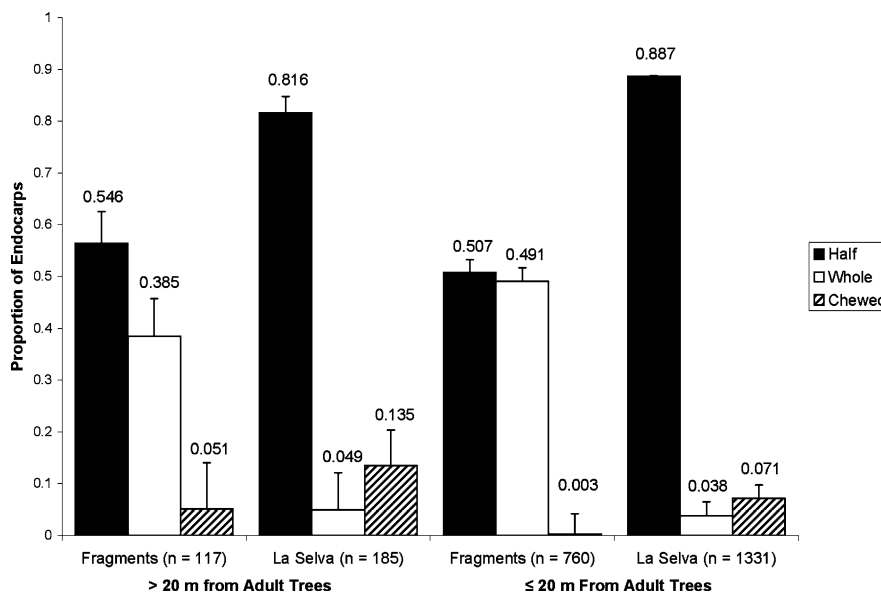

FIGURE 2.   The proportions of whole, half, and chewed endocarps of *D. panamensis* encountered away from adult trees (>20 m) and near adult trees (≤20 m) in two forest fragments and at La Selva Biological Station, Costa Rica. Error bars indicate one SE; numbers indicate exact proportions; N = number of endocarps.

density could simply be a reflection of site-specific adult density. But in our study we found higher seedling densities in the fragments, where the adult density was similar to or lower than at La Selva. The presence of larger (5–10 mm) diameter seedlings in the fragments suggests that this increased density may be more than an ephemeral trend. These larger, more robust individuals may represent fruiting events several years in the past, as Clark and Clark (1987) found that a 5-yr-old cohort of *D. panamensis* seedling averaged only 5 mm in diameter.

Our results agree with several recent studies that have documented decreased seed predation in heavily hunted and fragmented forests (Wright & Duber 2001, reviewed in Wright 2003, Wyatt & Silman 2004). Dirzo and Miranda (1991) noted greatly reduced herbivory in a hunted Mexican rain forest, accompanied by high seedling density and low understory diversity. De Steven and Putz (1984) observed lower seed predation and increased seedling recruitment at sites in Panama exposed to hunting. Wright *et al.* (2000) found altered seed predation patterns and increased seedling density for two palm species in forests with increased levels of hunting. Other research, however, has shown an increase in seed predation in fragments (Guariguata *et al.* 2002) and increased seed predation and seedling predation on small islands (Asquith *et al.* 1997).

Working in the same landscape as the present study, Guariguata *et al.* (2002) reached nearly opposite conclusions for *D. panamensis*, noting higher seed predation rates in fragments than at La Selva. They suggested that hunting pressure on larger mammals may have allowed an ecological release of smaller (<1 kg) seed consumers, which follows the Asquith *et al.* (1997) observation of high seed predation rates for *D. panamensis* on islands in Panama where spiny rats (*Proechimys semispinosus*) were the only resident fruit and seed consumers. The disparity between these results and the present study may arise in part from differences in methodology. Both Guariguata *et al.* (2002) and Asquith *et al.* (1997) defined seed predation as the removal of whole endocarps that were experimentally placed on the forest floor, which may overestimate the contribution of small mammals that eat the fleshy mesocarp but do not breach the endocarp to reach the seed, or that scatterhoard endocarps intact, some of which may later be forgotten. Conversely, our technique of assessing endocarp damage may underestimate predation by mammals that bury or cache endocarps out of sight.

Additional findings from these studies, however, also point to high predation pressure in fragments and on islands and cannot be explained by methodological differences. Asquith *et al.* (1997) followed the fate of *D. panamensis* seedlings at their small island sites and found extremely high rates of mortality from herbivory, presumably by spiny rats. Guariguata *et al.* (2002) measured seed dispersal and individual seed survival, noting higher seed dispersal and survival rates at La Selva than in fragments. Many authors have noted the complexity of interactions between defaunation and plant populations, suggesting that the impacts may be specific to the sites and biota involved (Asquith *et al.* 1997, Guariguata *et al.* 2002, Wright 2003, Wyatt & Silman 2004). Site and biota variation may be a factor here, as the fragments used by Guariguata *et al.* (2002) were considerably larger (>110 ha) than those used in our study (<55 ha), while the islands studied by Asquith *et al.* (1997)

have experienced major ecological shifts since their isolation from continuous forest (Putz *et al.* 1990), and may not be comparable with mainland fragments.

We suggest that hunting and fragmentation effects on mammalian seed predator populations offer a credible explanation for our results, but other factors may be involved. Natural fluctuations in seed predator abundance can also impact predation rates and seedling recruitment (Asquith *et al.* 1997, DeMattia *et al.* 2004). While our data reflect at least two fruiting periods, they may still represent a temporary disparity between predation activity in La Selva and the fragments. The timing of our sampling effort may also be relevant. At Barro Colorado Island in Panama, fruits mature from middle of December through early March (Bonnacorso *et al.* 1980) and seedling germination peaks several weeks after heavy rain events in late March or April (De Steven & Putz 1984). Our transects away from adults were conducted from the middle of January through early April, so it is possible that early sampling did not reflect a full season's fruit crop and that fruits had not long been exposed to predators, while later sampling may have captured more fruit-of-the-year seedlings. Endocarps from previous years would not be affected by this variation, nor would the near-adult transects, which were all carried out in July. Reduced predation activity may account for the higher seedling density we observed in fragments, but *D. panamensis* seedling survival is also influenced by light conditions (De Steven & Putz 1984, De Steven 1988), invertebrate herbivory and litterfall (Clark & Clark 1985), and fungal pathogens (De Steven & Putz 1984). Further research is needed on the influence of these factors in fragments, as well as on site-specific predator abundance and compensatory predation rates that could clarify our results in light of previous work.

Seed and postgermination predation by mammals has been called the most significant barrier to seedling recruitment for *D. panamensis* (De Steven & Putz 1984). The higher density of seedlings in fragments suggests that this barrier may be breaking down, both near and away from adult trees, while the presence of larger individuals suggests it is more than an ephemeral trend. If so, it has implications for the spacing and genetic diversity of *D. panamensis* populations and may negatively impact the diversity of forest fragment tree communities.

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