

Functional differences within a guild of tropical mammalian frugivores

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Abstract. Many plants interact with groups of mutualist pollinators and seed dispersers. A key issue for both basic ecology and conservation is whether the different species within these guilds of mutualist animals are functionally equivalent. Comparing the relative effects of sympatric mutualists is important for understanding the evolution of multispecies mutualisms and for predicting mutualism stability in the face of anthropogenic change. However, empirical comparisons of the population-level impacts of mutualist animals on their host plant are rare, particularly for seed dispersal mutualisms in species-rich ecosystems. We compared the influence of three seed-dispersing tropical mammals, lar gibbons (*Hylobates lar*), sambar deer (*Rusa unicolor*), and red muntjac deer (*Muntiacus muntjak*), on the demography of a shared host tree in Thailand, *Choerospondias axillaris* (Anacardiaceae). Sambar and muntjac dispersed far more *C. axillaris* seeds than did gibbons. While sambar deposited many seeds under female tree canopies, muntjac were the only disperser to move seeds to open microhabitats, where *C. axillaris* seed germination, seedling survival, and initial growth are enhanced. Using stage-based population models, we assessed how disperser-specific seed dispersal, variation in the frequency of canopy gap formation, and their interaction influenced the potential population growth of *C. axillaris*. Large differences in dispersal quantity and small differences in dispersal quality among sambar and gibbons resulted in similar and negligible impacts on the tree's population dynamics. Muntjac, by taking some of the seeds to open microhabitats, are projected to have a greater positive impact on *C. axillaris* demography than either sambar or gibbons. Model comparisons of population-level species impacts may allow us to predict which ecological interactions are at risk from loss of critical species.

Key words: biodiversity; *Choerospondias axillaris*; demography; dispersal effectiveness; gap dynamics; gibbons; muntjac deer; mutualism; redundancy; sambar deer; seed dispersal; tropical seasonal forests, Thailand.

INTRODUCTION

Mutualistic interactions are widespread in nature (Bronstein 1994, Ness et al. 2006). Historically, consideration of mutualisms has centered on highly specialized and tightly coevolved interactions where a single species interacts with only one partner (Stanton 2003). Yet it is increasingly clear that most mutualisms are more complex, often involving networks of interacting species. Presently, we lack a comprehensive understanding of how the different species within these mutualist guilds compare in the overall effects on their host (Waser et al. 1996, Stanton 2003). That is, do different mutualist partners have different impacts on host fitness or abundance, or are mutualists in the same guild functionally similar? Answers to these key questions remain elusive (Stanton 2003, Howe and Miriti 2004).

Determining the relative benefits that different mutualists provide to their host is essential for understanding how multiple-species mutualist assemblages are maintained, given the potential for competition among the mutualists (Palmer et al. 2008). Distinguishing the relative costs and benefits of associations with particular mutualists can also shed light on whether hosts can select for those mutualists that are most beneficial (Yu et al. 2001, Palmer et al. 2003). Finally, quantifying the relative effectiveness of different mutualist partners can elucidate how changing ecological context (Bronstein 1994) may influence the spatial mosaic of the coevolution of mutualistic traits (Gomulkiewicz et al. 2003).

In this paper we are particularly interested in how different mutualist partners may similarly or differentially influence the population dynamics of their host. This is of critical importance to conservation. Since species loss from mutualist guilds is an increasingly recognized problem (Cordeiro and Howe 2001, Peres and Palacios 2007), it is imperative that we understand whether particular species have disproportionately strong effects on their host (Christian 2001). Plant–

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disperser systems are excellent cases for comparing the relative effectiveness of different mutualist partners because seed dispersers usually differ in both dispersal quantity and quality (sensu Schupp 1993). For a given plant species, some animals may remove more fruit (Howe and Vande Kerckhove 1981), disperse seeds farther (Russo et al. 2006, Jordano et al. 2007), take seeds to better microhabitats (Reid 1989), be more effective at seed scarification (Figueroa et al. 2002), or destroy fewer of the seeds that they consume (Jordano 1983). Yet we know surprisingly little about whether this variation in dispersal effectiveness has meaningful effects on plant demography, abundance, or population dynamics. Most seed-dispersal studies have not quantified how variation in dispersal effectiveness influences plant abundance or dynamics (Howe and Miriti 2004). In one of the only studies that has explored population-level effects of different dispersers of the same plant, the “effectiveness” (relative abundance \times visitation rate \times seed handling \times probability of safe-site deposition) of a bat species in dispersing a Mexican columnar cactus was 4–5 orders of magnitude greater than that of four avian seed dispersers (Godinez-Alvarez et al. 2002). Yet the modeled cactus population growth rate attributable to each of the five animal species differed only slightly because of the high variability and low elasticity of seed dispersal relative to other vital rates (Godinez-Alvarez et al. 2002). Thus the relationship between disperser effectiveness and relative impacts on plant population dynamics is not necessarily straightforward (Godinez-Alvarez and Jordano 2007).

Assessing the relative effectiveness of different mutualist partners is especially critical in the tropics because many plants rely on multiple seed-dispersing species (Estrada and Fleming 1986, Bascompte and Jordano 2007). Moreover, many tropical frugivores are at risk of extinction from habitat loss and fragmentation (Cordeiro and Howe 2001) as well as overhunting (Peres and Palacios 2007). In the simplest case, plants that lose their sole disperser species can clearly be negatively affected demographically (Traveset and Riera 2005). But for the more common case, where plants are dispersed by several or many frugivore species (Bond 1995), it is unclear how loss of any one frugivore species might affect host-plant abundance. The general issue of whether diversity within frugivore mutualist assemblages buffers host plants from the negative effects of loss of any single mutualist species remains an open question.

In this study, we compare the demographic effects of seed dispersal by gibbons (*Hylobates lar*), red muntjac deer (*Muntiacus muntjak*), and sambar deer (*Rusa unicolor*; syn. *Cervus unicolor*) on the canopy tree *Choerospondias axillaris* (Roxb.) Burt & Hill (Anacardiaceae) in tropical seasonal forest of Thailand. We quantified how these three dispersers vary in the effectiveness of their seed dispersal by determining both the quantity of seeds they disperse and the microhabitat into which they bring seeds. We then assessed how

variation in dispersal effectiveness affects *C. axillaris* abundance by combining results from observations, demographic monitoring, and experiments into a staged-based matrix model of *C. axillaris* population growth. This approach is fairly novel in two respects. First, ours is one of the few attempts to model how variation in dispersal effectiveness that influences seed and seedling fate translates into long-term changes in plant population growth. Second, like many tropical trees (Whitmore 1989), *C. axillaris* recruitment may depend on forest canopy gaps; thus the potential effects of dispersers cannot be fully assessed without an understanding of gap dynamics. Therefore, we combine our stage-based population model with a separate matrix model that depicts realistic rates of canopy-gap formation and subsequent fill-in. This enabled us to put seed dispersal in a biologically realistic context and explore how dispersal may interact with microhabitat dynamics to influence the demographic impacts of each disperser.

METHODS

Study area and species

Khao Yai National Park (14°26' N, 101°22' E; 2166 km²) straddles a large plateau, approximately 700–900 m elevation, with seasonal evergreen or mixed evergreen–deciduous forest types throughout most of the area and mixed deciduous forest on the steep edges (Smitinand 1977). Mean annual rainfall is ~2200 mm, mostly occurring during May–October; there is a pronounced dry season from November through April. Abundances of many large-mammal species in the central portion of the park is high (Lynam et al. 2006). A 30-ha “forest-dynamics” plot was established in 1993 in the central western portion of the park; all woody stems ≥ 1 cm in diameter at breast height (dbh; 130cm) have been mapped, marked, and identified. The plot contains 200 tree species ≥ 10 cm dbh, where *Choerospondias axillaris* is the 24th most abundant by density (1.2% of trunks ≥ 10 cm dbh), and third most abundant by cumulative basal area (5.9% of total; W. Y. Brockelman, unpublished data). The plot contained 159 adult *C. axillaris*, of which 59 trees were female.

Choerospondias axillaris (syn. *Spondias axillaris* Burt & Hill) is a large (up to 30 m tall) canopy tree widely distributed in tropical Asia. It is dioecious and females bear fruits from June through October; the fruits are 2–3 cm long, and are composed of a pericarp surrounding fibrous, watery flesh, with a single stone inside $\sim 1.9 \times 1.4$ cm in size. Each stone (hereafter “seed”) has a very hard covering over five embryos. In Khao Yai, fruits are consumed almost entirely by gibbons, sambar, and red muntjac (Kunsakorn 2001, this study). While rodents consume some fruits and may perform primary or secondary dispersal of seeds, relatively few seeds are dispersed by rodents relative to total fruit production (see *Results: Seed dispersal* . . . , below). *C. axillaris* is often present in early successional habitats, and may be dependent on gaps for seedling survival, but persists into

mature mixed-evergreen seasonal forest. *C. axillaris* is highly unusual among tropical Asian trees in that its fruits drop off the tree when ripe rather than hanging on until eaten or rotten (Corlett 1996). Moreover, fruits and seeds are too large to be dispersed by most birds, and the fibrous pulp adheres strongly to the seed coat, a fruit anatomy not favored by hornbills (Bucerotidae; P. Poonswad, *personal communication*). These may be “partner selection mechanisms” (sensu Stanton 2003) whereby the tree promotes consumption of its fruits by terrestrial, non-volant frugivores. We explored this possibility by comparing the seed dispersal effectiveness of arboreal gibbons (*Hylobates lar*) and two species of terrestrial deer, sambar and red muntjac. Gibbons consume *C. axillaris* fruits before they fall and later defecate the seeds. Gibbons are common in much of Khao Yai; the forest-dynamics plot includes the entire home range of one group of animals (“Group A” composed of two adults plus, generally, two other individuals usually, but not always, their young) that have been studied since 1980 and are habituated to the presence of researchers. Sambar and red muntjac are large (109–260 kg) and small (20–28 kg) deer, respectively, that are distributed widely across tropical Asia. Muntjac density in the vicinity of the forest-dynamics plot during the time of this study was estimated at 0.7–4.2 deer/km² (Lynam et al. 2006); no such data are available for sambar. Both deer species primarily consume foliage, but they also eat large quantities of *C. axillaris* fallen fruit when available. Deer regurgitate “cleaned” *C. axillaris* seeds, usually while bedding and ruminating (W. Y. Brockelman and J. F. Brodie, *personal observations*). Although dispersal of undispersed fallen fruit is often considered secondary dispersal (Howe and Smallwood 1982), we treat it here as primary dispersal because of the tree’s unique trait of dropping fruits when ripe, possibly to attract terrestrial dispersers.

Seeds of *C. axillaris* fall or are dispersed during the monsoon season (July–November), and remain on the ground to germinate the following wet season; we have detected no seed bank (see *Results: Seed dispersal . . .*, below). The seeds germinate equally well whether they are defecated by gibbons, regurgitated by deer, or the fruits are uneaten (Kunsakorn 2001); variance in germination is mainly due to microhabitat differences among deposition sites (see *Results: Seed dispersal . . .*, below). Seeds are sufficiently large, conspicuous, and easily identifiable that they can be sampled with transects rather than seed traps.

Field sampling

We established 15 belt transects (500 × 4 m each) across the forest-dynamics plot (accounting for 10% of the plot). We surveyed these transects weekly for 10 weeks from mid-July to September in 2003 and 2004. We recorded the number of dispersed *C. axillaris* seeds, the number of seeds in the pile in which they had been deposited, and the identity of the disperser. Disperser

identity was easily determined because gibbons defecate seeds whereas deer regurgitate them. The identity of the deer species that dispersed seeds could be determined by the size of tracks and scat. Because fieldwork took place during the rainy season, the forest floor stayed continually moist and deer tracks could generally be found under the leaf litter. The quantity of seeds dispersed by deer and the microhabitats to which all frugivores dispersed seeds were measured from these transect data. The deer deposited very shiny piles of regurgitated seeds and we are confident that, with our regular sampling, we missed very few deer-dispersed seeds. Gibbon-defecated seeds, however, were somewhat less conspicuous. Therefore we assessed the quantity of seeds dispersed by gibbons by following individuals all day for 5–6 days per month and recording exactly how many *C. axillaris* seeds were defecated. To calculate the total number of seeds dispersed by gibbons on the plot during the study period, we divided the total number of seeds dispersed by single gibbons on observation days by the proportion of the study period during which observations took place and multiplied by the estimated mean number of gibbons on the plot at any one time.

We measured seed germination and predation experimentally to determine how canopy cover, seed-pile size, and being under an adult female *C. axillaris* canopy influenced the seed-to-seedling transition. We treated “under adult female canopy” as a separate microhabitat because it was nearly always high canopy cover, yet could also have had elevated seed and seedling mortality from seed-predator attraction or host-specific pathogens (cf. Janzen 1970, Connell 1971). In 2003 and 2004 we set up closed wire cages (30 × 30 × 15 cm wire enclosures pinned to the ground) with arrays of seeds at four densities (2, 8, 30, or 100 seeds/pile, which spans the range of observed deposition-pile sizes). These arrays were replicated across 15 sites that spanned the range of forest canopy-cover conditions; one third of sites were under adult female canopies (total of 2100 seeds/yr). The mesh size of the closed cages was ~1 cm², which excluded vertebrate seed predators but not small insects or fungi. Previous work in Khao Yai has shown that seed handling (i.e., fruit pulp intact vs. defecation by gibbons vs. regurgitation by deer) does not affect germination (Kunsakorn 2001), so we did not test this effect further in this study. In order to examine rates of post-dispersal seed predation, we repeated the seed-addition experiment described above, at the same sites, using “open” cages (same wire mesh as above but in a 3-cm-tall ring surrounding the seeds; total of 2100 seeds/yr). The open cages prevented the seeds from rolling away but allowed access by seed predators.

The numbers of seedlings in closed cages and remaining seeds in open cages were recorded the year following the initiation of each experiment. We performed multiple logistic regressions of seed-pile size, canopy-cover proportion (see below), and female canopy (a binary measure of whether the site was under

a fruiting adult) vs. germination (closed cages) and seed removal rates (open cages). We report R^2 values for full multiple linear-regression models, log-likelihood (LL) values for multiple logistic regressions (both significant at $\alpha = 0.05$), and both individual parameter coefficients (β) and partial P values.

To assess whether removed seeds were secondarily dispersed or destroyed by small mammals, we set out piles of 10 seeds at each planting-array site in each year (200 seeds each year), to which we had glued 60 cm of thin nylon string (cf. Forget and Milleron 1991). We returned 14 days later and scoured a 5-m-radius circle around the point where the pile had been placed, looking for strings, which we followed to the attached seeds to determine whether they had been destroyed or were still intact.

We marked all naturally occurring seedlings on the transects ($N = 670$ seedlings) and measured their survival and growth from 2003–2004 and 2004–2005. We assessed the effects of canopy cover, height, and mother-tree canopy on seedling survivorship using multiple logistic regressions and on seedling growth using linear multiple regressions.

Individuals of *C. axillaris* >1.3 m tall but smaller than 18 cm dbh were considered juveniles, those >18 cm dbh were defined as adults, as this was the smallest size of any observed fruiting tree. Juvenile survival and growth and adult survival were measured from repeat censuses of all marked individuals on the entire 30-ha plot. We estimated tree fecundity by visual counts (with 8×40 binoculars) of fruit crop at the beginning of the fruiting season in a random sample ($N = 14$ trees) of the total adult female population. We also measured the proportion of the total fruit crop that had dropped or been dispersed during the field season by repeating these visual counts (and counting seeds on the ground under the canopies) at the end of the field season. We compared fruit crop between years, and assessed its relationship to tree diameter using multiple linear regressions.

We measured canopy cover at all naturally dispersed seed piles with hemispherical canopy photographs, at locations where we found seedlings on transects, and at sites where we placed experimental seed arrays. All photographs were taken 1 m above the ground and analyzed for canopy-cover proportion using HemiView 2.1 (Delta-T Devices, Cambridge, UK). To assess the change in forest cover over time, we set up 218 permanent photo points across a range of canopy conditions on 10 of the 15 transects. At each, we took hemispherical canopy photos every year, 2003–2005. We then constructed an annual transition matrix for microhabitat types.

Population model

We used female-only, post-birth census, stage-based matrix projection models to assess the influence of seed dispersers on the population dynamics of *C. axillaris*. This model includes both demographic transitions for *C.*

axillaris and transitions among microhabitat states, since forest microhabitat is dynamic through time and the demographic performance of *C. axillaris* is enhanced in light gaps. We used six stage–microhabitat classes: seedlings underneath female canopies, seedlings with 11–30% canopy cover, seedlings with 31–70% canopy cover, seedlings with 71–100% canopy cover, juveniles (>1.3 m tall but <18 cm dbh), and adults (>18 cm dbh). No points in the forest had less than 11% canopy cover. The seedling-stage boundaries were based on graphical inspection of the relationships between canopy cover and germination and seedling survivorship (cf. Morris and Doak 2002). Most (98%) of the microhabitat underneath adult females was in the 71–100% canopy-cover range, but this was considered a separate class because seedling survivorship was significantly lower (see *Results: Seed dispersal...*, below). Only adults reproduced, with fecundity estimated from measured fruit crops at the beginning of the two fruiting seasons. Seed dispersal to different microhabitats by different frugivores was measured from the transect data and expressed as a proportion of the total fruit crop available to the frugivores during the study period (i.e., total fruit crop produced minus the proportion of seeds remaining on or underneath the trees at the end of the study period). All vital rates were calculated from data pooled across years.

We used the microhabitat transitions probabilities measured from the repeat canopy photographs to construct a microhabitat transition matrix (C), rescaled so that each column summed to 1. Seedlings could “move” among microhabitats via gaps opening up or closing in above them, measured by microhabitat transition probabilities, C_{ij} . Gap formation was modeled to occur at a predictable time of year (cf. Pascarella and Horvitz 1998), specifically at the end of the rainy season (August–October) when winds increase (W. Y. Brockelman, *personal observation*). Therefore the order of events in the model was: seed dispersal > microhabitat transition > germination, seedling survivorship, and seedling growth. Germination, seedling survivorship, and seedling growth were measured at the median canopy-cover values for each microhabitat, using logistic (germination and seedling survival) or linear (seedling growth) regressions of each vital rate vs. canopy cover. We multiplied seed removal by the proportion of the removed seeds that had been predated (from the string experiments), to estimate total seed predation probabilities. Annual seedling-to-juvenile transition probabilities ($\text{Trans}_{j,\text{juv}}$) were measured as microhabitat-specific seedling growth (in vertical centimeters; from linear regressions of seedling growth vs. canopy cover) accounting for size structure within the seedling stages (cf. Crouse et al. 1987):

$$\text{Trans}_{j,\text{juv}} = \frac{\left(\text{Surv}_j^{(\text{SG}_j/\text{Hgt})^{-1}}\right) \times (1 - \text{Surv}_j)}{1 - \text{Surv}_j^{(\text{SG}_j/\text{Hgt})}} \quad (1)$$

where SG_j and $Surv_j$ are growth (in vertical centimeters) and annual survivorship, respectively, of seedlings in microhabitat j , and Hgt is the height cutoff between seedlings and juveniles (1.3 m).

Vital rates for juveniles and adults were independent of microhabitat, partly due to lack of microhabitat-specific data for these classes, and also because “canopy cover” loses much of its meaning for an adult tree that is itself part of the canopy. We therefore calculated transition of juveniles to adults using a formula identical to Eq. 1 except substituting juvenile growth (measured as centimeters in diameter) and survivorship for the seedling equivalents, and using a diameter stage boundary (18 cm) between juveniles and adults. (See Appendix A for details of model construction.)

We assessed the influence of the frugivore species (alone and all three combined) on *C. axillaris* population dynamics. For each of 10000 bootstrap iterations we resampled (with replacement) the raw data to estimate vital rates and constructed five population projection matrices that differed only in the seed-dispersal term (i.e., no dispersal, gibbon dispersal, muntjac dispersal, sambar dispersal, and dispersal by all frugivores combined). We then estimated the difference in *C. axillaris* lambda ($\Delta\hat{\lambda}$) for dispersal by each frugivore vs. no dispersal at all, and generated 95% bootstrap confidence intervals around these differences.

RESULTS

Seed dispersal and Choerospondias axillaris demography

Of the 8202 seeds naturally dispersed in 103 piles across both years, we could confidently identify the disperser for 79.6% of piles and 95.8% of total seeds. For these, all of the seeds were dispersed by gibbons, muntjac, and sambar except 22 seeds (0.3% of total) that were dispersed by a bear (*Ursus thibetanus* or *Helarctos malayanus*), 3 seeds (<0.1%) by an elephant (*Elephas maximus*), and 7 seeds (0.1%) by a civet (Viverridae). Handling by rodents was also evident in 1.4% of seeds, but it is unclear whether this represents primary or secondary dispersal. Of the dispersed seed piles where we could not definitively identify the disperser species (4.2% of total seeds), 37% were dispersed by deer (based on the shiny regurgitated seeds). However, due to a lack of distinct tracks (or tracks of both deer species) near the seeds we could not identify the species of deer.

The three frugivores differed in the quantity of *C. axillaris* seeds dispersed (ANOVA: $F_{2,3} = 171.37$, $P < 0.01$). Muntjac and sambar dispersed more seeds than gibbons (Tukey post hoc comparisons: $P < 0.01$), but there were no significant differences in dispersal quantity between the two deer ($P = 0.27$; Fig. 1). There were no significant differences between years in the proportions of seeds dispersed to the different microhabitats for gibbons ($\chi^2_3 = 0.51$, $P = 0.92$), muntjac ($\chi^2_3 = 0.02$, $P = 0.99$), or sambar ($\chi^2_3 = 0.16$, $P = 0.98$). Seeds were dispersed to different microhabitats roughly in propor-

tion to the availability of those microhabitats for gibbons ($\chi^2_3 = 1.31$, $P = 0.73$) and muntjac ($\chi^2_3 = 0.37$, $P = 0.95$). Sambar dispersed more seeds than expected by chance to the “underneath adult female canopy” microhabitat and fewer than expected to the other three microhabitats ($\chi^2_3 = 8.65$, $P = 0.03$). A majority of sambar-dispersed seeds were found under female *C. axillaris*, whereas muntjac and gibbons dispersed most of their seeds away from female canopies to forest in the 31–70% canopy-cover range (also see Appendix B). Muntjac were the only dispersers to deposit seeds in the two highest-light microhabitats (Fig. 1).

Fruit crop at the beginning of the fruiting season did not differ significantly between years (linear regression: $R^2 = 0.11$, $df = 24$, $P = 0.75$), and was not significantly related to tree diameter (β [individual parameter coefficient] = -11.84 , $P = 0.13$). Fruit production was 801 ± 106 (mean \pm SE) fruits per tree; on average $70.8\% \pm 4.1\%$ of seeds produced were dispersed by the end of the field season (i.e., were not still on or underneath the canopy). The percentage of seeds that were dispersed did not vary significantly between years (linear regression: $R^2 = 0.09$, $df = 24$, $P = 0.21$) or as a function of tree diameter ($\beta = 0.00$, $P = 0.49$).

Germination in experimental seed piles was negatively affected by canopy cover ($\beta = -3.75$, $P < 0.01$; see Fig. 2) and was significantly higher in 2003 than in 2004 (logistic regression: log likelihood (LL) = -148.8 , $df = 2009$, $P = 0.04$). However, seed germination was not significantly affected by seed pile size ($\beta = 0.00$, $P = 0.24$) or by being under an adult-female canopy ($\beta = -12.02$, $P = 0.82$). While germination under female trees was zero in our trials, this is at least partly an experimental artifact since seedlings do occur under female canopies in nature. All 2003 seeds that did not germinate and were not removed by 2004 ($N = 3350$ seeds) were monitored for the following year, and none germinated. Percentages of seeds removed from the open cages were $34\% \pm 5\%$ and $37\% \pm 6\%$ (mean \pm SE) for 2003 and 2004, respectively ($N = 2100$ seeds in each year); seed removal was not significantly affected by canopy cover, being under a female canopy, or seed-pile size. Post-dispersal seed predation was not significantly affected by canopy cover or location under a female canopy. Of removed seeds with strings attached, $80\% \pm 13\%$ and $84\% \pm 6\%$ (mean \pm SE) were recovered within 5 m in 2003 and 2004, respectively. Of these recovered seeds, the percentages of post-removal seed predation were $86\% \pm 14\%$ and $64\% \pm 11\%$ in 2003 and 2004, respectively.

Seedling survivorship was negatively affected by canopy cover ($\beta = -3.75$, $P = 0.01$; Fig. 2) and by being under an adult female canopy ($\beta = -0.89$, $P = 0.01$), but not by seedling height ($\beta = 0.03$, $P = 0.28$). Seedling survivorship (logistic regression: LL = -212.4 , $df = 580$, $P = 0.99$) and growth (linear regression: $R^2 = 0.07$, $df = 90$, $P = 0.17$) did not differ significantly between years. Seedling growth, however, was significantly negatively

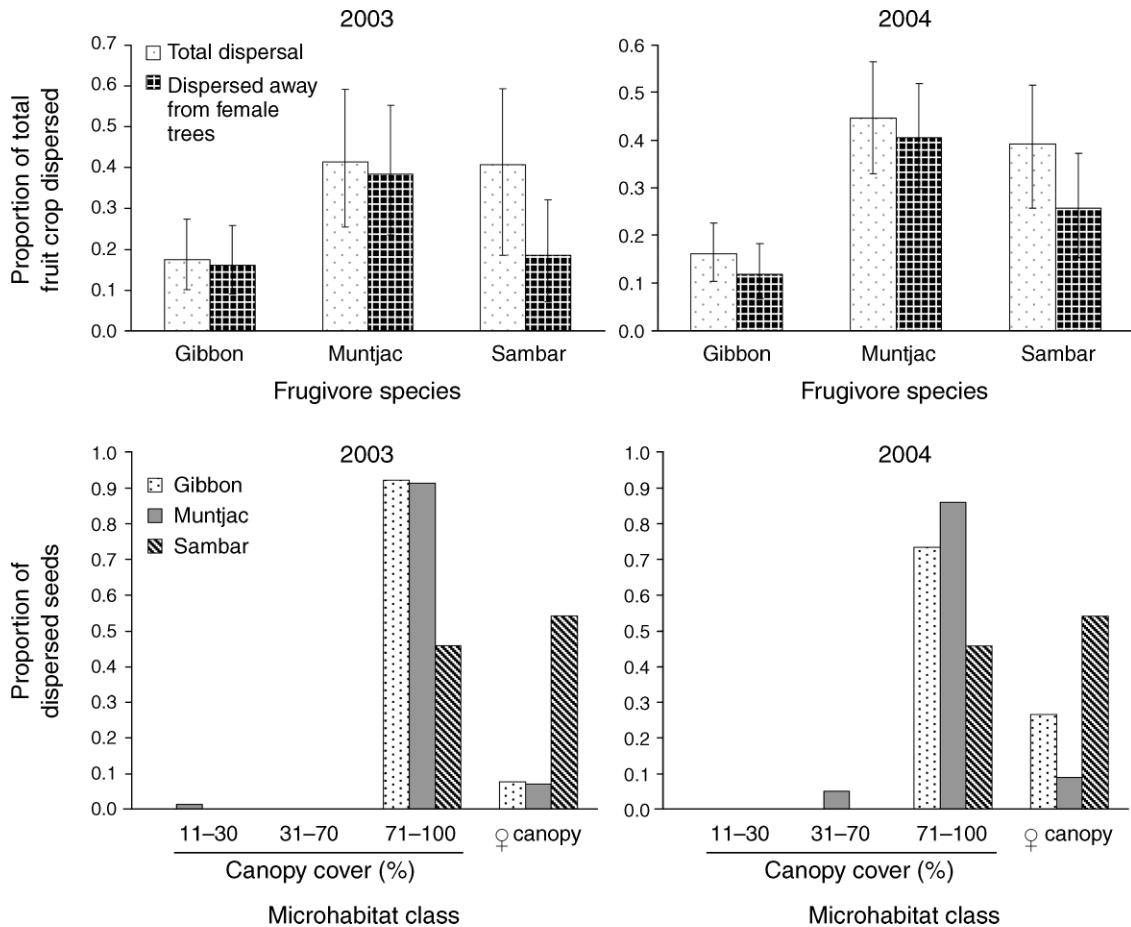


FIG. 1. (Top panels) Relative seed dispersal by each frugivore, expressed as a proportion of total fruit crop on the plot across two years. Error bars show 95% bootstrap confidence intervals. (Bottom panels) Deposition microhabitats of dispersed seeds across two years.

associated with increasing canopy cover ($\beta = -11.58$, $P = 0.01$; Fig. 2), but not by seedling height ($\beta = 0.08$, $P = 0.36$). Presence under an adult female canopy did not significantly affect seedling growth ($\beta = 0.93$, $P = 0.53$), but only 16 seedlings under female canopies survived (both yearly transitions combined), so we had low power to detect this effect.

Of the 15 juvenile *C. axillaris* on the Khao Yai forest-dynamics plot in 2002, 14 trees (93.3%) survived to the re-census three years later, resulting in a mean annual survivorship estimate of 0.98. Juvenile tree diameter did not significantly affect survivorship (logistic regression: $LL = 0.00$, $df = 14$, $\beta = 37.35$, $P = 0.84$) or growth (linear regression: $R^2 < 0.01$, $df = 14$, $\beta = 0.01$, $P = 0.93$). Juvenile growth was $1.89 \text{ cm} \pm 0.43 \text{ cm/yr}$ (mean \pm SE). Of the 159 adults on the plot at the first census, 152 adults (95.6%) survived to the re-census; estimated mean annual survivorship was 0.99. Adult tree diameter did not significantly affect survivorship (logistic regression: $LL = -27.75$, $df = 158$, $\beta = 0.03$, $P = 0.19$) or growth (linear regression: $R^2 < 0.01$, $df = 158$, $\beta = 0.01$, $P = 0.71$).

Gap dynamics

Forest cover across the biodynamics plot ranged from 11% to 98%. Forest canopy in gaps can increase over time as they fill in with vegetation, or decrease as wind continues to knock down trees and branches on their edges. Repeat canopy photography at permanent photo points revealed that overall the forest canopy cover is slowly increasing. Excluding the female-canopy microhabitat (with a canopy cover of 0.89 ± 0.06 [mean \pm SD]), the majority of photography points showed increases in canopy cover as they filled in with vegetation.

Population model

We first asked how the microhabitat into which seeds were dispersed might affect *C. axillaris* population growth. Here we assumed an unchanging microhabitat with no inherent gap dynamics. In this case, canopy cover significantly influenced *C. axillaris* population-growth rates. $\hat{\lambda}$ was higher in the 11–30% canopy-cover microhabitat (1.123 ± 0.042) than in the 31–70%, 71–100%, and “under female canopy” microhabitats (0.985

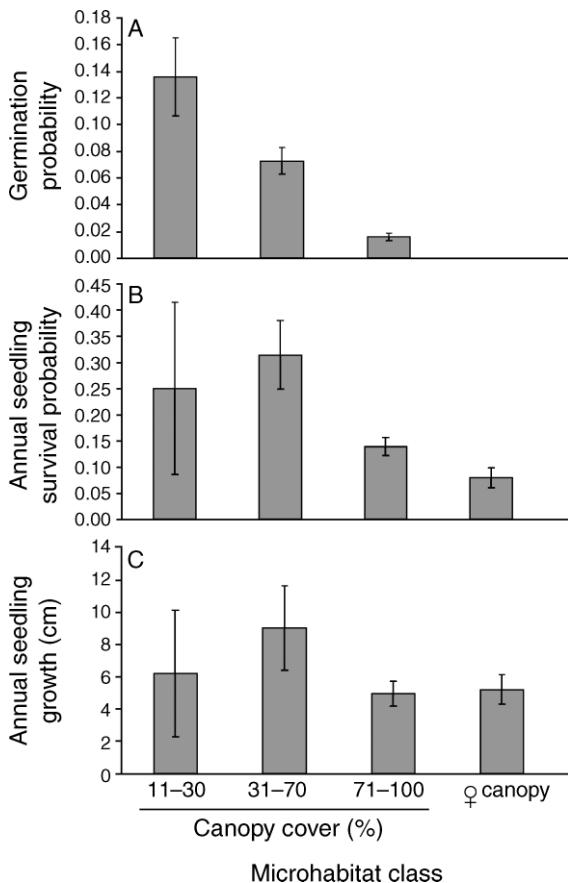


FIG. 2. (A) Germination ($N = 4200$ seeds), (B) seedling survivorship ($N = 1182$ seedlings), and (C) seedling growth ($N = 91$ seedlings) across microhabitat types. Data are means \pm SE.

± 0.005 for all three) (mean \pm SD). The bootstrapped 95% confidence intervals (see Fig. 3) of the 11–30% canopy cover microhabitat did not overlap those of any other microhabitat; population growth was positive only in the 11–30% canopy-cover microhabitat.

We then assessed how the three dispersers individually or together affected *C. axillaris* population growth (also see Appendix D). In a changing environment (i.e., canopy gaps forming and filling in) seed dispersal had only limited effects on $\hat{\lambda}$. The effects of dispersal are likely limited because unsuitable microhabitat for seed germination can turn into suitable microhabitat (i.e., gaps), causing seed dispersal under initially higher canopy covers to be sufficient in some instances. Under this scenario, dispersal by either gibbons or sambar (as opposed to no dispersal) had negligible effects, raising the tree's population growth rate ($\Delta\hat{\lambda}$) by a mean of 0.000 (95% confidence interval [CI]: 0.000, 0.001), for both mammals. Only seed dispersal by muntjac raised the *C. axillaris* population growth rate significantly, by 0.005 (95% CI: 0.001, 0.015); dispersal by all the frugivores combined raised $\Delta\hat{\lambda}$ by 0.004 (95% CI: 0.001, 0.013). Adult survival followed by juvenile

survival had the highest elasticities among the vital rates. Elasticities of fecundity, seed dispersal, seed predation, seedling survival, juvenile growth, and microhabitat transitions were roughly equal (Appendix E).

DISCUSSION

Despite a vast literature on zoochorous seed dispersal, studies that examine seed dispersal within the context of an entire plant's life cycle are still surprisingly rare (Howe and Miriti 2004, Godinez-Alvarez and Jordano 2007). Using this approach, we showed that *Choerospondias axillaris* demography is gap dependent. Similar to other tropical trees (Whitmore 1989), modeled *C. axillaris* population growth was positive only in microhabitats with relatively low canopy cover. Indeed the population on the Khao Yai (Thailand) forest-dynamics plot may be declining ($\hat{\lambda} = 0.989$; dispersal by all frugivores combined) because the overall forest is getting darker (increasing canopy cover), reducing the availability of high-light microhabitats. More importantly, against this backdrop of gap dependence, our results suggest that the three dispersers servicing *C. axillaris* do not have similar effects on the tree's population dynamics. Instead, muntjac deer appear to be the most important dispersers for *C. axillaris* primarily because they are the sole transporter of seeds (albeit rarely) to the most favorable, open-canopy environments. The $\Delta\hat{\lambda}$ confidence intervals for seed dispersal by muntjac do not overlap those for seed dispersal by gibbons or sambar deer, suggesting that they are significantly more effective mutualists for *C. axillaris* under these forest conditions. Gibbons and sambar have the same impacts on *C. axillaris* population dynamics. These results imply that not all frugivore species affect their shared host equivalently. In the absence of numerical or behavioral compensation by the other species, we estimate that loss of muntjac could have an order-of-magnitude greater impact on *C. axillaris* population dynamics than loss of gibbons or sambar (as measured by their mean $\Delta\hat{\lambda}$ s).

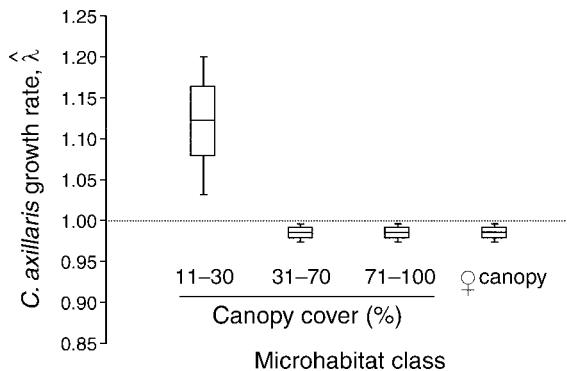


FIG. 3. Microhabitat-specific *Choerospondias axillaris* rate of population growth. Boxes and error bars show mean \pm SD and 95% bootstrap confidence intervals, respectively.

The issue of behavioral or numerical compensation for the loss of muntjac, however, is not trivial. Clearly gibbons could not compensate for the loss of muntjac, since the former already have sole access to the fruits before they fall, and gibbons do not forage on the ground. Whether sambar abundance or foraging would change following removal of muntjac is unknown; studies in other systems have certainly demonstrated the plausibility of such compensation (Weins 1989, Renjifo 1999). Moreover, we documented the relative impacts of the three frugivores on *C. axillaris* demography in one habitat (seasonal forest) in a small part of the geographical range occupied by these four species. These impacts could very plausibly be significantly different in other areas or habitat types (Bronstein et al. 2003), or for other plant species.

In contrast to other studies that have found that the most effective dispersers (generally the largest-bodied species) are the first to be lost following excessive hunting (e.g., Peres 2000, Peres and Palacios 2007), muntjac in hunted forests in Thailand usually persist longer than either gibbons or sambar (J. F. Brodie, unpublished data). Gibbons are among the first mammals lost in over-hunted forests in Southeast Asia (J. F. Brodie, unpublished data) likely because of their sociality and conspicuous vocalizations (Brockelman and Sriksamatara 1993). Sambar are more social and much larger than muntjac, both factors that probably contribute to their increased vulnerability (Purvis 2001).

The positive role of deer in plant population dynamics is often overlooked since the seed-dispersal role of ungulates is generally thought to be overshadowed by their impacts as seedling predators (Russell et al. 2001, Horsley et al. 2003). Yet recent studies suggest that deer in temperate ecosystems may play important seed-dispersal roles (Myers et al. 2004, Brathen et al. 2007, Eycott et al. 2007, Williams et al. 2008). Here we show that two deer species in the Asian tropics are also effective seed dispersers, one being the most important dispersal agent for a common and widespread canopy tree.

For such an abundant and prolifically fruiting tree, *C. axillaris* has remarkably few seed dispersers. Although the fruit pulp is clearly edible to primates (including humans) and ruminants, it may contain secondary compounds that deter other animals; phenolic allergens are common in the Anacardiaceae (Judd et al. 2002). The related and ecologically similar *Spondias mombin* of the Neotropics was thought to be adapted for dispersal by gomphotheres (Pleistocene proboscideans; Janzen 1985). Yet, although modern Asian elephants are abundant in Khao Yai, we only found three *C. axillaris* seeds in elephant scat (two of which were crushed), despite thorough examinations of nearly 50 scat piles from 2003 through 2005. Other frugivores could possibly remove seeds to communal roosts (e.g., Pteropodid fruit bats) or latrines (e.g., civets), avoiding our detection on transects. However, only a small proportion of the seeds

were unaccounted for; our estimation of the total number of seeds dispersed was actually slightly higher than the total number of seeds available on the forest dynamics plot (due either to measurement error or immigration of seeds from outside the plot; in the model the proportion of the total fruit crop on the plot that was dispersed could not exceed 1; see Fig. 1).

Gibbons, muntjac, and sambar differ both in where they deposit seeds and in the number of seeds they leave in deposition piles. Although deposition location clearly affects seed germination and seedling survival, the size of seed-deposition piles does not appear to play an important demographic role since germination and first-year seedling survivorship were not affected by seed-pile size. Moreover, due to overall low seedling survivorship across different-sized seed piles there was no evidence for density-dependent seedling mortality (cf. Russo and Augspurger 2007), even for seeds that germinated out of large deposition piles.

Neither secondary dispersal (further movement by animals of seeds that had already been dispersed once) nor seed dormancy appear to play a major role for *C. axillaris*. Although 30–40% of seeds are removed from their primary deposition locations, most do not travel more than 5 m (and are therefore unlikely to change microhabitats), and most are destroyed. We occasionally encountered caches of *C. axillaris* seeds in the forest, likely brought there by squirrels, but these were rare and, again, many of the seeds had been destroyed. Moreover, *C. axillaris* seeds must germinate within the year following their dispersal, otherwise they do not appear capable of germination; out of the 3350 seeds deposited in 2003 but that had not germinated by mid-2004, none germinated by mid-2005.

The stage-structured population model we employed places differences in seed dispersal in an ecologically realistic context that includes demographic transitions as well as transitions in microhabitat state. We suggest that this approach may be generally useful for evaluating the population-level consequences of dispersal, especially for tropical trees that depend on abiotic disturbance for successful recruitment. We note, however, that our model makes several assumptions that may affect the robustness of its output. Perhaps most importantly, juvenile vital rates in our model are microhabitat independent. If juvenile growth or survival were actually strongly enhanced in canopy gaps, seed dispersal to gaps could be even more important than our results suggest. Moreover, as our seedling vital-rate measurements are based on two annual transitions, we cannot accurately assess variance in demography over time. Because *C. axillaris* is so highly benefited by canopy gaps, its long-term demography may depend on periodic cycles of intense forest disturbance by cyclones (W. Y. Brockelman, personal observation). To explore this possibility, we ran population models (as described in *Methods: Population model*, above) that simulated an intense storm every 10 years which sent 50% of the forest to the

0.11–0.30 proportion canopy cover microhabitat without killing any *C. axillaris* individuals. Interestingly, even this extreme and unrealistically beneficial storm regime had little qualitative effect on estimated differences among frugivores in their impact on *C. axillaris* $\hat{\lambda}$ (see Appendix F). According to our model, the *C. axillaris* population we surveyed is slowly declining. This decline may be real; as noted, our microhabitat transition measurements suggest that the forest is getting darker over time (Appendix C), reducing the availability of light gaps where *C. axillaris* germination is enhanced. Alternatively, the apparent decline may be an artifact of the low sample sizes used to estimate the two highest-elasticity vital rates, adult and juvenile survival. If six of the adults that died had instead survived, *C. axillaris* $\hat{\lambda}$ for the total dispersal scenario (all frugivores combined) would equal 1.00. The relative differences in $\Delta\hat{\lambda}$ for each frugivore, however, change only slightly; muntjac $\Delta\hat{\lambda}$: gibbon $\Delta\hat{\lambda}$ and muntjac $\Delta\hat{\lambda}$: sambar $\Delta\hat{\lambda}$ ratios both decline by 8.9%.

The demographic importance of seed dispersal, and therefore the potential for differences in effectiveness among sympatric frugivores, is strongly affected by variation in tree life history. Although seed dispersal is statistically advantageous for *C. axillaris* demography in this population (the $\Delta\hat{\lambda}$ confidence intervals for muntjac dispersal did not overlap zero; see Fig. 4), its life history buffers it from variation in disperser effectiveness. Although seed dispersal to existing open microhabitats is beneficial for *C. axillaris*, even seeds initially deposited in the shade experience opportunities for success if the forest canopy opens above them. Moreover, *C. axillaris* seeds do not require ingestion in order to germinate. Thus the seed-removal component of dispersal is less important to *C. axillaris* than where the seeds end up. Other tree species, that either require seed scarification (Traveset 1998) or have lower seedling survival and are thus more dependent on immediate dispersal to sites favorable for germination (Bond 1995), tend to exhibit greater demographic reliance on seed dispersal (Bond 1995). As a result, these species may be more sensitive to functional differences among their attendant frugivores.

Combining models of microhabitat changes with plant demography may be a particularly useful approach for studying the population-level impacts of dispersers. In our case, this joint approach illustrated the pitfalls of estimating disperser impact solely by comparing how many seeds are dispersed by different animals. We found that sambar remove over twice as many seeds as gibbons, yet this does not result in stronger impacts on plant abundance, likely because many of the seeds that sambar ingest get “dispersed” right back under adult trees. This is in contrast to the general correlation reported between the visitation rate of a given frugivore species and its “total effect” on the plant (e.g., Vazquez et al. 2005, Bascompte et al. 2006). Likely this discrepancy is due to the above correlation assuming high variation in visitation rate that washes

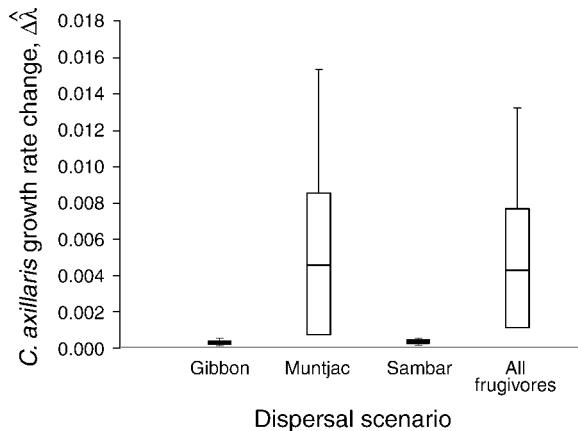


FIG. 4. Change in *Choerospondias axillaris* rate of population growth due to interaction with its seed dispersers; $\Delta\hat{\lambda}$ represents the change in lambda (population growth rate) when there is no seed dispersal compared to dispersal by each frugivore in isolation and all three combined. Boxes and error bars show mean \pm SD and 95% bootstrap confidence intervals, respectively (for muntjac and all frugivores, the lower error bar coincides with the lower CI).

out smaller differences in frugivore effectiveness. In our system, variation in dispersal quality is large enough to outweigh differences in visitation rate. It is not clear why sambar may not disperse seeds far from parent trees whereas muntjac disperse seeds to microhabitats roughly in proportion to the availability of those microhabitats. We speculate that the disparity may be due to behavioral differences between the species (Russo et al. 2006). For example muntjac, unlike sambar, are territorial (Odden and Wegege 2007, Bagchia et al. 2008); perhaps their daily movement rates are higher as they patrol their home ranges. We suggest that our ability to accurately predict the ramifications of disperser loss will require studies that explicitly quantify and compare the relative impacts of frugivore species across habitats (Bronstein et al. 2003). Simple counts of individuals, or their visitation rates, may be insufficient to accurately assess the importance of particular dispersers in the same guild.

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APPENDIX A

Structure of *Choerospondias axillaris* population projection matrix (*Ecological Archives* E090-048-A1).

APPENDIX B

Histogram of distances from dispersed seed piles to the nearest adult female *Choerospondias axillaris* (*Ecological Archives* E090-048-A2).

APPENDIX C

Mean microhabitat transition matrix, C_{ij} (*Ecological Archives* E090-048-A3).

APPENDIX D

Mean *Choerospondias axillaris* projection matrices for each dispersal scenario (*Ecological Archives* E090-048-A4).

APPENDIX E

Sensitivity of *Choerospondias axillaris* population-growth rate (for all dispersers combined) to demographic vital rates (*Ecological Archives* E090-048-A5).

APPENDIX F

Assessment of storm impacts on the relative importance of seed dispersal to *Choerospondias axillaris* population dynamics (*Ecological Archives* E090-048-A6).