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Effects of seed dispersal by gibbons, sambar, and muntjac on *Choerospondias axillaris*  
demography, and the disruption of this mutualism by wildlife poaching

By

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B.A., University of California, Santa Cruz, California, 1997

Dissertation

presented in partial fulfillment of the requirements  
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Seed dispersal of *Choerospondias axillaris* by gibbons, sambar, and muntjac, and its disruption by wildlife poaching.

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Rampant illegal hunting threatens wildlife populations inside many tropical protected areas, compromising their long-term effectiveness. A critical question concerns whether such harvest has indirect effects on non-hunted organisms that interact with the game species. For example many tree species are demographically reliant on seed dispersal by vertebrates that are threatened by hunting; the anthropogenic disruption of this animal-plant mutualism can severely alter the composition of tropical forests. Here I show that illegal poaching has reduced or extirpated several mammal species from national parks in northern Thailand. This, in turn, has negatively affected the demography of the canopy tree *Choerospondias axillaris*, which is dependent on the dispersal of its seeds to light gaps by gibbons (*Hylobates lar*), sambar deer (*Cervus elaphus*), and muntjac deer (*Muntiacus muntjak*). In parks where these mammals are heavily hunted, far fewer seeds are dispersed to light gaps and seedling abundance is significantly reduced. These results suggest that anthropogenic impacts such as overharvest can indirectly ramify through communities.

I also assessed the functional equivalence of the three seed-dispersing mammals in terms of their demographic impact on *C. axillaris*. Sambar and muntjac dispersed far more seeds than gibbons. Sambar deposited many seeds under female tree canopies; muntjac were the only disperser to deposit seeds in the most open habitats, which are beneficial for *C. axillaris* seed germination, seedling survival and growth. Using stage-based population models, I assessed how disperser-specific seed dispersal, variation in the frequency of canopy gap formation, and the interactive effects of these factors on plant demography influence the long-term population growth of *C. axillaris*. Large differences in dispersal quantity and small differences in dispersal quality, when placed in a biologically complex population-level context, resulted in only marginal variation in the impacts of these frugivores on tree abundance. Tree species more highly dependent on zoochorous seed dispersal will have more room for skewed interaction strengths among their dispersers. In measuring functional redundancy or in trying to predict the role of diversity in species interactions, we must explicitly account for variation in life-history traits.

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# CHAPTER 1: BIODIVERSITY AND THE RESISTENCE OF SEED DISPERSAL MUTUALISMS TO ANTHROPOGENIC DISRUPTION

## Introduction

The relationship between diversity and ecosystem processes constitutes a growing sub-field of ecology. Research over the last decade has examined effects of diversity on invasion resistance (reviewed by Levine et al., 2004), ecosystem stability (Tilman et al., 1994; Tilman and Downing, 1994), ecosystem reliability (Naeem and Li, 1997), primary production (reviewed by Hooper et al., 2005), bacterial decomposers (Stephan et al., 2000), and litter decomposition rates (Blair et al., 1990; Williams, 1994). The relationship between diversity and ecosystem function has risen to such prominence in part because of the current biodiversity crisis. Conservationists urgently need to understand the broader impacts of species losses in order to make informed policy recommendations. Studies on biodiversity and ecosystem function clearly attempt to address this need (e.g. Hooper et al., 2005; O'Connor and Crowe, 2005).

Yet the majority of studies on the relationship between diversity and ecosystem process have occurred in greatly simplified systems such as laboratory mesocosms or heavily disturbed grasslands (Naeem, 2001; Hooper et al., 2005). These studies have involved only one (Hooper et al., 2005) or at most two trophic levels (Duffy, 2002), and have examined the consequences of species loss in assemblages that, for logistical reasons, are relatively species-poor. Studies of biodiversity and ecosystem function have clearly advanced our understanding of the mechanisms by which diversity influences ecological processes (e.g. Hooper and Vitousek, 1997). But these studies have yet to provide insight into the emergent impacts of species loss in diverse ecosystems with complex food webs; precisely those systems where species loss is of greatest concern.

Most studies of diversity and ecosystem function have ignored interactions such as mutualisms, herbivory, parasitism, and predation, which are known determinants of both community structure and ecosystem function. One of the first effects of biodiversity loss is disruption of these interactions, which often leads to further impacts on ecosystem function (Terborgh et al., 2001; Ebenman and Jonsson, 2005; Larsen et al., 2005). Extinctions arising from anthropogenic activities are distinctly non-random (Reed, 1999;



Fagan et al., 2001; Larsen et al., 2005). Large-bodied predators and mutualists are often the first species to go, particularly in biodiverse systems that suffer substantial human pressure (Garcia and Tarifa, 1991; Peres, 2000). Moreover these first species to be lost are often functionally-crucial strong interactors (Larsen et al., 2005). Therefore diversity loss in complex natural systems may have very different ecosystem impacts than random reductions of algal diversity in terraria or plant diversity in invaded grasslands. In some instances the structure of food webs can have more impact than diversity within the basal trophic levels on ecosystem processes (Mikola and Setälä, 1998; Laakso and Setälä, 1999). Studies that examine the importance of biodiversity at larger spatial scales, and in systems that include ubiquitous interactions other than interspecific competition, are likely to provide important new insight into the ecological consequences of biodiversity loss.

Here we develop a predictive framework for how diversity may affect the resistance of communities to the anthropogenic disruption of mutualisms between zoochorous plants and frugivorous animals. We focus on animal-mediated seed dispersal because frugivores and fruit-bearing plants are dominant components of biodiverse ecosystems, particularly in the tropics (Terborgh, 1983; Gautier-Hion et al., 1985; Estrada et al., 1993; Peres, 1999). Furthermore frugivores may be more susceptible to anthropogenic-induced declines than other guilds (Terborgh and Winter, 1980; Ribon et al., 2003; Sekercioglu et al., 2004).

We currently lack a synthesis of research that examines how human-caused diversity loss in frugivore assemblages may indirectly influence plant communities and how diversity may buffer communities from negative effects of altered plant-seed disperser interactions. We focus here on ‘endozoochorous’ dispersal, where animals are attracted to and “rewarded” by fleshy fruit, nutritious seeds, or elaiosomes (see Snow, 1981), and we exclude exozoochorous syndromes where seeds attach themselves to animal pelage. This analysis is primarily concerned with human-mediated changes in plant-seed disperser interactions, but the same anthropogenic forces that disrupt seed dispersal can simultaneously drive a host of other changes in natural communities, the impacts of which can be difficult to untangle from those of dispersal limitation. For example, habitat fragmentation and selective logging can lead to the loss of seed-

dispersing vertebrates but also alter abiotic conditions within the remnant forests (Laurance et al., 2002) in ways that influence plant demography (Jules, 1998; Bruna and Oli, 2005).

In this paper we argue for the importance of estimating indirect (in addition to direct) effects of biodiversity loss, in particular for plant-animal seed dispersal mutualisms. We then offer four predictions for how seed dispersal mutualisms may respond to anthropogenic disruption, based on theory from the biodiversity and ecosystem function literature, and assess the empirical evidence supporting or refuting them. Finally we discuss the theoretical potential and evidence for functional redundancy and frugivore compensation mediating disperser guild responses to disruption.

#### The importance of estimating indirect effects of biodiversity loss

The disruption of food web structure is a common early consequence of diversity loss (Terborgh et al., 2001; Ebenman and Jonsson, 2005; Larsen et al., 2005). Declines in animal diversity at higher trophic levels of complex food webs can produce cascading effects that alter community and ecosystem structure. For example forest fragments deprived of their full complement of frugivores can have lowered seed dispersal, seedling diversity, and juvenile abundance (Chapman and Onderdonk, 1998; Asquith et al., 1999; Cordeiro and Howe, 2003), usually due to altered seed removal patterns (Chapman et al., 2003; Galetti et al., 2003; Stoner et al., 2007; Wang et al. 2007) and very low germination rates of undispersed seeds, particularly of large-seeded species (Chapman and Chapman, 1995, 1996; Cochrane and Reef, 2003). These effects will be especially strong in plants whose seeds are dependent on passage through animal digestive tracts for germination (see Traveset, 1998). Even the direction of influence of anthropogenic indirect effects varies with food web structure. Hunting, whether in intact forest (Redford, 1992) or in synergy with habitat fragmentation (Tabarelli et al., 2004), can have serious impacts on plants via the disruption of seed dispersal; yet forests with defaunated mammal communities can have either increased (Wright et al., 2000; Wright and Duber, 2001) or decreased (Asquith et al., 1997; Roldan and Simonetti, 2001) tree seedling recruitment depending on simultaneous impacts on seed predators (Wright et al., 2007).

Reductions in diversity influence not only single species, but entire systems (Loreau et al., 2001; Hooper et al., 2005). For example, forests with reduced frugivore diversity show important shifts in plant species composition, with wind- and gravity-dispersed trees increasing in abundance relative to animal dispersed species (Van Ruremonde and Kalkoven, 1991; Tabarelli et al., 1999; Cordeiro and Howe, 2001; Stoner et al., 2007). Moreover animal-dispersed trees do not only interact with their frugivores; loss of such trees will in turn affect assemblages of secondary dispersers, seed predators, pollinators, and herbivores. We need to broaden the scope of what is considered an “ecosystem function” when considering effects of biodiversity loss.

### Frugivore diversity and plant communities

Impacts of diversity loss on ecosystem function depend greatly on the trophic level at which the losses occur (Duffy, 2002; Thebault and Loreau, 2005). We present several predictions for the ways in which frugivore and plant diversity affect the structuring of communities via the ecological integrity of their mutualistic interaction. These predictions arise out of current understanding of how diversity should influence the stability of ecological systems (e.g. Doak et al., 1998; Tilman, 1999; Duffy, 2002; Hooper et al., 2005).

Prediction 1: *Greater diversity in the zoochorous plant assemblage should buffer that assemblage from changes in frugivore abundance.* This is the “statistical averaging” (Doak et al., 1998) or “portfolio effect” (Tilman et al., 1998) -the idea that greater diversity decreases temporal variability in community properties because individual components of larger data sets have less influence on the mean. These effects have been demonstrated in plant communities, where diverse assemblages: 1) show less temporal variability in biomass due to altered abiotic conditions than do less diverse assemblages (Tilman and Downing, 1986) and experience smaller biomass reductions from grazers than depauperate assemblages (Thacker et al., 2001; McNaughton, 1985). Additionally, more diverse plant assemblages are more stable in the face of consumption because higher diversity groups are more likely to contain species with higher resistance to

consumption (the “sampling effect”; Hooper et al., 2005). By analogy, highly diverse zoochorous plant assemblages may be more likely to contain species that are less vulnerable to loss of their seed dispersing animals, or that are serviced by frugivores less susceptible to anthropogenic influence. Increased diversity should thereby reduce the overall impacts of selective frugivore extirpation on the combined plant assemblage.

For the sampling effect to operate in seed dispersal interactions, species must vary in their reproductive life-history. Indeed, zoochorous plants display high variance in their vulnerability to seed dispersal loss. Shorter-lived plants with high disperser specificity (low diversity of frugivores providing dispersal services), high disperser dependence (where dispersal is critical for germination or recruitment), and important effects of current-year seeds on overall demography (high elasticity of the seed germination vital rate) all have relatively high vulnerability to dispersal loss (Bond, 1995). Large-seeded fruits tend to have higher disperser specificity (Martin, 1985; Peres and Van Roosmalen, 2002; Meehan et al., 2002; Alcantara and Rey, 2003) and greater reliance on biotic processes for recruitment (Jordano, 1995); they therefore tend to be at higher risk (but see Beckman and Muller-Landau, 2007). Peres and Van Roosmalen (2002) list 102 genera of large-seeded woody plants in Amazonia that could be at risk of disperser failure due to overhunting. The inability to recruit under conspecifics indicates high dependence on seed dispersal (Chapman and Chapman, 1995), and increased demographic vulnerability to frugivore loss.

However, the relationship between species diversity and life-history diversity is not yet clear. Tropical rainforests and the South African fynbos are spectacularly speciose plant communities yet have very high proportions of species with large seeds or otherwise vulnerable life history traits (Bond, 1995; Kitamura et al., 2005). Counter to the statistical averaging and sampling effect arguments, these diverse systems may therefore be highly vulnerable to loss of their seed dispersing animals. Indeed, these are the systems where some of the best examples of community-wide effects of native seed disperser declines are manifest; i.e. where important changes in plant diversity follow frugivore extirpations (e.g. Silva and Tabarelli, 2000; Christian, 2001; Cordeiro and Howe, 2001). Diversity alone is not enough to buffer a zoochorous plant assemblage without the requisite variation in vulnerable characteristics among component species.

Prediction 2: *Greater diversity of frugivores should reduce variation in total frugivore numbers or biomass due to anthropogenic disruption.* Nearly all of the diversity and ecosystem function literature examines richness of plants or microbes, yet the theory is often extrapolated to include animal assemblages (Hooper et al., 2005). If frugivore species vary in their susceptibility to anthropogenic disruption, we would expect higher diversity assemblages to be more likely to include species resistant to anthropogenic disruption or able to compensate for extirpated species (Hooper and Vitousek, 1997; Duffy, 2002; Hooper et al., 2005).

Although the negative impacts of human activities on frugivores as a group are severe, there is high variation within tropical faunas in their responses to anthropogenic disruption (Naughton-Treves et al., 2003; Laurance et al., 2007; Peres and Palacios, 2007). Some animals respond positively to moderate levels of human disturbance, whereas others respond negatively (Janzen and Vasquez-Yanes, 1991). Large-bodied species are among the most vulnerable (Redford, 1992; Fa et al., 2005; Peres and Palacios, 2007) because they are often preferentially hunted (Cowlshaw and Dunbar, 2000), they require larger home ranges for persistence (Estrada et al., 1993; Cosson et al., 1999), and because large body size is tightly correlated with low reproductive rate (Harvey and Purvis, 1999). Wide-ranging species are particularly at risk because of their increased probability of interacting with humans, particularly at reserve edges (Woodroffe and Ginsburg, 1998). Social animals tend to be more vulnerable to hunting, presumably as a result of being easier to detect and more profitable to pursue (Peres, 1990; Cowlshaw and Dunbar, 2000).

The degree to which human activities directly influence a frugivore assemblage also affects the degree to which those activities indirectly impact the zoochorous plant assemblage. Therefore a corollary to this prediction posits that diversity in the frugivore assemblage should buffer the zoochorous plant assemblage against changes in frugivore abundance or diversity. Clearly, plant species with obligate one-to-one dispersal syndromes are at risk if their single disperser is extirpated (Traveset and Riera, 2005), and habitat fragmentation has stronger negative effects on tree species serviced by single frugivores, as compared to those serviced by more diverse assemblages (Ganzhorn et al.,

1999; Hewitt and Kellman, 2002). Nevertheless we have no empirical validation of whether frugivore diversity buffers the entire plant assemblage (as opposed to individual species) against anthropogenic disruption.

Prediction 3: *Reductions in frugivore diversity should increase temporal variability in the indirect impacts on zoochorous plants.* Populations of frugivores within an assemblage may vary independently or negatively with each other due to competition; thus the total abundance of frugivores (across species) in diverse assemblages should be less variable than in depauperate assemblages (Doak et al., 1998; Tilman et al., 1998). Lower variability in frugivore abundance should lead to reduced annual variation in the number of seeds dispersed, and lower year-to-year variance in reproduction at the population level. Smaller variance in reproduction across years should lead to higher long-term population growth rates, as variability in annual population change decreases the long-term growth rate of populations, even if the arithmetic mean of the annual changes remains constant (Morris and Doak, 2001). Therefore, by reducing year-to-year variation in seed dispersal, diverse frugivore assemblages are predicted to confer higher population growth rates on the plants they service, as compared to less diverse groups.

To our knowledge there are no existing data that allow us to test this hypothesis. In practice the effect may often be damped by synchronous population reductions across all frugivore species in the assemblage. Hunting by humans often drastically reduces the populations of all large-bodied mammals in an area (Garcia and Tarifa, 1991; Peres, 1990). Smaller-seeded plant species may then fall back on small-bodied frugivores, but large-seeded plants may have no such recourse (Meehan et al., 2002).

Prediction 4: *Successive eliminations of frugivore species will have non-linear impacts on the demography or biomass of zoochorous plants.* As species diversity in plant assemblages rises, metrics of ecosystem-function generally increase up to some asymptote (Hooper et al., 2005). For example, plant productivity often rises with increasing species richness up to a point, after which further increases in species richness have little effect on productivity. This asymptotic relationship between diversity and ecosystem function would predict that as species are lost the effects on ecosystem

function may be minimal at first, but at some point reach a threshold where increasing declines in species produce steep declines in ecosystem function. If diversity affects interspecific interactions as it does ecosystem function, the progressive removals of frugivore species from an assemblage should have increasingly dramatic effects on zoochorous plant demography or biomass (Hooper et al., 2005; also see Fig 1, line A).

Yet there is real reason to expect the opposite result in nature; the most dramatic effects of frugivore removals should follow the loss of the first few species. Diversity-ecosystem function experiments usually utilize random assemblages, but anthropogenic removal of species in nature are distinctly non-random (Peres, 1990, 2000; Peres and Palacios, 2007). Large-bodied animals are particularly vulnerable to hunting and fragmentation, and these species are often the most important seed dispersers in frugivore assemblages because they consume a wide variety of seed sizes (Martin, 1985; Peres and Van Roosmalen, 2002; Alcantara and Rey, 2003) and may disperse seeds away from the parent canopy more frequently than smaller bodied frugivores (Howe, 1993). Thus the first frugivores to be removed from assemblages will often be the most effective seed dispersers, implying that initial disturbance to a system could have immediate, drastic indirect effects on the zoochorous plants (Fig 1, line B).

Even before the large-bodied, vulnerable frugivores are extirpated, reductions in their density can disproportionately reduce their effectiveness as dispersers. This non-linearity is primarily due to two factors: 1) differences in foraging efficiency between conspecifics (Redford and Feinsinger, 2001, Table 17.2, and references therein), and 2) density-dependent foraging behavior (Redford and Feinsinger, 2001; McConkey and Drake, 2006). Variation in individual foraging behavior suggests that the loss of particular individuals may disproportionately affect dispersal services. Modest declines in frugivore numbers might have minimal effects on seed dispersal, but there may be thresholds beyond which extant frugivore populations cease to provide effective disperser services in their communities. Our understanding of when and where these thresholds exist is quite poor. We have almost no knowledge of how reduction (short of complete extirpation) of frugivore species will affect their relative interaction strengths and dispersal efficacies.

This prediction has grave implications; even moderate disturbance to forest communities can severely impact seed dispersal. Extractive reserves where hunting is “sustainable” in terms of maintaining wildlife populations may still suffer the loss of effective seed dispersal as the abundance of the most efficacious dispersers is reduced beyond their “ecologically effective” threshold (Soule et al., 2003).

Important to all four of these predictions, we have very little understanding of how seed dispersal affects zoochorous plant demography. This is difficult to assess a priori. On the one hand, the importance of seed dispersal could very plausibly be swamped by the myriad other factors affecting individual plant fitness between the germinating-seed and reproducing-adult life stages. Seed-seedling transitions often have very low elasticity values (Silvertown et al., 1993; Howe and Mariti, 2004). On the other hand, even differences between species that initially appear small can turn out, over longer time periods, to be very important (Brown et al., 2001) and vital rates with low elasticity but high variation can still have important impacts on population dynamics (Mills et al., 1999; Howe and Mariti, 2004).

#### Functional redundancy in seed dispersal interactions

Central to the above predictions is the issue of functional redundancy. If frugivore species in an assemblage are functionally equivalent, the loss of one disperser will be compensated for by the remaining species (Howe, 1984; Pizo, 1997; Loiselle and Blake, 2002), and reductions in the diversity of seed dispersers should have little impact on the effectiveness of seed dispersal. Alternatively, if members of a disperser guild differ significantly in their effectiveness then the identity of the species that are lost can critically influence plant dispersal and persistence. The amount of functional redundancy in a seed disperser guild may be related to the number of species in the assemblage, with higher diversity implying a greater degree of redundancy (Loiselle and Blake, 2002). This implies that species diversity has little relationship to functional diversity, so that speciose communities have higher diversity within functional groups but not necessarily more functional groups. Yet this has never been explicitly tested. We still have very little understanding of the relationship between species- and functional-diversity.



Frugivore species nearly always vary in the dispersal services they provide. Many animal-dispersed plants are serviced by a wide range of frugivores in different taxa (Fig 2; also see Bond, 1995), and these frugivore assemblages can be highly variable (Howe, 1983; Jordano, 1994; Fuentes, 1995). The effectiveness of frugivore species can vary, sometimes quite widely (Howe and Vande Kerckhove, 1980; Bond and Slingsby, 1984; Murray, 1988; Reid, 1989; Howe, 1993; Pizo, 1997; Santos et al., 1999; Alcantara et al., 2000; Figuerola et al., 2002; Ness et al., 2004; Wehncke et al., 2004; Dominy and Duncan, 2005). Very few of the many frugivores visiting a given plant may actually provide beneficial dispersal (Howe, 1977; Cordeiro et al., 2004). These differences in dispersal effectiveness suggest that functional redundancy may be low within frugivore assemblages.

However, though frugivore-specific differences in dispersal efficacy are common, whether these differences are manifest at the plant population level remains largely unknown. As discussed above, we have very little understanding of how seed dispersal affects plants demographically, and therefore how differences among seed dispersing animals matter to plant population dynamics. In one of the only studies to assess the relative effects of frugivores on plant population dynamics, seed dispersal by a species of bat led to positive population growth for a columnar cactus, while dispersal by three bird species led to negative growth (Godinez-Alvarez et al., 2002), though the confidence intervals were broadly overlapping. It makes sense to use plant population growth rates attributable to specific frugivore species as the measure of one-way interaction strength (frugivores on plants), as per Godinez-Alvarez et al. (2002). Much more data is needed on the population-level impacts of different dispersers on plants; the claim made over a decade ago by Schupp (1993: 26) that, "...more emphasis should be placed on quantifying the consequences of dispersal by different disperser species" still holds true. Knowledge of the variation in demographic susceptibility to disperser loss among plant populations is a necessary first step towards an eventual understanding of the mechanisms by which impacts on frugivore diversity ramify throughout natural communities.

We must also consider functional redundancy in the zoochorous plant assemblage. Frugivores in systems with many fruit species should be less affected by, for

example, the overharvest of particular fruit species by humans. Wild fruits collected by humans in developing countries are commonly consumed by large birds and mammals (Hladik et al., 1993). The widespread harvest of wild fruits by humans affects wild frugivore populations, behavior, and species richness (Chapman and Onderdonk, 1998; Moegenburg and Levey, 2003).

Finally, we lack understanding of the relationship between species diversity and functional diversity. Do frugivore assemblages with more species span greater ranges of body size, gape width, effective seed handling, or gut retention time? We badly need research to assess whether repeated patterns will allow us to predict combinations of animal taxa that provide redundancy in seed-disperser assemblages.

#### Compensation in seed dispersal interactions

Functional redundancy is usually implied to be temporally static, yet the degree to which zoochorous plants are affected by the loss of certain disperser species is also importantly influenced by the changes in density or behavior (“compensation”) of the remaining dispersers. Indeed, communities under anthropogenic stress often show important changes in species composition or within-taxon abundance without clear impacts on ecosystem function (Folke et al., 1996); this implies that potential for functional compensation may be common in natural communities. Persistent seed dispersers could increase in density or alter feeding behavior in ways that make their dispersal more efficacious, thereby potentially compensating –at the level of the plant populations- for the loss of other disperser species. They might also expand their diet breadth to include fruit species not previously exploited, thereby compensating at a community level. This illustrates an important problem with using static functional redundancy to assess mutualism vulnerability. Snapshot assessments of frugivore species composition and functional attributes give us no a priori knowledge of the interactions between the frugivores themselves (see Berlow, 1999), and therefore no way of predicting the responses of non-target species to population or behavioral changes in anthropogenically affected species.

One approach used to examine functional redundancy among frugivores is to assess the degree of overlap in tree species they service (Gautier-Hion et al., 1985;

Kitamura et al., 2002; Poulsen et al., 2002). This approach can provide useful information at the scale of the entire community but cannot tell us whether the respective frugivores differ in the effectiveness of the dispersal services they provide to a single plant species. Furthermore these studies of dietary overlap rarely, if ever, account for the possibility of compensation. Poulsen et al. (2002) convincingly demonstrated that hornbills (*Ceratogymna* spp.) and arboreal primates feed on different suites of fruit species in an Afrotropical forest, and from this the authors infer that loss of one group would not be compensated for by the persistence of the other (in terms of maintaining vegetation diversity). However, following the loss of the primates with which they had formerly competed, hornbills could plausibly expand their diet to include species that they had formerly ignored due to facultative resource partitioning in the presence of sympatric competitors.

Persistent frugivores on islands and habitat fragments can increase in density following extirpation of another species (Weins, 1989), even to the point where the total number of individuals in the community remains stable (Renjifo, 1999). For instance, all native frugivorous birds on Mangaia Island (southern Cook Islands archipelago) are extinct (Compton and McCormack, 1999), which would appear to doom *Ficus prolixa* – a primarily bird-dispersed strangler fig- to eventual extinction. However recruitment of the tree appears healthy, perhaps due to replacement seed dispersal by fruit bats (Compton and McCormack, 1999). Yet the remaining species might not be functionally similar to their eliminated counterparts. Reduction in frugivore diversity or abundance in small habitat fragments negatively affects seed dispersal and recruitment (Santos and Telleria, 1994; Pizo, 1997; Andresen 2003) as remnant plants in fragments are forced to rely on persistent yet less efficacious dispersers (Pizo, 1997; Santos et al., 1999). The strength, and even the direction, of these effects may vary by species. Several studies have shown weak effects of fragmentation on seedling:adult ratios, or decreased seed dispersal and increased seed predation in fragments (compared to contiguous forest) for some animal-dispersed species, but not for others (Githiru et al., 2002; Guariguata et al., 2002). We have a clear need for research to assess whether there are certain combinations of frugivore species or functional groups where compensation is likely to occur.

### Future directions

In this age of ever-increasing extinction it is important to understand the indirect effects of the loss of biological diversity on natural ecosystems. We must conduct studies at spatial scales and trophic complexity levels appropriate to complex natural communities where particular species are at genuine risk. How does species or functional group diversity affect the resistance of frugivore assemblages, and the zoochorous plant assemblages they service, to anthropogenic disruption? How does diversity in the plant assemblage affect its vulnerability to actual or functional loss of frugivores? What are the temporal and demographic effects of frugivore species loss on zoochorous plants? Of particular importance, we need a much better understanding of the degrees to which functional redundancy and the potential for numerical or behavioral compensation exist within natural frugivore assemblages of varying diversity. Is there any way of testing the potential for diet breadth expansion in frugivores? Perhaps preference tests similar to those used in evaluations of potential host range for biological control agents could be useful. If possible, can we identify traits that will allow us to predict the degree of functional redundancy or compensation potential within frugivore assemblages, so that we could identify a priori which plant communities might be at particular risk of negative indirect effects of anthropogenic impacts on their associated frugivore faunas?

Understanding how diversity affects the functioning of ecosystems is clearly an important task for ecologists, yet it must be undertaken at appropriate scales so that we can assess the potential impacts of real-world extinctions. Advances in our knowledge of the relationship between diversity and interaction stability could allow us to design conservation strategies based, not on single-species, but on the preservation of ecologically-crucial species interactions.

Figure 1.1: Potential effects of seed disperser removal on zoochorous plant diversity or biomass. Line A shows the prediction from diversity and ecosystem function theory (Hooper et al. 2005), which assumes random removal of species. Line B shows the predicted relationship accounting for the observation that the most efficacious dispersers are often the first to be lost in real-world systems.

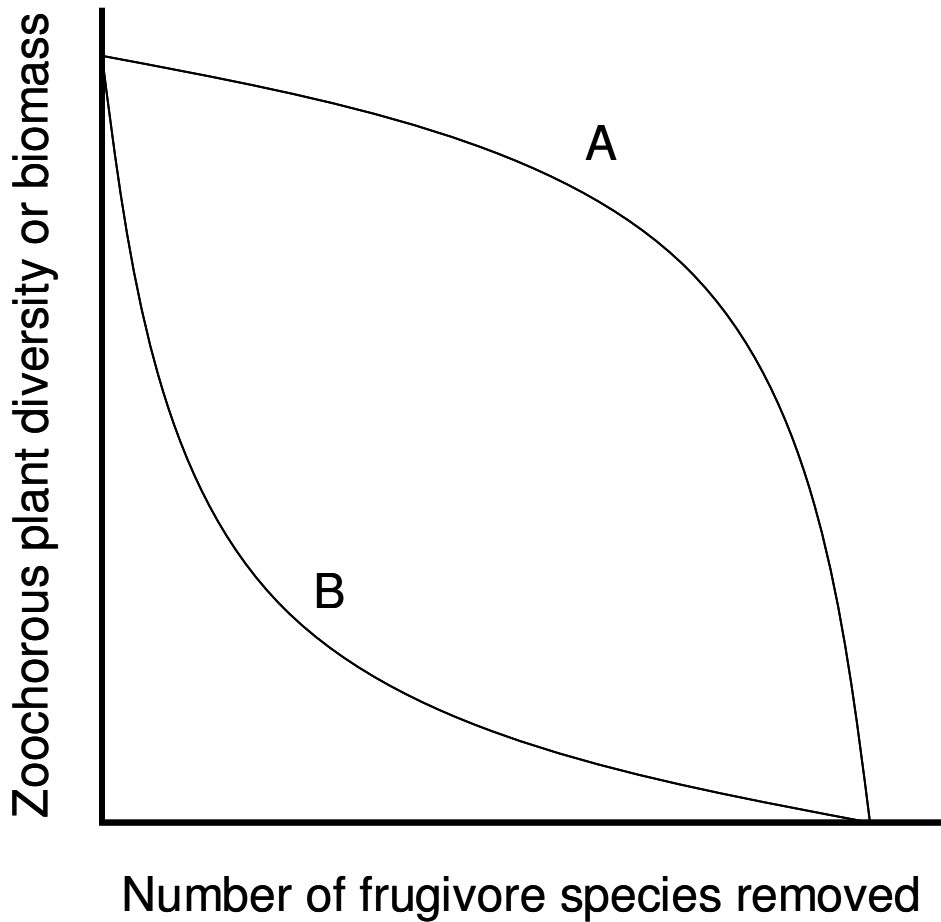
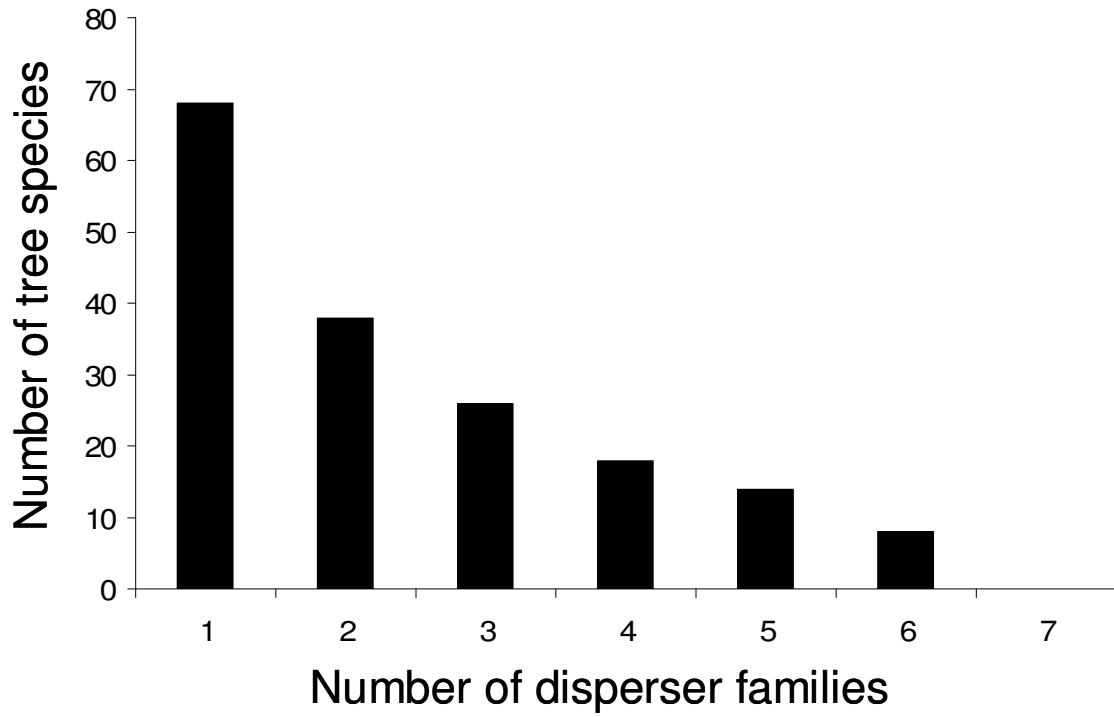


Figure 1.2: The number of tree species in a tropical seasonal forest in Thailand serviced by varying numbers of frugivore families. Species diversity within families varies from one (Asian elephant: Elephantidae) to seven (bulbuls: Pycnonotidae); from data in Kitamura et al. (2002).



## CHAPTER 2: AN EXPERIMENTALLY DETERMINED PERSISTENCE-RATE CORRECTION FACTOR FOR SCAT-BASED ABUNDANCE INDICES

### Introduction

Scat counts have long been used to indirectly assess mammal density in lieu of directly sampling the animals themselves (Bennett et al. 1940). If scat abundance proportionally relates to actual mammal abundance, scat counts provide a valuable index of population size (White 1992). If the functional relationship between the abundance estimate and true population size is known, then this index can be used to estimate population density (Krebs et al. 1987).

Scat-based indices and estimators have been shown to scale proportionally to known snowshoe hare (Krebs et al. 1987), deer (Marquez et al. 2001), and large carnivore (Stander 1998) density. Yet several studies comparing estimated deer population sizes from scat-based estimators to known populations in enclosures showed high variability in index-based estimates of deer abundance and relatively low correlations between the estimated and actual abundance values (Eberhardt and Van Etten 1956, Ryel 1959, Downing et al. 1965, Dzieciolowski 1976). Studies testing the relationships between deer abundance estimates calculated from scat-based estimators and other estimators (e.g. drive counts, line-transect samples) have showed weak relationships (Dasmann and Taber 1955, Fuller 1990) or relationships with substantial variation between years (Harris 1959) or habitats (White 1960).

An important source of variation in pellet numbers between locations in the above studies (and a potential partial explanation for the weakness of the relationships between pellet-based abundance estimators and actual population size) is that persistence of the scat pellets might vary between study sites or over time at the same location. There could be substantial spatial and temporal variation in the rates at which dung beetles, erosion, desiccation, and other factors cause scat to degrade or disappear. This variation could lead to fewer pellet piles being found at some sites than at others regardless of actual differences in animal density or behavior. Loss of scat due to natural degradation should minimally affect the usefulness of scat-based abundance indices, as long as the degradation rates are similar between study sites or periods. However, several studies

have demonstrated important differences in scat decay rates depending on the habitat into which the pellets were deposited (Low 1959, unpublished data, as cited by Neff 1968; Dzieciolowski 1976).

Marquez et al. (2001) suggest that a measure of persistence rate should be included as a parameter in the model used to convert raw scat counts into population estimators. Their method involves marking a sample of fresh pellets in the areas to be surveyed, and measuring their persistence rates over the months preceding the scat survey. While this approach should improve the accuracy of scat-based estimators, it has several potential problems. First, determinations of whether scat is fresh can at times be problematic. Van Etten and Bennet (1965) show that, under certain habitat and weather conditions, pellet piles up to 2 years old can appear fresh. Furthermore, in some areas it may be difficult to locate a sufficiently large sample of fresh pellet piles to allow accurate determinations of decay rates.

I propose a simple study design to experimentally measure scat persistence rates that can overcome the above sampling and logistical issues, and should improve accuracy in scat-based indices and the density estimators derived from them. The method, exemplified here for deer, works as follows: 1) scat pellets are collected from high animal-use areas, where they are known to be fresh, 2) pellets are air dried and mixed, 3) pellet piles are set out at random or systematic locations within the study area and marked with flagging, 4) concurrent with conducting the scat survey, the proportion of the experimental pellet piles still visible is measured to determine the scat persistence rate, and 5) observed scat counts (uncorrected indices) are divided by the persistence rate to create corrected index values.

Scat surveys generally use one of two general methodologies; the “clearance plot” method, whereby plots or transects are cleared of existing scat and then, usually several months later, resampled for scats that have been deposited in the intervening time, and the “standing crop” method whereby plots are not cleared beforehand (Marquez et al. 2001). Applying a persistence rate correction factor is especially important in the standing crop design since there is otherwise no way to determine the age of the observed pellet piles. But such correction factors should also be used in the clearance plot design to measure the rate at which pellet piles deposited since plot clearance have disappeared



before sampling takes place. In this case experimental piles can be set out at the time of plot clearance, and persistence measured during plot sampling, thus ensuring that factors promoting pellet pile decay act concurrently on experimental and naturally-occurring scat piles.

### Study Area

I experimentally tested the persistence rates of sambar scat pellet piles across sites in monsoon forests of northern Thailand, to assess whether the use of a persistence-based correction factor alters the qualitative results of a scat-based relative abundance survey. This work was part of an ongoing study on the effects of wildlife poaching on zoochorous tree seed dispersal in 4 National Parks: Doi Inthanon, Doi Sutep-Pui, Nam Nao, and Khao Yai. Khao Yai National Park (2,172 km<sup>2</sup>; 14°26' N, 101°22' E) is a large plateau, 700-900 m in elevation, with mixed deciduous forest on the steep slopes and evergreen seasonal or mixed evergreen-deciduous forest types throughout most of the area (Smitinand 1977). It receives about 250 cm of rain annually, mostly from May-October; there is a pronounced dry season from December to April. Abundance of many large mammals is high in the central portion of Khao Yai (Lynam et al. 2000, 2003). Nam Nao (966 km<sup>2</sup>; 16°44' N, 101°34' E) is a matrix of mixed evergreen-deciduous forest types with open, grassy, pine-dipterocarp woodland (Elliot 2001). All sampled plots in this park were in mixed evergreen forest. The understory vegetation in the mixed evergreen forest of both parks is fairly open with rattan palms (Arecaceae) and *Strobilanthes* spp. (Acanthaceae; especially in Khao Yai) common and much exposed leaf litter on the forest floor. There have not been any recent mammal density estimates in Nam Nao.

Other pellet-forming ungulates in these parks include the common muntjac (*Muntiacus muntjak*), Fea's muntjac (*Muntjac feae*; Nam Nao only), mouse deer (*Tragulus* spp.), and possibly the southern serow (*Naemorhedus sumatrensis*) and long-tailed goral (*Naemorhedus caudatus*; Lekagul and McNeely 1977, Srikosamatara and Hansel 2000). Serow and goral are unconfirmed in Nam Nao, and in Khao Yai they are rare and tend to reside in the hilly portion of the park (Srikosamatara and Hansel 2000),

not close to the sites used in this study. Muntjac and mouse deer scat is easily distinguished from that of sambar by size.

### Methods

I haphazardly selected 4 0.5ha plots in each park. Out of the 16 plots, only 6 showed evidence of sambar presence; the animals may be extirpated in Doi Sutep-Pui and Doi Inthanon, and only 2 of the sites in Nam Nao had sambar scat. Therefore only the 6 plots (four in Khao Yai, two in Nam Nao) with sambar scat were used for the analyses below. Within these plots I randomly chose four 50×4 m parallel belt transects in each plot, each  $\geq 10$  m apart. To limit variation in the number of scat pellet piles due to differences in habitat or presence of local food sources, transects were staggered so as to stay within forest cover (i.e. avoiding light gaps) and to avoid fruiting *Choerospondias axillaris* (Anacardiaceae) trees.

I cleared the transects of existing scat pellet piles at the beginning of the field season (mid-July) and sampled them for new pellet piles at the end of the season (mid-October). I conducted all surveys to reduce observer bias (Neff 1968).

I developed a plot-specific measure of scat persistence rates. In early July, I collected fresh sambar scat from the grassy lawn of the Lam Ta Khong campground in Khao Yai National Park, a site of very heavy sambar use. Pellets were dried in the sun, and then transported to the study sites. On the same days that transects were cleared of existing pellet piles, I initiated the pile persistence rate experiments. I placed 10 piles of 10 pellets each at randomly chosen locations within each plot, and marked them with pin flags. At the end of the season I determined whether the piles were still visible. Piles were scored as either “visible” or “not visible”, rather than by the proportion of the original pellets remaining. The proportion of the 10 original piles still remaining at the end of the season constituted the persistence-rate correction factor.

The uncorrected sambar abundance index was the mean number of pellet piles across the 4 transects on a plot. The uncorrected index value divided by the plot-specific persistence rate correction factor constituted the corrected index. If there was any loss of pellet piles at all, the corrected index value would be higher than the uncorrected value. But if scat persistence rates were similar across sites, the ratio of corrected to uncorrected

index values would remain relatively constant. I calculated these ratios for all 6 sites (treating the sites themselves as independent) and, separately, for the 2 parks (treating sites within the parks as replicates).

### Results and Discussion

The rank of the 6 sites, ordered by relative sambar abundance, changed when the persistence-rate correction factor was applied. The rank order based on the uncorrected abundances was  $KY1 > KY2 > KY3 = KY4 > NN3 > NN1$ ; the rank of the sites using the corrected sambar abundance was  $KY1 > KY4 > KY2 > KY3 > NN3 > NN1$  (Fig. 2.1). The ratio of corrected to uncorrected abundance values (Fig. 2.2) varied among sites by a factor of 2.7. The ratio of corrected to uncorrected abundance values between parks (Fig. 2.3) varied by a factor of 1.6. I speculate that the differences in scat persistence among sites and parks were due to variation in dung beetle abundance and local weather and habitat conditions; drier sites probably had higher persistence due to reduced direct impacts of precipitation on scat.

Many studies using indices seek to assess relative differences in population density between sites. The application of the persistence-rate correction-factor in this study changed the qualitative ranking of the sites, implying that differences in scat decay rates between environments could be an important source of bias in index measurements. This result is further supported by the observation of highly variable corrected:uncorrected index value ratios across sites and parks. The persistence-rate correction-factor proposed here should increase the accuracy of abundance indices, while serving as a necessary parameter in density estimator equations based on scat count data.

Figure 2.1: Sambar relative abundance indices with and without scat persistence rate correction factor. On the X-axis are sites in 2 National Parks where sambar presence was detected; standard error bars represent variation across transects within each site.

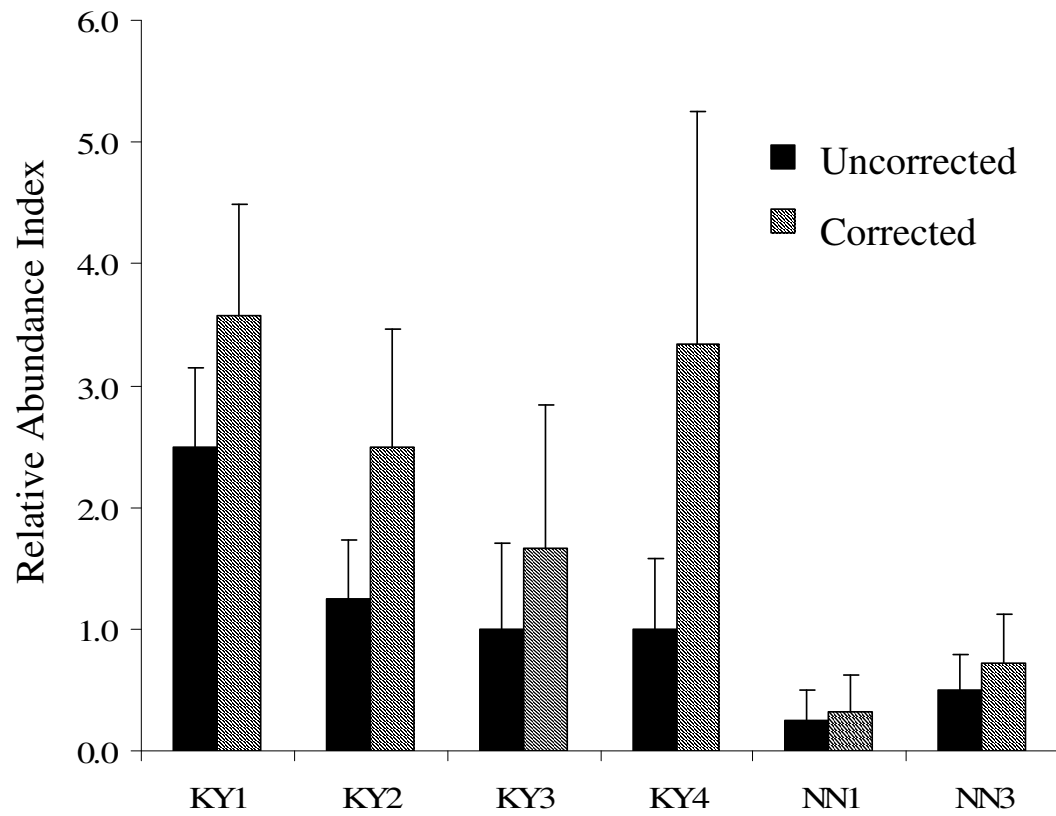


Figure 2.2: Ratios of corrected to uncorrected abundance index values across study sites.

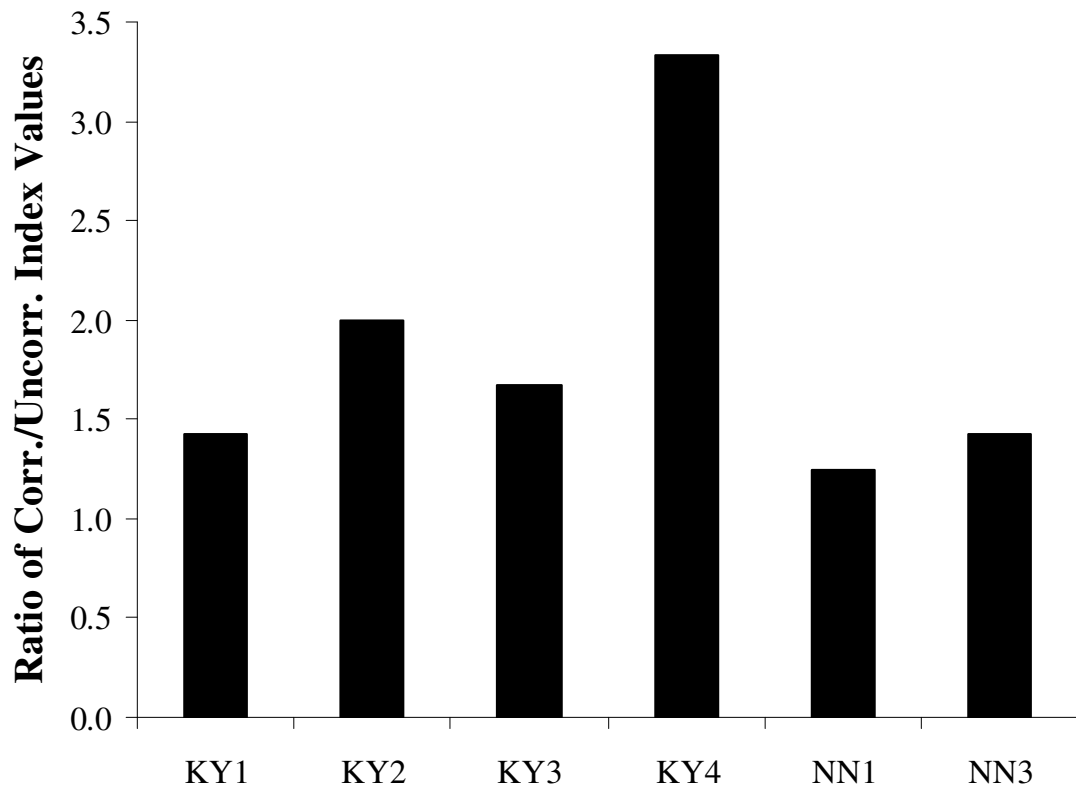
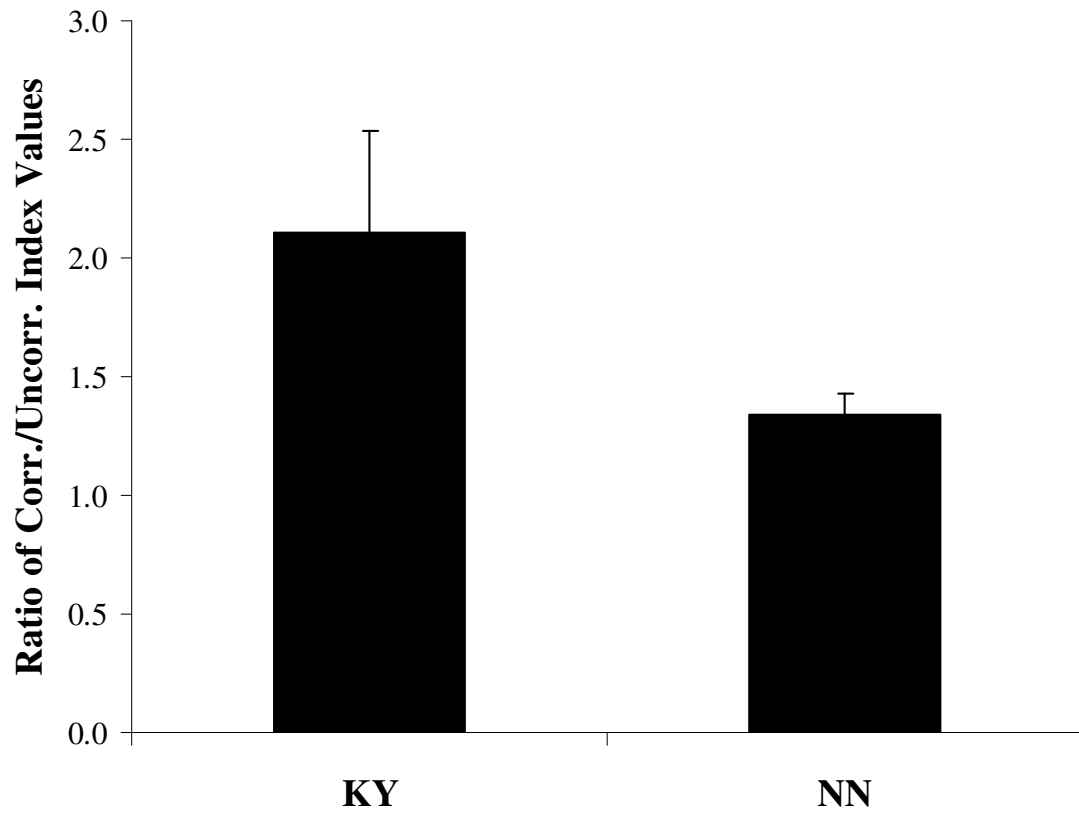


Figure 2.3: Ratios of corrected to uncorrected abundance index values across parks. Variation across sites within a park is represented by standard error bars.



## CHAPTER 3: CASCADING INDIRECT EFFECTS OF WILDLIFE POACHING IN PROTECTED AREAS

### Introduction

Overharvest is one of the most serious threats to tropical vertebrates worldwide (Robinson & Bennett 2000; Fa & Peres 2001; Milner-Gulland et al. 2003). “Bushmeat” hunting can reduce or eliminate mammals and birds in impacted areas (Robinson & Bennett 2000; Peres & Palacios 2007), leading to forests that are structurally intact but “empty” of large animals (Redford 1992). Indeed hunting rates of large vertebrates across the tropics are often so high as to be unsustainable (Fa et al. 2001; Bennett & Rao 2002; Milner-Gulland et al. 2003; Corlett 2007).

Although the direct effects of harvest on target species are of growing concern and have received considerable attention, hunted species represent only a small portion of the total biodiversity in any ecosystem. A critical, though largely unresolved, issue concerns the extent to which this harvest has cascading indirect effects that threaten non-hunted organisms (Springer et al. 2003; Frank et al. 2005), especially in complex tropical forests (Redford 1992; Brechin et al. 2003). Much of what we know about the indirect impacts of overharvest stems from marine systems where harvest is largely legal and measurable (Baum et al. 2003; Myers & Worm 2003; Frank et al. 2005). But in tropical terrestrial systems, most vertebrate harvest is illegal and extremely difficult to quantify. The annual black-market trade in wildlife is estimated at US \$8 billion, second only to the illegal traffic of drugs and arms (WCS 2002).

We do know that hunting in tropical forests can drastically reduce animal populations (O'Brien & Kinnaird 2000; Peres 2000; Peres & Palacios 2007), and that many of these hunted species are frugivores that disperse tree and shrub seeds (Redford 1992; Chapman & Chapman 1995; Stoner et al. 2007a; Stoner et al. 2007b). Indeed frugivores comprise the bulk of vertebrate biomass in some tropical forests (Gautier-Hion et al. 1985; Peres 1999), up to 85% of the total bird and mammal biomass at one site in Mexico (Estrada et al. 1993). As many as 70-90% of tree species in these habitats are adapted for animal-mediated seed dispersal (Howe 1977; Gautier-Hion et al. 1985). Yet

the cascading impacts of hunting on zoochorous seed dispersal are only beginning to be explored (Stoner et al. 2007a; Stoner et al. 2007b; Wright et al. 2007).

Although overhunting can reduce fruit removal (Wright et al. 2000; Wright & Duber 2001; Forget & Jansen 2007; Wang et al. 2007) and seed dispersal distances (Chapman & Onderdonk 1998), we have very little understanding of its effects on tree population dynamics. Largely this is because the demographic effects of seed dispersal itself are still poorly understood. On the one hand, reduced seed dispersal can lead to lower overall germination in a given fruit crop (Chapman & Chapman 1995; Forget & Jansen 2007). But on the other hand, the chances that any given seed (dispersed or not) will survive to become a reproductive adult are extraordinarily slim (Howe & Smallwood 1982). Seed dispersal and germination often have very low elasticities, or low ability, relative to other vital rates, to affect population dynamics (Silvertown et al. 1993; Howe & Mariti 2004). This is especially true for long-lived organisms such as tropical trees, where population growth is nearly always driven by adult survival rather than reproduction or the survival of younger age classes (Pfister 1998). Therefore, to address the potentially cascading indirect effects of overhunting on animal-dispersed trees, we must place alterations in seed dispersal and germination in a population-level context.

We capitalized on large-scale variation in poaching pressure across four national parks in northern Thailand (Fig. 1) to examine how reductions in several mammalian frugivore species might influence the recruitment and population growth rate of *Choerospondias axillaris* (Roxb.) Burt & Hill (Anacardiaceae), a widespread canopy tree. We surveyed four parks that protect tropical seasonal mixed-evergreen forest, including populations of *C. axillaris*. These parks vary in their abundance of white-handed gibbons (*Hylobates lar*), sambar deer (*Cervus unicolor*), and common muntjac (*Muntiacus muntjak*), the tree's primary seed dispersers (Kunsakorn 2001). We measured relative density of these mammals in each park, and quantified levels of seed dispersal and seedling abundance of *C. axillaris*. We then used a stage-structured population model, based on demographic data collected in Khao Yai, to ask how *C. axillaris* population growth and persistence in this park would be affected if hunting were to increase and *C. axillaris* dispersal were to decrease to levels observed in other parks.



## Methods

### Study sites

Prior to extensive deforestation, northern Thailand was dominated by seasonal (or “monsoon”) forests; many trees are deciduous or semi-deciduous (Gardner et al. 2000; Maxwell & Elliott 2001). The southwest monsoon usually occurs from May or June through October or November, and there is a pronounced dry season from December to March (Smitinand 1977; Maxwell & Elliott 2001). Doi Suthep-Pui (DS; 18°48’N, 98°55’E) is the most recently established of the four parks we surveyed, and the smallest. Most of the park lies on a 350-1685 m mountain with two peaks; the study sites were located in mixed evergreen-deciduous forest at mid-elevations near the center of the park where *C. axillaris* is considered of “medium abundance” (Maxwell & Elliott 2001). Mean annual rainfall is approximately 2095 mm (Maxwell & Elliott 2001). Chiang Mai, one of Thailand’s largest cities, is only a few kilometers from the border of Doi Suthep-Pui, and at least four villages of ethnic Hmong people live inside the national park (approx. 5000 individuals as of 1999), practicing agriculture and illegal hunting (Maxwell & Elliott 2001). Nearly all large birds (Round 1984) and mammals (Maxwell & Elliott 2001) have been extirpated from the park by overhunting, including sambar and gibbons; muntjac remain extant but very rare (Maxwell & Elliott 2001). Doi Inthanon national park (DI; 18°32’N, 98°33’E) is larger than DS and within the same topographic zone and forest complex (Leimgruber et al. 2003). It also has villages inside its boundaries (Hmong and Karen people), with attendant hunting and some illegal forest conversion. None of our study sites were affected by forest conversion (though a *C. axillaris* tree on one of our plots was poached after the study concluded). Gibbons (along with many other large mammals and birds) are almost certainly extirpated from this park; sambar and muntjac are uncommon (JFB, pers. obs.). Nam Nao national park (NN; 16°44’N, 101°34’E) is in the somewhat drier eastern plateau. Much of the forests are relatively open and dominated by *Dipterocarpus*, *Pinus*, and *Quercus* species (JFB, pers. obs.); there are also extensive patches of mixed evergreen-deciduous forest (in wetter areas), in which we located our study plots. Nam Nao is bisected by a major highway and several smaller roads. Little is known about its hunting pressure or mammal densities; sambar and muntjac appear relatively common though gibbon abundance is

likely very low (JFB, pers. obs.). Khao Yai (KY; 14°26'N, 101°22'E) is Thailand's oldest and one of its largest parks. It lies on a large plateau, 700-900 m in elevation, dominated by mixed evergreen-deciduous forests (Smitinand 1977). Annual rainfall is approximately 2500 mm. Khao Yai is nearly surrounded by towns and villages, but the steep slopes on the flanks of the plateau make access to the interior on foot difficult. There are no villages (other than park staff quarters) inside the park, and the small roads that cross the park are guarded by entry kiosks. Poaching is rife on the periphery of the park, but the density of many large mammals in the central portion of the park is quite high (Lynam et al. 2006), suggesting a more limited impact of poachers. Deer, gibbons, large birds such as hornbills (Bucerotidae), and elephant (*Elephas maximus*) sign are observed almost daily in Khao Yai, unlike in any of the other parks (JFB, pers. obs.). A 30 ha Forest Biodynamics plot was established in 1993 in the central western portion of the park ("Mo Sing To" area). All trees over 1 cm DBH have been marked, mapped, and identified.

#### Field work

In 2002, we established four plots each in Khao Yai and Doi Suthep-Pui. In 2003 these were resurveyed, and four plots each established in Doi Inthanon and Nam Nao. All plots were resurveyed in 2004. Each plot was 50×100 m and separated from others in the same park by 1-4 km; plots in Khao Yai were located systematically, and in other parks were placed in areas that resembled the Khao Yai plots as closely as possible in terms of forest type and *C. axillaris* density. We estimated fruit crop on all trees in the plots by counting fruits on a portion of each tree's canopy using 8×40 binoculars and dividing this count by the proportion of the canopy sampled. We estimated the *C. axillaris* fruit crop on all adult female trees per plot at the beginning (July) of the fruiting season to determine the available fruit crop on each sampling plot. At the end of the fruiting season (October) we measured the proportion of seeds that remained undispersed (i.e. were underneath or still on the parent tree). The distances over which *C. axillaris* seeds are dispersed is a function of movement and gut retention time in the frugivores which, being large-bodied, mobile, mammals, could be quite high. Therefore seed deposition through the forest is likely quite random with respect to location of the mother tree, and should not decay as a predictable function of distance from the mother, as it

would with smaller frugivores or those that spit seeds rather than ingesting them (Bodmer 1991). Thus, to detect dispersed seeds, we established four parallel 50×4 m transects randomly on each plot (away from the parent canopies and light gaps), instead of radiating out from mother tree trunks. We surveyed these at the end of each fruiting season to measure the density of seeds dispersed to the forest (“shade dispersal”). Current-year seeds could be easily distinguished in this species (and were the only ones we counted); older seeds exhibited extensive decay. Finally, since *C. axillaris* seed germination is enhanced in light gaps, we wanted to examine the probability of seeds being dispersed to these microhabitats in particular across our study sites. We randomly located three 10×10 m plots in light gaps on each plot (or, if there were not three gaps on a plot, on the nearest gaps to the plot). Light gaps were defined as <60% canopy cover, determined with a spherical densitometer, as this was an inflection point in seed germination probabilities (see Results and Fig. 5A below). We surveyed these gaps for dispersed seeds (“light gap dispersal”) and seedlings at the end of each fruiting season.

We measured gibbon abundance using auditory sampling of their vocalizations, a standard method for surveying forest primates (Brockelman & Ali 1987; Brockelman & Srikosamatara 1993). At each plot, we measured the maximum number of groups heard calling during a one-hour period per day for five days. The mean maximum number of groups heard across five days was the gibbon abundance index. We measured relative abundance for muntjac and sambar using scat pellet counts (Bennett et al. 1940; Neff 1968) on the same transects used to measure seed dispersal levels. Transects were cleared of scat at the beginning of the season and sampled at the end. The relative abundance index was the total number of scat piles per plot divided by an experimentally determined “scat persistence rate” (Brodie 2006).

In 2003 and 2004 we set up planting arrays on the Khao Yai forest biodynamics plot to assess germination and seed predation across deposition environments (15 sites over a range of canopy cover conditions, ¼ of which were under adult female *C. axillaris* canopies). We used two cage types: “closed” to measure rates of germination and beetle predation and “open” to measure rates of seed predation by small mammals. Germination is not affected by seed handling (i.e. defecation vs. regurgitation vs. not ingested) (Kunsakorn 2001) so this effect was not tested. The number of remaining intact

seeds (open cages) and seedlings (closed cages) were recorded the year following the initiation of each experiment. We also compared germination and seed predation across parks, using 6 open and 6 closed cages per plot, half in light gaps and half in the shade, each with 40 *C. axillaris* seeds.

We marked naturally-occurring seedlings ( $n = 668$ ) on the Khao Yai forest biodynamics plot and followed their fates from 2003-2005 to assess survivorship and growth rates.

We also administered written (in Thai) questionnaires to a haphazard sample of 10 park rangers in each park (c.f. Wright et al. 2000), asking them to qualitatively assess poaching pressure in their park and whether it had affected gibbon, sambar, and muntjac populations.

### Population model

We assessed the importance of seed dispersal and its disruption for the population dynamics of *C. axillaris* using a stage-based, habitat-explicit matrix projection model. Much of the vital rate data for the model came from the Khao Yai forest biodynamics plot. The model was female-based and used a post-birth census with five stage classes: seedlings under mother trees, seedling dispersed away from mother trees but in the shade ( $\geq 60\%$  canopy cover), seedlings in light gaps ( $< 60\%$  canopy cover), juveniles ( $> 1.3$  m tall), and adults ( $> 18$  cm DBH; the smallest diameter at which trees begin fruiting; WYB, unpublished data). Only adults produced seeds, and there was no seed bank (JFB, unpublished data).

The number of seedlings in habitat  $i$  ( $sdlg_i$ ) produced by each adult per year was:

$$sdlg_i = S_A \times F_A \times P_{Female} \times D_i \times G_i \quad (1)$$

where  $S_A$  is the annual survivorship of adults (measured by repeat censuses on the biodynamics plot),  $F_A$  is the annual fecundity of adults (annual fruit counts of female trees on the biodynamics plot for 3 consecutive years),  $P_{Female}$  is the proportion of seeds that are female (assumed to be the same as the measured sex ratio of adults on the biodynamics plot),  $D_i$  is the proportion of fecundity dispersed to habitat  $i$ , and  $G_i$  is the germination of seeds in habitat  $i$  (measured experimentally in Khao Yai; see Fig. 5A). For the “under mother tree” habitat,  $D_i$  was the proportion of seeds that remained undispersed (Fig. 4A); for the two dispersed habitats:

$$D_i = (1 - P_U) \times \left( \frac{Y_i}{Y_i + Y_j} \right) \quad (2)$$

where  $P_U$  is the proportion of seeds undispersed,  $Y_i$  is the density of dispersed seeds in habitat  $i$  (see Fig. 4B & 4C) and  $Y_j$  is the density of dispersed seeds in the other of the two “dispersed” habitats.

Seedlings in given habitats could die, survive and remain seedlings in that habitat, or transition to become juveniles. These transition rates ( $J_i$ ) were based on habitat-specific survival and growth rates (see Fig. 5B & 5C), the cutoff point ( $Z$ ) between seedlings and juveniles (1.3 m), and accounted for size structure within the seedling stages (c.f. Crouse et al. 1987):

$$J_i = \frac{S_{s,i}^{(G_{s,i}/Z)-1} \times (1 - S_{s,i})}{1 - S_{s,i}^{(G_{s,i}/Z)}} \quad (3)$$

where  $S_{s,i}$  and  $G_{s,i}$  are the annual survival and growth, respectively, of seedlings in habitat  $i$ .

Survival of juveniles and adults, and the transition of juveniles to adults were estimated from repeat censuses of the forest biodynamics plot (WYB, unpublished data).

As most of the vital rate data come from Khao Yai, we could not make any inference about population growth rates in other parks. Rather, we used the matrix model to ask how, if hunting were to increase in Khao Yai to the levels we see in the other parks, would *C. axillaris* population growth be affected? For each of 10,000 bootstrap iterations, we re-sampled (with replacement) from the raw data to estimate vital rates and build four matrices that were identical except for the seed dispersal terms (which varied according to that observed in each park). We calculated the dominant eigenvalue of each matrix ( $\hat{\lambda}$ ) and took the differences in growth rate ( $\Delta\hat{\lambda}$ ) between the Khao Yai matrix and each of the “increased hunting” matrices. These bootstrap  $\Delta\hat{\lambda}$  arrays were ordered by rank and the 250<sup>th</sup> and 9750<sup>th</sup> used as lower and upper, respectively, 95% confidence limits. We also calculated the exponential decay half-life of the population as:

$$T_{1/2} = \frac{\log_e(2)}{\log_e(\hat{\lambda})} \quad (4)$$

to provide a simple metric for how changes in deterministic  $\hat{\lambda}$  might affect population persistence.

## Results

### Field work

Twice as many park rangers interviewed in Doi Suthep-Pui indicated that historical poaching had been “moderate” or “severe” as “light” or “none”. In Khao Yai half of the respondents said that poaching had been “moderate”, the other half either “light” or “none”. 70% of respondents in Doi Inthanon and Nam Nao said that poaching had been “moderate”. No rangers in any park indicated that current poaching was “severe” (see Fig. 2).

Relative density of the three mammals differed strongly among the parks in 2003 (gibbons: ANOVA,  $F_{3,12} = 520.273$ ,  $p < 0.001$ ; muntjac:  $F_{3,12} = 11.910$ ,  $p = 0.001$ ; sambar:  $F_{3,12} = 33.552$ ,  $p < 0.001$ ) and 2004 (gibbons:  $F_{3,12} = 173.400$ ,  $p < 0.001$ ; muntjac:  $F_{3,12} = 9.428$ ,  $p = 0.002$ ; sambar:  $F_{3,12} = 23.675$ ,  $p < 0.001$ ; see Fig. 3). Gibbons were consistently abundant in Khao Yai in both years and were never detected in Doi Suthep-Pui or Doi Inthanon; one group was heard calling once in Nam Nao (from very far off) in 2003, but none were detected in 2004. Muntjac and sambar densities were relatively high in Khao Yai and lower in Nam Nao; muntjac but not sambar were detected in Doi Inthanon. Neither of the deer were detected on our transects in Doi Suthep-Pui, though muntjac scat was observed on one occasion in the park (also see Maxwell & Elliott 2001).

The proportion of *C. axillaris* fruits remaining undispersed at the end of the field season (i.e. those that were still on or underneath the mother trees) differed strongly between parks in 2003 (ANOVA;  $F_{3,38} = 24.68$ ,  $p < 0.001$ ) and in 2004 ( $F_{3,38} = 13.22$ ,  $p < 0.001$ ). The proportion of undispersed fruits ranged from 80-94% in Doi Suthep-Pui to 15-21% in Khao Yai (Fig 4A). The density ( $m^{-2}$ ) of seeds dispersed away from mother trees but remaining in the shade ( $\geq 60\%$  canopy cover) varied significantly among parks in 2004 (ANOVA;  $F_{3,12} = 19.60$ ,  $p < 0.001$ ), but not in 2003. The density of seeds dispersed to light gaps varied significantly among parks in 2004 ( $F_{3,12} = 4.03$ ,  $p = 0.034$ ), but not in 2003 (Fig. 4). In general the density of dispersed seeds and the proportion of

undispersed seeds positively and negatively (respectively) track variation in mammal density across the parks, though our small sample size ( $n = 4$  parks) precludes effective formal correlation analysis.

We pooled *C. axillaris* seedling density ( $\text{m}^{-2}$ ) data within plots across all years since, unlike seeds (which were always from the current year fruit crop), seedlings could survive to be counted in consecutive years. The density of seedlings away from parent canopies but in the shade did not vary significantly among parks, but the density of seedlings in light gaps did ( $F_{3,12} = 6.07$ ,  $p = 0.009$ ). Seedling density in light gaps was higher in Khao Yai than in any other park (Tukey post-hoc comparisons; Doi Inthanon:  $p = 0.050$ ; Doi Suthep-Pui:  $p = 0.010$ ; Nam Nao:  $p = 0.026$ ). In Doi Suthep-Pui, where large mammals are all but extinct, no *C. axillaris* seeds or seedlings were found in light gaps.

Seed germination in light gaps, determined experimentally in Khao Yai, was higher than in the shade (ANOVA;  $F_{2,116} = 8.31$ ,  $p < 0.001$ ; Fig. 5). Germination under adult females was zero in our experiments, but this is partly an experimental artifact since seedlings can be found under female trees in nature. There were no differences in rates of seed predation among habitats. Seedling growth was higher in light gaps than in the shade or under mother trees (growth:  $F_{2,88} = 4.84$ ,  $p = 0.010$ ; Fig. 5).

Seed addition experiments showed no difference in germination rates across parks either in forest (ANOVA;  $F_{3,44} = 0.67$ ;  $p = 0.577$ ) or in light gaps ( $F_{3,44} = 0.12$ ;  $p = 0.947$ ). Seed predation rates, measured with open cages to which rodents and insects had access to seeds, did vary across parks in the forest ( $F_{3,43} = 3.05$ ;  $p = 0.039$ ): they were lower in Nam Nao than in Doi Inthanon (Tukey post-hoc comparison:  $p = 0.050$ ). They did not vary significantly in light gaps ( $F_{3,44} = 2.48$ ;  $p = 0.073$ ). Annual survivorship did not differ among parks for seedlings under parent trees ( $F_{3,148} = 1.15$ ;  $p = 0.332$ ), dispersed but still in the shade ( $F_{1,38} = 0.11$ ;  $p = 0.774$ ), or in light gaps ( $F_{2,78} = 0.18$ ;  $p = 0.838$ ). Surviving seedlings in the shade were too scarce in any park to test for differences in their growth rates. Annual growth of seedlings under parent trees did not differ ( $F_{3,13} = 0.35$ ;  $p = 0.793$ ), though growth in light gaps did ( $F_{2,12} = 7.16$ ;  $p = 0.009$ ), due to lower rates in Khao Yai (mean = 7.96 cm/year) than in Doi Inthanon (mean = 10.00 cm/year;  $p = 0.009$ ).

### Population model

The mean *C. axillaris* population growth rate in Khao Yai was estimated at 0.990. As seed dispersal declined across the “increased hunting” scenarios, the population growth rate dropped, though very slightly. Nam Nao seed dispersal levels reduced the Khao Yai  $\hat{\lambda}$  by 0.003 (95% CI: 0.000, 0.018), Doi Inthanon seed dispersal levels by 0.006 (0.000, 0.029), and Doi Suthep-Pui levels by 0.009 (0.000, 0.048; see Fig. 6). The exponential decay half-life for the Khao Yai *C. axillaris* population, based on the best-estimate  $\lambda$ , is 69.0 years. As seed dispersal and  $\hat{\lambda}$  in the “increased hunting” scenarios decline, the population half-life is reduced by 17.2 years for Nam Nao hunting levels (95% CI: 0.0, 44.6), 24.6 years for Doi Inthanon hunting levels (0.0, 51.7), and 31.9 years for Doi Suthep-Pui levels (0.0, 57.3).

The analytical elasticity (sensu Caswell 2001) of seed dispersal (to all habitats combined) is the fourth-highest (0.014) out of 15 vital rates, following adult survivorship (0.792), juvenile survivorship (0.110), and the survivorship of seedlings in light gaps (0.034).

### Discussion

Parks with extensive hunting exhibit lower seed dispersal and fewer *C. axillaris* seedlings. Gibbons, muntjac, and sambar in Khao Yai transport a high proportion of *C. axillaris* seeds away from the parent canopy, and some of them to light gaps, where germination and seedling survival are enhanced. In the other parks, where the abundance of these mammals is lower, seed dispersal is curtailed; the density of seeds dispersed to the forest and to light gaps is lower and the proportion of seeds that remain undispersed is higher. The density of *C. axillaris* seedlings in light gaps positively tracks both gibbon and deer density and the level of seed dispersal to gaps.

Previous studies have shown that hunting in Neotropical and Afrotropical forests can disrupt seed dispersal mutualisms by reducing the quantity of seeds removed (Wright et al. 2000; Wright & Duber 2001; Forget & Jansen 2007; Wang et al. 2007) or the distance which they are dispersed (Chapman & Onderdonk 1998). Our results corroborate these findings for a widespread canopy tree of the Indomalayan tropics, and place the results in a population-level context. In national parks with severe hunting, we



estimate that the long-term population growth rate and persistence of *C. axillaris* is reduced, albeit slightly. Model output suggests that disruption of this seed dispersal mutualism by illegal hunting can lower the abundance and time to extinction of this zoochorous tree.

Although our results suggest that reductions in dispersers may decrease population growth of *C. axillaris*, this decrease in population growth rate is slight; even a massive reduction in mammal density, from quite high in Khao Yai to essentially zero in Doi Suthep-Pui, results in only a very small drop in *C. axillaris*  $\hat{\lambda}$  (see Fig. 6A). This is likely explained by the relatively low elasticity of seed dispersal. In other words, even if no regeneration were to go on at all, it would still take a very long time for the adults in the population to slowly fade from attrition. But the declines, though slow, are real. As mammalian frugivores are reduced or removed from tropical forests, the persistence and population dynamics of the trees that depend on them for seed dispersal may be affected, even if actual extinction could take many decades or longer.

Because our study, like all others on the topic, uses a natural experiment rather than a controlled manipulation, we cannot exclude the possibility that factors other than hunting explain the variation in mammal abundance across these parks. The lowest relative abundance of all three mammals surveyed was in the smallest park, Doi Suthep-Pui. We think it unlikely, however, that the observed mammal abundances are strongly influenced by fragmentation effects (c.f. Terborgh et al. 2001; Cordeiro & Howe 2003; Laurance et al. 2006), since all the parks are embedded in larger forest complexes (Fig. 1) that substantially increase their effective area (Leimgruber et al. 2003). There are no diseases or introduced species known to affect primate or ungulate populations in any of these parks. The high proportion of drier, more open forests in Nam Nao could account for the very low gibbon density there. But in the absence of hunting these forests should, if anything, support higher deer densities than closed-canopy moist tropical forest (Dinerstein 1982; Robinson & Bennett 2004). Indeed hunting pressure is often a better predictor than forest type for mammal density in tropical areas (Bennett et al. 2000). Likewise, Doi Suthep-Pui and Doi Inthanon have villages inside their boundaries and some associated conversion of forest to agricultural fields; while this habitat alteration would undoubtedly have negative effects on the strictly arboreal gibbons, in the absence

of hunting it should not be detrimental to the deer (Dinerstein 1982; Robinson & Bennett 2004). Hunting is known to be unsustainably high across Southeast Asia (WCS 2002; Lynam et al. 2006), to have caused the extirpation of large-bodied vertebrates within protected areas of northern Thailand (Round 1984; Maxwell & Elliott 2001; Tungittiaplakorn & Dearden 2002; Lynam et al. 2006), and to be "...the greatest threat to wildlife and wild lands in Asia" (WCS 2002: 31). Despite small sample sizes, our interviews suggest that historically, poaching in Khao Yai was less intense than in the other three parks.

Likewise, factors other than seed dispersal limitation could potentially explain the differences in *C. axillaris* seedling abundance across parks. *C. axillaris* seed germination, seed predation, and seedling survivorship rates did not differ importantly among parks. Seedling growth was lower in Khao Yai than in Doi Inthanon, but clearly this cannot explain the higher seedling abundance in the former. Though much of Nam Nao is drier than the other parks, the study sites in each park were broadly similar in forest type and approximate *C. axillaris* density.

We use a structured population model to assess the cascading effects of overhunting, and suggest that this approach can be highly valuable for evaluating the population-level consequences of mutualism disruptions in complex systems and on large geographic scales. However, inherent in this approach are several assumptions that may affect the robustness of its results. First, we assume that the only way for seeds to get to light gaps is to be dispersed there by animals, when in nature gaps can form (by falling trees or branches) above undispersed seeds. But a more detailed model that includes such habitat transitions results in only very slight (<0.01%) changes in *C. axillaris*  $\hat{\lambda}$  (JFB, unpub. data). Second, the model does not incorporate environmental stochasticity or density dependence, both of which could influence population dynamics. Moreover some of the vital rates used to construct our model are based on relatively small sample sizes: two annual transitions for seedlings and repeat censuses three years apart for juveniles and adults. Indeed these low sample sizes could explain the fact that *C. axillaris*  $\hat{\lambda}$  in Khao Yai is <1; if 5 of the 7 adults that died (out of 159 individuals) had lived instead,  $\hat{\lambda}$  in Khao Yai would equal 1.000. However, even under if we assume that  $\hat{\lambda}$  in Khao Yai equals 1 (and adjust adult survivorship to make this so) the relative

differences ( $\Delta\hat{\lambda}$ ) between Khao Yai and the increased-hunting scenarios (i.e. the other national parks) would change only slightly;  $\Delta\hat{\lambda}_{NN}$ ,  $\Delta\hat{\lambda}_{DI}$ , and  $\Delta\hat{\lambda}_{DS}$  would be reduced by 17.6%, 21.4%, and 20.0% respectively. Thus, if our baseline estimate of *C. axillaris* population growth rate in Khao Yai were biased low, true declines in  $\hat{\lambda}$  across the increased-hunting scenarios would be lower than we report here. However, 1) there would still be statistically real declines in  $\hat{\lambda}$  in parks with higher hunting, and 2) estimates of relative differences in  $\hat{\lambda}$  among parks that vary in poaching would change only slightly.

The direct ecological impacts of hunting by humans in protected areas can be severe, and may in turn precipitate indirect negative effects on a widespread canopy tree. Even tree species such as *C. axillaris*, with multiple seed dispersers, are susceptible to the indirect effects of poaching if those dispersers are large mammals. The mere establishment of protected areas is insufficient to fulfill conservation goals. Effective enforcement, the active engagement of local people in protected area management, and education about the ecological effects of hunting are also required.

Figure 3.1: Northern Thailand showing locations of four national parks with the area of the park (NP) and the greater ecosystem (GE) within which it resides (Leimgruber *et al.* 2003).

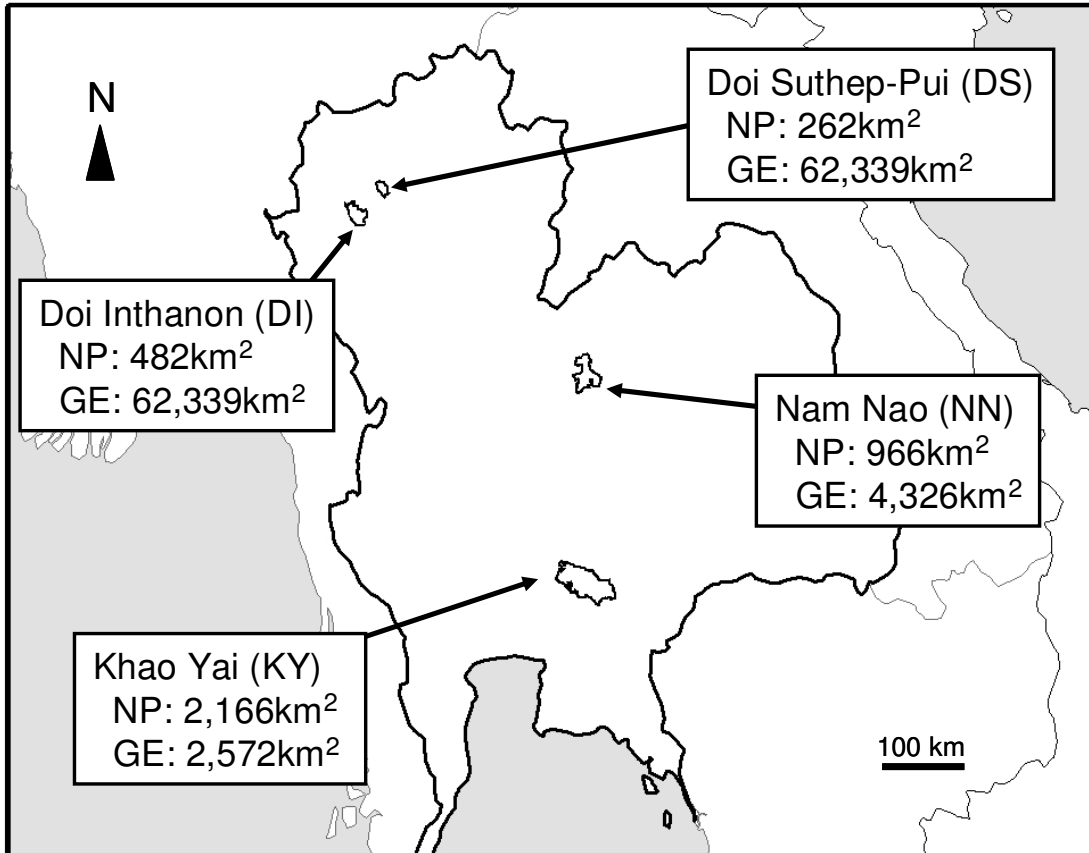


Figure 3.2: Responses by park rangers interviewed in Doi Suthep-Pui (top row), Doi Inthanon (second row), Nam Nao (third row), and Khao Yai (bottom row), asked to qualitatively assess poaching pressure “since the park was formed” (left column) and “currently” (right column) on gibbons, muntjac, and sambar.

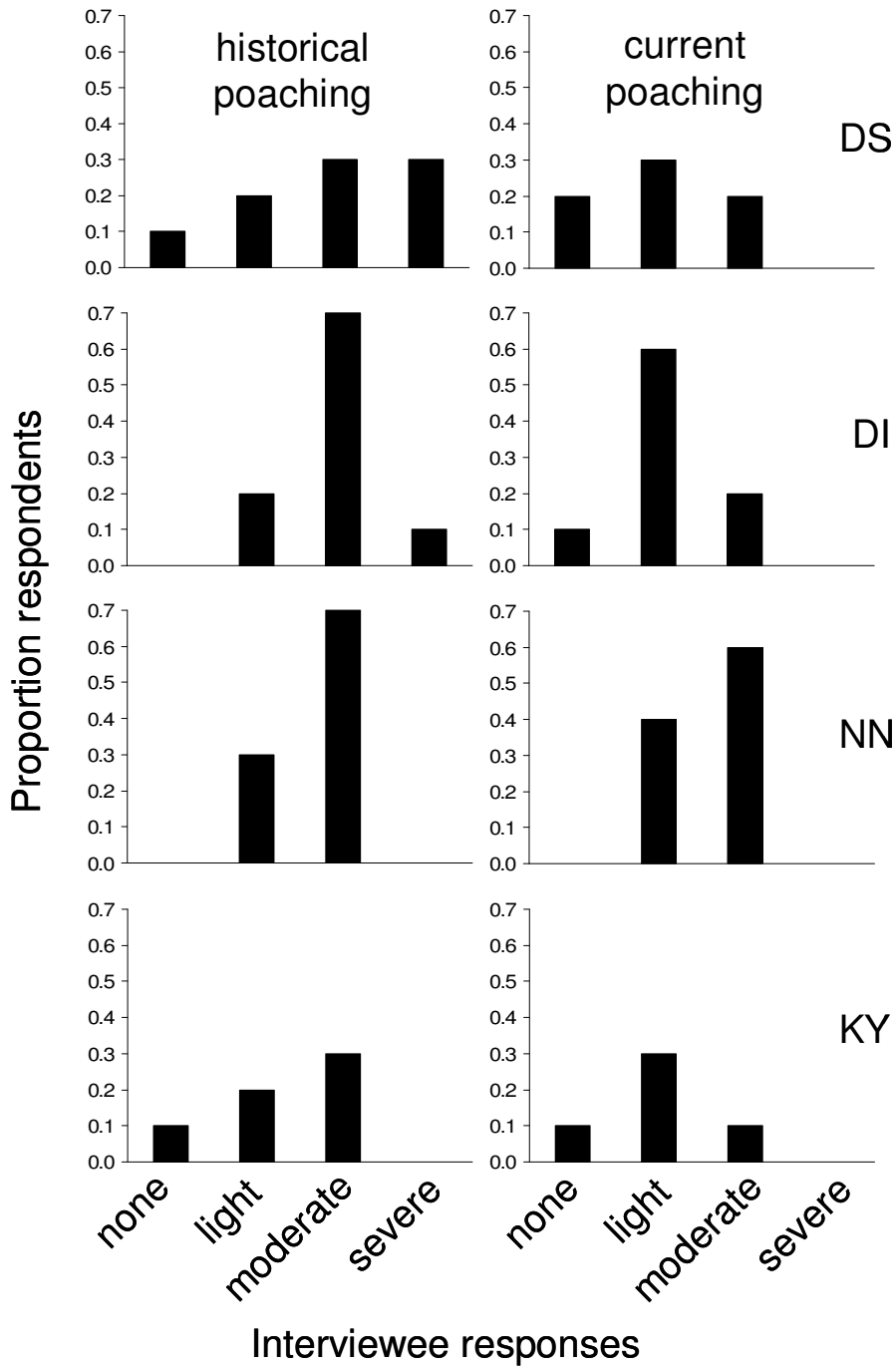


Figure 3.3: Mean (+SE) relative mammal density across parks.

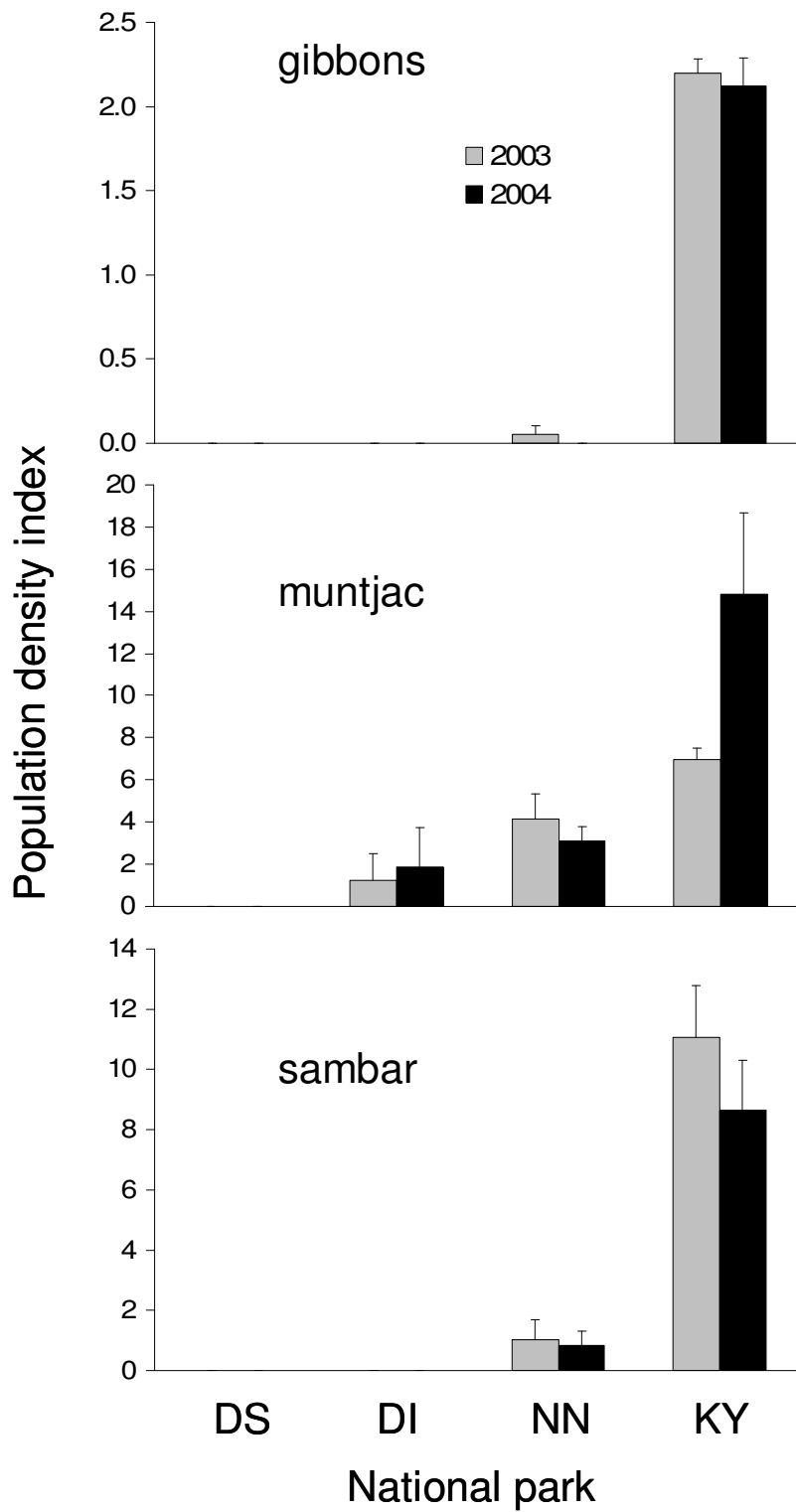


Figure 3.4: Mean (+SE) proportion *C. axillaris* fruits left undispersed (still on or underneath mother trees) at end of field seasons (A); density of seeds dispersed away from mother trees to shady habitats (B) and light gaps (C).

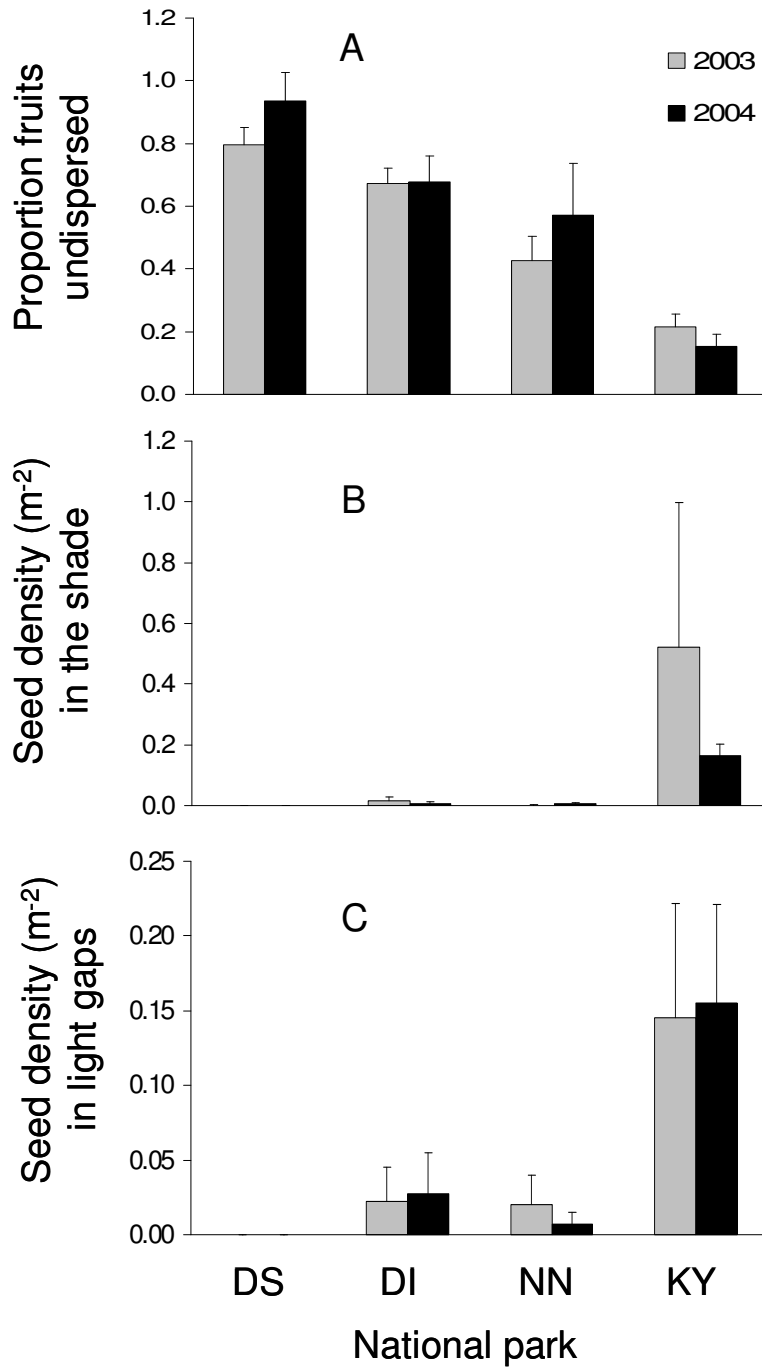


Figure 3.5: Mean (+SE) *C. axillaris* germination (A), seedling survivorship (B), and seedling growth (C) across habitats.

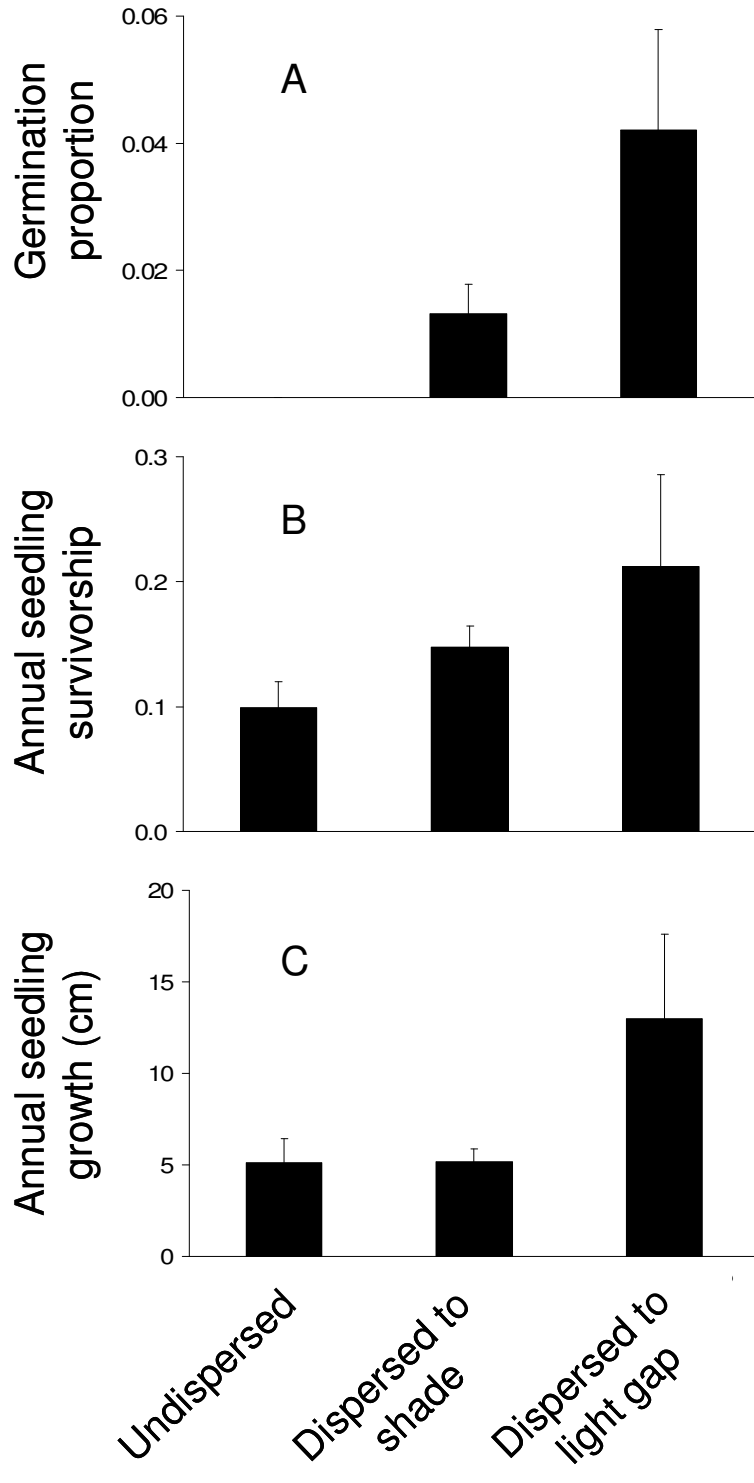
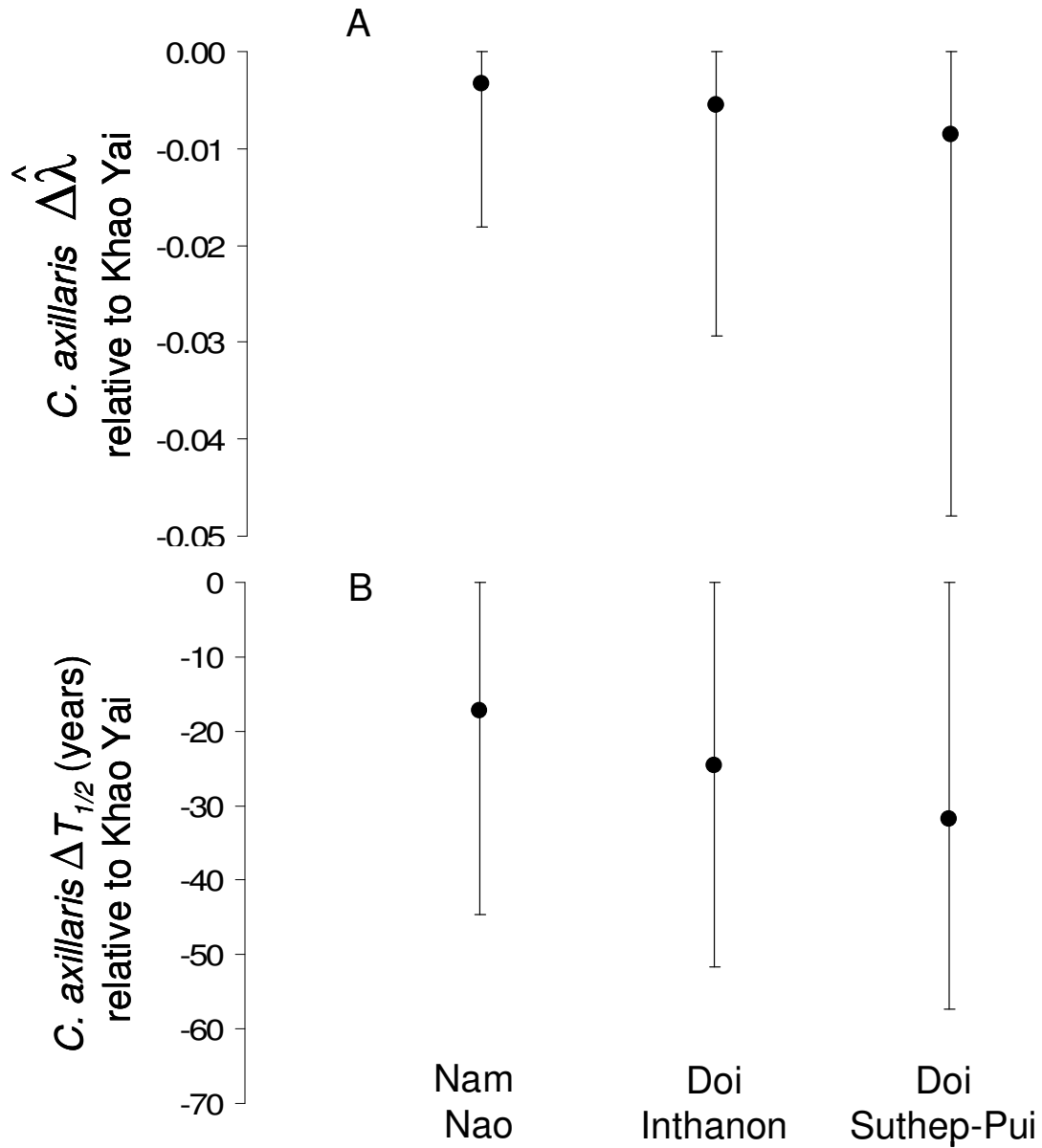




Figure 3.6: Estimated change in *C. axillaris* population growth rate (A) and exponential decay half-life (B) in Khao Yai if hunting in that park were to increase (and seed dispersal correspondingly decrease) to the levels seen in the other parks. Bootstrap mean and 95% confidence intervals shown. Exponential decay half-life under Khao Yai hunting scenario is 69.0 years.



## CHAPTER 4: FUNCTIONAL EQUIVALENCE OF TROPICAL MAMMALIAN FRUGIVORES

### Introduction

The current extinction crisis has generated increasing interest in how loss of species will affect community stability (Tilman and Downing 1994) and ecosystem function (Hooper et al. 2005). Functional redundancy in natural ecosystems is a crucial determinant of these effects. Ecological function can be measured in several ways. Here we use the metric of interaction strength as measured by demographic impact on interacting species (Power et al. 1996, Godinez-Alvarez et al. 2002); if two species in a guild have similar influence on the population growth rate of a third species, they are considered functionally equivalent. If communities are composed of many functionally equivalent species, loss of one or a few would not be expected to have major ecological ramifications. But if there is large variability in the strength of interactions among species, loss of the most strongly-interacting agents will have critical impacts on the assemblage. Analyses of trophic interactions in intertidal (Raffaelli and Hall 1995, Wootton 1997) and grassland (Fagan and Hurd 1994) communities suggest that predator guilds in nature are usually composed of many weak and a few strong interactors, implying low functional equivalence. Yet we have little data on the distribution of interaction strengths in other systems or types of guilds.

Here we use field observations and population modeling to infer how variation in the efficacy of seed dispersal among a group of tropical mammalian frugivores influences the demography and population growth of a canopy tree whose seeds they disperse. We ask how variation in the quantity of seeds dispersed, the microhabitat they are dispersed to, and the frequency of canopy gap formation affects the population-level impacts of these frugivores on their host tree. Although quantifying interaction strengths among species has historically been accomplished through a purely experimental approach (e.g. Paine 1992), this is difficult in complex tropical systems that harbor many long-lived species. Our approach combines observations, small-scale experiments, and stage-based matrix modeling to infer how different dispersers may differentially influence tree abundance. We assess seed dispersal in a biologically realistic context that includes the

complete life-cycle of the zoochorous tree as well as changes in the habitat in which it dwells.

Zoochorous seed dispersal is a mutualism critical to the function of many tropical forests, and has the potential for disruption by anthropogenic impacts on frugivorous vertebrates (Bond 1995). Many tropical trees obligately rely on birds and mammals for seed dispersal (Estrada and Fleming 1986, Hamilton 1999). Frugivores are susceptible to population decline and local extinction from human activities such as habitat fragmentation (Cordeiro and Howe 2001) and wildlife hunting (Redford 1992). In systems where a plant is serviced by one frugivore, loss of that disperser can negatively affect the plant's reproduction and regeneration (Traveset and Riera 2005). But more commonly, several or many frugivores service a single plant species (Howe and Smallwood 1982, Bond 1995), and how diversity in the frugivore guild affects a tree's susceptibility to loss of dispersal services is a critical hole in ecological knowledge (Loiselle and Blake 2002). If different frugivore species are functionally similar, loss of one disperser can be compensated for by the services of the remaining species, and reductions in the diversity of seed dispersers should have little impact on the effectiveness of seed dispersal. Alternatively, if members of a disperser guild differ significantly in the effectiveness of their services, the loss of a primary disperser may force plants to rely on less efficient secondary dispersers (Santos et al. 1999), with negative implications for the demography of the plant.

Numerous comparisons of seed dispersal services within frugivore guilds have found differences among the component species. For a given plant species, some animals may remove more fruit (Howe and Vande Kerckhove 1981), disperse seeds farther (Howe 1993, Jordano et al. 2007), take them to better microhabitats (Reid 1989), or be more effective at seed scarification (Figuerola et al. 2002). Yet we have very little understanding of the extent to which these differences manifest at the plant population level. Fruit removal or seed dispersal distance may vary among frugivore species by orders of magnitude (Vazquez et al. 2005; and references therein), yet this still does not necessarily allow us to predict how these differences affect zoochorous plant population dynamics. Among dispersers of a Mexican columnar cactus, the "effectiveness" (relative abundance  $\times$  visitation rate  $\times$  seed handling  $\times$  probability of safe-site deposition) of a bat

species was four to five orders of magnitude greater than that of four avian seed dispersers (Godinez-Alvarez et al. 2002). Yet the cactus population growth rate attributable to each of the five animals individually differed only slightly, with highly overlapping confidence intervals (Godinez-Alvarez et al. 2002).

For functional redundancy to be important at the population level, seed dispersal must have net positive effects on plant demography; yet even this is rarely quantified (Howe and Miriti 2004). On the one hand, the impressive energetic investment of many plants to the production of animal-attracting fruits suggests that, over evolutionary time scales, seed dispersal must be important (Howe 1977, Howe and Smallwood 1982). On the other hand, myriad factors affect the fitness of an individual plant from seed to reproductive adult stages, potentially swamping the demographic importance of seed dispersal. Thus studies of seed dispersal mutualisms must place seed dispersal within a broader demographic context by explicitly accounting for seed and seedling survivorship, growth, and variation in habitat quality that can influence these vital rates. When such an approach is taken, it is often found that reproductive parameters such as seed dispersal for long-lived organisms like tropical trees have low elasticities (Pfister 1998), that is, little ability, relative to other vital rates, to affect population growth. This would suggest that variation in seed dispersal might have minimal impacts of plant dynamics. Alternatively, if the vital rates are highly variable (e.g. due to the differential efficacy of different seed disperser species), even those with low instantaneous elasticity can still importantly affect population dynamics (Mills et al. 1999, Howe and Miriti 2004). Yet empirical comparisons of the demographic and population-level consequences of species-specific variation in seed dispersal are limited.

Here we compare the demographic and population-level effects of seed dispersal by gibbons, common muntjac deer, and sambar deer on the canopy tree *Choerospondias axillaris* (Roxb.) Burt & Hill (Anacardiaceae) in tropical seasonal forest of Thailand. All three frugivore species are subject to intense illegal hunting pressure in protected areas across Thailand; thus it is of great interest to understand how declines in the abundance of one or several of these species might influence the abundance of their host tree, *C. axillaris*.

## Methods

### Study area and species

Khao Yai National Park (14°26' N, 101°22' E; 2166 km<sup>2</sup>) straddles a large plateau, approximately 700-900 m elevation, with mixed deciduous forest on the steep edges and seasonal evergreen or mixed evergreen-deciduous forest types throughout most of the area (Smitinand 1977). Annual rainfall is approximately 2500 mm, mostly occurring from May-Oct.; there is a pronounced dry season from Dec.-April. Abundance of many large mammals in the central portion of the park is high (Lynam et al. 2006). A 30 ha Forest Biodynamics plot was established in 1993 in the central western portion of the park; all trees over 10 cm diameter at breast height (DBH; 130cm) were mapped, marked, and identified by 2002, a re-census (including measurements of individuals 1-10 cm DBH) occurred in 2005. The plot contains over 200 tree species, where *C. axillaris* is the 24<sup>th</sup> most abundant by frequency (1.2% of adult trunks), and 3<sup>rd</sup> most abundant by cumulative basal area (5.9% of total; WYB, unpub. data).

*C. axillaris* (syn. *Spondias axillaris* Burt & Hill) is a large (up to 30 m tall) canopy tree widely distributed in tropical Asia from central Thailand to Nepal to Taiwan. It is dioecious and females bear fruits from Jun.-Oct.; the fruits are 2-3 cm long, and are composed of a pericarp surrounding fibrous, watery flesh, with a single stone inside. Wet mass of the fruit pulp contains, on average, 84% moisture, 2.7% protein, 0.6% fat, and 3.0% sugars (Chen et al. 2001). Each stone (hereafter “seed”) has a very hard covering over 5 embryos. In Khao Yai, fruits are consumed almost entirely by gibbons, sambar, and common muntjac (Kunsakorn 2001, Kitamura et al. 2002, this study). 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, pers. comm.). 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’ below). *C. axillaris* is often present in early successional habitats, but persists into mature mixed-evergreen seasonal forest (Maxwell and Elliott 2001).

White-handed gibbons (*Hylobates lar*) are frugivorous arboreal apes (4-8 kg; Lekagul and McNeely 1977); they are the most widely distributed gibbon in Southeast

Asia, and are common in much of Khao Yai. The forest dynamics plot includes the entire range of one group of animals (“Group A” composed of 2 adults plus varying numbers of young and juveniles) that have been studied since the 1980s and are habituated to the presence of researchers. Sambar and common muntjac are large (109-260 kg) and small (20-28 kg; Lekagul and McNeely 1977) deer respectively; both have extensive distributions across tropical Asia. Gibbons consume *C. axillaris* fruits before they fall and defecate the seeds. Both of the deer species primarily consume foliage, but are occasionally frugivorous and eat large quantities of *C. axillaris* fruit when it is available (JFB, pers. obs.). They consume the fallen fruits and regurgitate cleaned seeds, usually while bedding and ruminating (WYB, JFB, pers. obs.).

*C. axillaris* seeds fall or are dispersed during the monsoon season (Jul.-Nov.), and remain on the ground to germinate the following wet season; we have detected no seed bank (see Results). 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 habitat differences among deposition sites (see “Results”). Seeds are so 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 total surface area of the plot). We surveyed these transects weekly for 10 weeks from mid-July to September in 2003 and 2004. Each transect was surveyed in two 2 m-wide passes. We recorded the number of dispersed *C. axillaris* seeds, the density of 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 (Kanjavanit 2004) and scat. Because field work occurred during the rainy season, the forest floor stayed continually moist and deer tracks could easily 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/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 assessed whether the proportion of seeds dispersed to different habitats differed by frugivore or year with chi-squared tests.

We assessed seed germination and predation experimentally, and determined 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 (c.f. Janzen 1970). To do this, in 2003 and 2004 we set up arrays of seeds at different densities (2, 8, 30, 100 seeds/pile; spanning the range of observed deposition pile sizes), and in different microhabitats (15 sites across a range of canopy cover conditions, ¼ of which were under adult female *C. axillaris* canopies). In order to examine rates of post-dispersal seed predation, we placed seeds in “closed” or “open” cages (30×30×15 cm wire enclosures pinned to the ground; total of 4200 seeds/year). 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. The number of seedlings remaining in open and closed cages was recorded the year following the initiation of each experiment. Therefore “germination” as used here includes germination per se and first-year seedling survival (many of these seeds were destroyed by beetles or fungus), and seed removal by small mammals (open cages) is cumulative for an entire year. We performed multiple logistic regressions of seed pile size, canopy cover proportion, and female canopy (a binary measure of whether the site was under a fruiting adult) versus germination and seed removal rates. 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 individual parameter coefficients ( $\beta$ ) 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/year; c.f. Forget and Milleron 1991), to which we had glued 60 cm of thin nylon string. 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 predated or were still intact.

We measured canopy cover at all naturally dispersed seed piles, at locations where we found seedlings on transects, and at sites where we placed experimental seed arrays with hemispherical canopy photographs (2004, 2005) or a spherical densitometer (2003; standardized using a regression of densitometer vs. photography cover values). All photographs were taken 1 m above the ground and analyzed for canopy cover proportion using HemiView 2.1 (Dynamax Inc.). Tropical forests are mosaics of dense tree cover, light gaps, and areas in between (Whitmore 1998). 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 from 2003-2005. We then constructed an annual transition matrix for habitat types.

We marked all naturally-occurring seedlings on the transects ( $N = 670$ ) 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 regressions.

Individuals  $>1.3$  m tall (“breast height”) 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 plot. We measured fecundity by visual counts (with 8×40 binoculars) of fruit crop at the beginning of the fruiting season in a random sample of the total adult female population. We also measured the proportion of total fecundity 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 fecundity (fruit crop at the beginning of the fruiting season) between years, and assessed its relationship to tree diameter using multiple linear regressions.

### 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* as well as transitions for habitat state, since forest habitat is dynamic through time and the demographic performance of *C. axillaris* is enhanced in light gaps. We used 6 stage classes: habitat 0 seedlings (underneath female canopies), habitat 1 seedlings (0.11-0.3 proportion canopy cover), habitat 2 seedlings (0.31-0.7 proportion canopy cover), habitat 3 seedlings (0.71-1.0 proportion canopy cover), juveniles (over 1.3m tall but <18 cm DBH), and adults (>18 cm DBH). No points in the forest had less than 0.11 proportion canopy cover. The seedling stage boundaries were determined from graphical inspection of the relationships between canopy cover and germination and seedling survivorship. Habitat 0 (underneath adult females) essentially mimicked the canopy cover range of habitat 3 (98% of habitat under female canopies was in the 0.71-1.0 proportion canopy cover range), but was considered a separate class because seedling survivorship was significantly lower (see “Results”). Only adults reproduced, with fecundity estimated from measured fruit crops at the beginning of the two fruiting seasons. Seed dispersal to different habitats by different frugivores was measured from the transect data and expressed as a proportion of the total fecundity available to the frugivores during the study period (i.e. total fecundity 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 habitat transitions probabilities measured from the repeat canopy photographs to construct a habitat transition matrix ( $C$ ), rescaled so that each column summed to 1. Seedlings could “move” among habitats via gaps opening up or closing in above them, measured by habitat transition probabilities,  $C_{ij}$ . Gap formation was assumed to occur at a predictable time of year (c.f. Pascarella and Horvitz 1998), specifically during the dry season (Dec.-Mar.) when winds increase. Therefore the order of events in the model was: seed dispersal > habitat transition > germination, seedling

survivorship, and seedling growth. Germination, seedling survivorship, and seedling growth were measured at the median canopy cover values for each habitat, using logistic (germination and seedling survival) or linear (seedling growth) regressions of each vital rate versus 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 ( $trans_{j,juv}$ ) were measured as habitat-specific seedling growth (in vertical cm; from linear regressions of seedling growth versus canopy cover) accounting for size structure within the seedling stages (c.f. Crouse et al. 1987):

$$trans_{j,juv} = \frac{\left(surv_j^{(sgj/ht)-1}\right) \times (1 - surv_j)}{1 - surv_j^{(sgj/ht)}} \quad (1)$$

where  $sgj$  and  $surv_j$  are growth (in vertical cm) and annual survivorship, respectively, of seedlings in habitat  $j$ , and  $ht$  is the height cutoff between seedlings and juveniles (1.3 m).

Vital rates for juveniles and adults were independent of habitat, partly due to lack of habitat-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 calculated transition of juveniles to adults using a formula identical to Eq. 1 except substituting juvenile growth (in cm 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 constructed separate matrices for each frugivore (using different seed dispersal data), and measured the *C. axillaris* population growth rate ( $\hat{\lambda}$ ) attributable to each frugivore independently and all of them combined. These frugivore-specific lambda estimates were our measures of interaction strength. We generated bootstrap confidence intervals around each  $\hat{\lambda}$  by resampling from the original data to re-create vital rate estimates for each iteration, and used 10,000 iterations per matrix.

The confidence intervals around frugivore-specific estimates of lambda include variance from all of the vital rates in the population matrix, yet we also wished to assess the differences in *C. axillaris*  $\hat{\lambda}$  due solely to variance in seed dispersal among the mammals. Thus we also constructed confidence intervals around the difference in  $\hat{\lambda}$  due to dispersal by each frugivore compared to no dispersal at all. For each of 10,000

bootstrap iterations we resampled the original data to estimate vital rates and constructed 5 matrices that differed only in the dispersal term. We then estimated the difference in lambda ( $\Delta\hat{\lambda}$ ) for dispersal by each frugivore versus no dispersal at all, and generated 95% confidence intervals around these differences.

## Results

### Field sampling

Of the 8202 seeds dispersed in 103 piles across both years, we were able to confidently identify the disperser for 79.6% of piles (95.8% of total seeds). Thirty seven percent of the unidentified dispersers were deer (based on the shiny regurgitated seeds), but due to a lack of distinct tracks near the seeds we could not identify the species of deer. All of the seeds were dispersed by gibbons, muntjac, and sambar except 22 (0.3% of total) by a bear (*Ursus* sp.), 3 (<0.1%) by an elephant (*Elephas maximus*), and 7 (0.1%) by either a large civet (*Viverra* sp.) or a macaque (*Macaca nemestrina*). Handling by rodents was also evident in 1.4% of seeds, but it is unclear whether this represents primary or secondary dispersal.

Muntjac dispersed more seeds than gibbons or sambar, and dispersed a higher proportion of their seeds away from female canopies (Fig. 1). There were no differences between years in the proportions of seeds dispersed to the different habitats for gibbons ( $\chi^2_{[3]} = 0.51, p = 0.917$ ), muntjac ( $\chi^2_{[3]} = 0.02, p = 0.999$ ), or sambar ( $\chi^2_{[3]} = 0.16, p = 0.984$ ). Seeds were dispersed to different habitats roughly proportionally to the availability of those habitats for gibbons ( $\chi^2_{[3]} = 1.31, p = 0.727$ ) and muntjac ( $\chi^2_{[3]} = 0.37, p = 0.946$ ). Sambar dispersed more seeds than expected to the “underneath adult female canopy” microhabitat and fewer than expected to the other three microhabitats ( $\chi^2_{[3]} = 8.65, p = 0.034$ ). 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 0.31-0.7 proportion canopy cover range (also see Appendix B). Muntjac were the only dispersers to deposit seeds in the highest-light microhabitat (0.11-0.3 canopy cover; Fig. 1).

Fruit crop at the beginning of the fruiting season did not differ between years (linear regression:  $R^2 = 0.11, df = 24, p = 0.754$ ), and was not significantly related to tree

diameter ( $\beta = -11.839$ ,  $p = 0.127$ ). Mean ( $\pm$ SE) fecundity was 800.81 ( $\pm$ 106.45) 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 between years (linear regression:  $R^2 = 0.09$ ,  $df = 24$ ,  $p = 0.208$ ) or as a function of tree diameter ( $\beta = -0.002$ ,  $p = 0.487$ ).

Germination was significantly higher in 2003 than in 2004 (logistic regression:  $LL = -148.8$ ,  $df = 2009$ ,  $p = 0.041$ ), and was negatively affected by canopy cover ( $\beta = -3.745$ ,  $p < 0.001$ ; see Fig. 2). However, seed germination was unaffected by seed pile size ( $\beta = 0.004$ ,  $p = 0.238$ ) or by being under an adult female canopy ( $\beta = -12.015$ ,  $p = 0.822$ ). While germination under female trees was zero in our trials, this is at least partly an experimental artifact since seedlings occur under female canopies in nature. All 2003 seeds that did not germinate and were not removed by 2004 ( $n = 3350$ ) were monitored for the following year, and none germinated. Mean ( $\pm$ SE) proportions of seeds per plot removed from the open cages were 0.341 ( $\pm$ 0.047) and 0.372 ( $\pm$ 0.059) for 2003 and 2004, respectively; seed removal was not significantly affected by canopy cover, being under a female canopy, or seed pile size. Post-removal seed predation was not significantly affected by canopy cover or location under a female canopy. Of removed seeds with strings attached, 0.80 ( $\pm$ 0.133) and 0.84 ( $\pm$ 0.055) were recovered within five meters in 2003 and 2004 respectively. Of these recovered seeds, the mean proportion of post-removal seed predation was 0.857 ( $\pm$ 0.143) and 0.636 ( $\pm$ 0.105) in 2003 and 2004, respectively.

Seedling survivorship did not differ between years (logistic regression:  $LL = -212.4$ ,  $df = 580$ ,  $p = 0.991$ ). Survivorship was negatively affected by canopy cover ( $\beta = -3.746$ ,  $p = 0.003$ ; Fig. 2) and by being under an adult female canopy ( $\beta = -0.889$ ,  $p = 0.004$ ), but not by seedling height ( $\beta = 0.026$ ,  $p = 0.276$ ). Seedling growth did not differ between years (linear regression:  $R^2 = 0.07$ ,  $df = 90$ ,  $p = 0.168$ ). Growth was significantly, negatively affected by canopy cover ( $\beta = -11.579$ ,  $p = 0.012$ ; Fig. 2), but not by seedling height ( $\beta = 0.083$ ,  $p = 0.359$ ). Presence under an adult female canopy did not significantly affect seedling growth ( $\beta = 0.925$ ,  $p = 0.530$ ), 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 (93.3%) survived to the re-census three years later, resulting in a mean annual survivorship estimate of 0.977. Juvenile tree diameter did not significantly affect survivorship (logistic regression:  $LL = 0.00$ ,  $df = 14$ ,  $\beta = 37.349$ ,  $p = 0.838$ ) or growth (linear regression:  $R^2 < 0.01$ ,  $df = 14$ ,  $\beta = 0.011$ ,  $p = 0.927$ ). Mean ( $\pm$ SE) juvenile growth was 1.89 cm ( $\pm 0.43$  cm) per year. Of the 159 adults on the plot at the first census, 59 were female and 152 (95.6%) survived to the re-census; estimated mean annual survivorship was 0.985. Adult tree diameter did not significantly affect survivorship (logistic regression:  $LL = -27.75$ ,  $df = 158$ ,  $\beta = 0.034$ ,  $p = 0.190$ ) or growth (linear regression:  $R^2 < 0.01$ ,  $df = 158$ ,  $\beta = 0.006$ ,  $p = 0.704$ ).

Gaps in the forest canopy can become darker over time as they fill in with vegetation, or lighter as wind continues to knock down trees and branches on their edges. Repeat canopy photography at the permanent photo points revealed that the forest is slowly becoming darker. Excluding the female canopy habitat (with a mean [ $\pm$ SD] canopy cover of 0.89 [ $\pm 0.06$ ]), darker-tending elements in the habitat transition matrix (below the diagonal; see Appendix C) sum to 0.60, lighter-tending elements (above the diagonal) to 0.15, and stasis elements to 2.25.

#### Population model

Using simplified matrices with no microhabitat transitions and where the *C. axillaris* lifecycle played out entirely in single microhabitats, we calculated habitat-specific population growth rates. Mean ( $\pm$ SD)  $\hat{\lambda}$  was higher in the 0.11-0.3 proportion canopy cover habitat (1.123  $\pm$  0.042) than in the 0.31-0.7, 0.71-1.0, and “under female canopy” habitats (0.985  $\pm$  0.005 for all three). The bootstrapped 95% confidence intervals (see Fig. 3) of habitat 1 (0.11-0.3 cover) did not overlap those of any other habitat; only in habitat 1 was population growth positive.

Under a scenario of no seed dispersal (all seeds deposited in habitat 0), our model projected *C. axillaris* population growth as 0.989 ( $\pm 0.006$ ). Growth rate point estimates were marginally higher for the various dispersal scenarios (gibbon only: 0.991  $\pm$  0.006; muntjac only: 0.994  $\pm$  0.007; sambar only: 0.992  $\pm$  0.006; and all dispersers combined: 0.993  $\pm$  0.007; also see Appendix D). Nevertheless the confidence intervals for these growth rate estimates overlapped broadly, and all point estimates were included in the

confidence intervals of all other dispersal scenarios (Fig. 4A). Running the model without habitat transitions (i.e. seeds and seedlings stay, grow, and survive where they are dispersed; Appendix F) did not affect relative differences among dispersal scenarios, but slightly increased *C. axillaris*  $\hat{\lambda}$  attributable to each. The differences in lambda ( $\Delta\hat{\lambda}$ ) between each frugivore and no dispersal at all show only small differences among the scenarios. None of the  $\Delta\hat{\lambda}$  confidence intervals overlapped zero, but all were broadly overlapping with each other (Fig. 4B). Adult survival followed by juvenile survival had the highest elasticities (sensu Caswell 2001) among the vital rates. Elasticities of fecundity, seed dispersal, seed predation, seedling survival and growth, juvenile growth, and habitat transitions were roughly equal (see Appendix E).

### Discussion

The *C. axillaris* population growth rates attributable to each of the three primary frugivores are remarkably close. Moreover the differences between dispersal by each frugivore and no dispersal at all ( $\Delta\hat{\lambda}$ ) have broadly overlapping confidence intervals. Together these results suggest that *C. axillaris* seed dispersal by its three mammalian mutualists is largely equivalent and that the frugivores exhibit a relatively high degree of functional redundancy in their seed dispersal services. The importance of each frugivore to *C. axillaris* appears roughly equal, in contrast to previous documentation of strong skew in interaction strengths within guilds (Raffaelli and Hall 1995, Wootton 1997). Other authors have suggested that frugivore visitation rate scales to interaction strength (e.g. Bascompte et al. 2006). Yet in this study, muntjac and sambar removal of over twice as many seeds as gibbons did not appear to result in noticeably stronger interactions. Indeed sambar and gibbons have nearly identical interaction strengths with *C. axillaris*, likely because many of the seeds that sambar ingest get “dispersed” right back under adult trees. Differences in seed dispersal among the mammals may prove important for *C. axillaris* genetic structure or colonization of new habitats (c.f. Jordano et al. 2007), but are relatively unimportant for the population dynamics of this established population.

This study measures interaction strength as the total effect of each mammal species on *C. axillaris* population growth. It is possible that differences among

frugivores would be more pronounced if we corrected for relative population density or biomass (e.g. per capita interaction strength). A very rough estimate of the mean number of gibbons on the plot at any one time is approximately 2-6 individuals (WYB, pers. obs.), for a total biomass of 8-48 kg. Estimated muntjac density in the vicinity of the plot during the time of this study was 0.7-4.2 km<sup>-2</sup> (Lynam et al. 2006); abundance and biomass estimates for the 30 ha plot are therefore 0.2-1.26 individuals and 4-35.3 kg, respectively. No such data are available for sambar. The overlap in total species effect between gibbons and muntjac is unlikely to be due to differences in relative abundance or biomass, which appear qualitatively similar.

For such an abundant and prolifically-fruiting tree, *C. axillaris* has remarkably few seed dispersers. While 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). *C. axillaris* may be adapted for dispersal by terrestrial frugivores; it is the only one of 255 fruiting tree species in a Hong Kong forest whose fruit drops undamaged when ripe (Corlett 1996). 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 3 *C. axillaris* seeds in elephant scat, despite detailed examinations of nearly 50 scat piles from 2003-2005. 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 total fecundity 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 the location where seeds are dispersed can have clear effects on seed germination and seedling survival, the size of seed deposition piles did 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-dependence even for seeds that germinated out of large deposition piles.

Secondary dispersal does not appear to play a major role for this species. Though 30-40% of seeds are removed from their primary deposition locations, most do not travel more than 5 m, and most are predated. We occasionally encountered caches of *C. axillaris* seeds in the forest, possibly brought there by tree or ground squirrels, but these were rare and, again, many of the seeds had been destroyed. Likewise *C. axillaris* does not appear to have a seed bank; if seeds do not germinate a year after they are deposited, they do not seem to germinate at all.

The stage-structure population model we employed places differences in seed dispersal in an ecologically realistic context that includes demographic transitions as well as transitions in habitat state. We suggest that this approach is necessary for evaluating the population-level consequences of species interactions, especially for tropical trees that depend on canopy gaps for successful recruitment. Yet our model also makes several assumptions that may affect the robustness of its output to uncertainty in particular vital rates. Perhaps most importantly, juvenile vital rates in our model are habitat-independent. If juvenile growth or survival were actually strongly enhanced in canopy gaps, seed dispersal to gaps could be more important than our results suggest. Moreover our model does not explicitly account for two factors known to importantly influence population dynamics: environmental stochasticity and density dependence. 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 (WYB, pers. obs.). We explored this possibility by running the population model as described above, but including an intense storm every 10 years that sent 50% of the forest to habitat stage 1. Interestingly, this had little qualitative effect on estimates of population growth rate or differences among dispersal scenarios (see Appendix F). According to our model, the *C. axillaris* population we surveyed is slowly declining (Fig. 4A). This decline may be real; as noted, our habitat transition measurements indicate 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 1.000. The relative differences in  $\hat{\lambda}$  attributable to each frugivore would, however, remain almost unchanged;  $\hat{\lambda}_{\text{muntjac}}:\hat{\lambda}_{\text{gibbon}}$  and  $\hat{\lambda}_{\text{muntjac}}:\hat{\lambda}_{\text{sambar}}$  ratios both decline by 0.09%. Interestingly the exclusion of habitat transitions from the model (Appendix F) actually raises population growth rate estimates; this is likely due to the fact that the habitat transition matrix makes the forest generally move toward darker habitats.

The potential for redundancy in seed disperser assemblages will be strongly affected by variation in life-history traits across tree species. Part of the explanation for the small differences among frugivore interaction strengths in this study lies in the fact that although seed dispersal is statistically advantageous for *C. axillaris*  $\hat{\lambda}$  in this population (none of the  $\Delta\hat{\lambda}$  confidence intervals overlapped zero; see Fig. 4B), the advantages are only slight. And differences in dispersal among frugivores should decrease in magnitude as dispersal itself becomes less important. *C. axillaris* seeds do not require ingestion in order to germinate. While seed dispersal to open habitats does appear to be beneficial, seedlings can also change habitats as forest canopy opens or closes above them. Tree species that are more dependent on, for example, seed scarification or dispersal to gaps tend to exhibit increased demographic reliance on seed dispersal (Bond 1995) and may show larger functional differences among their attendant frugivores. Quantification of the distribution of interaction strengths in frugivore guilds, and an understanding of how tree life-history influences these distributions, will help alert us to situations where particular tree species may be at demographic risk from loss of crucial, non-redundant seed dispersers.

Figure 4.1: Quantity of seeds dispersed by each frugivore, expressed as proportions of total fecundity on the plot in 2003 (A) and 2004 (B; error bars represent 95% bootstrap confidence intervals). Deposition habitats of dispersed seeds in 2003 (C) and 2004 (D): habitat 0 = underneath an adult female canopy, habitat 1 = 0.11-0.3 proportion canopy cover, habitat 2 = 0.31-0.7 canopy cover, habitat 3 = 0.71-1.0 canopy cover.

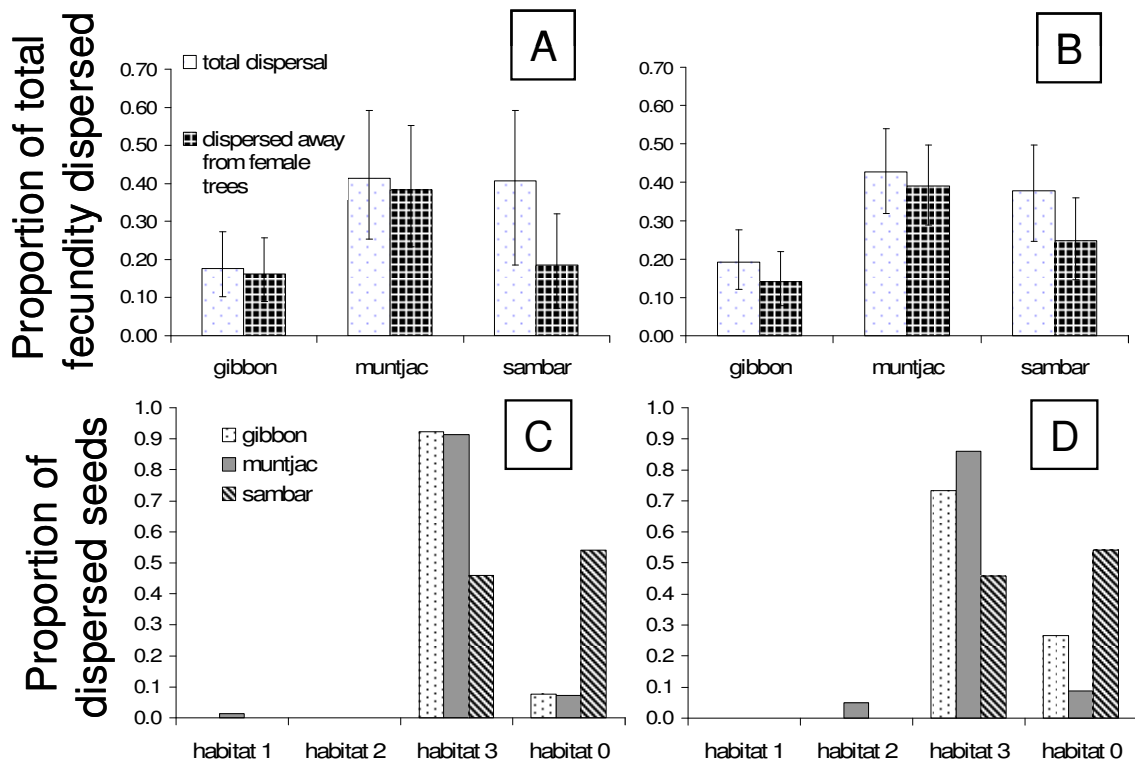


Figure 4.2: Mean ( $\pm$ SE) germination (A), seedling survivorship (B), and seedling growth (C) across habitat types.

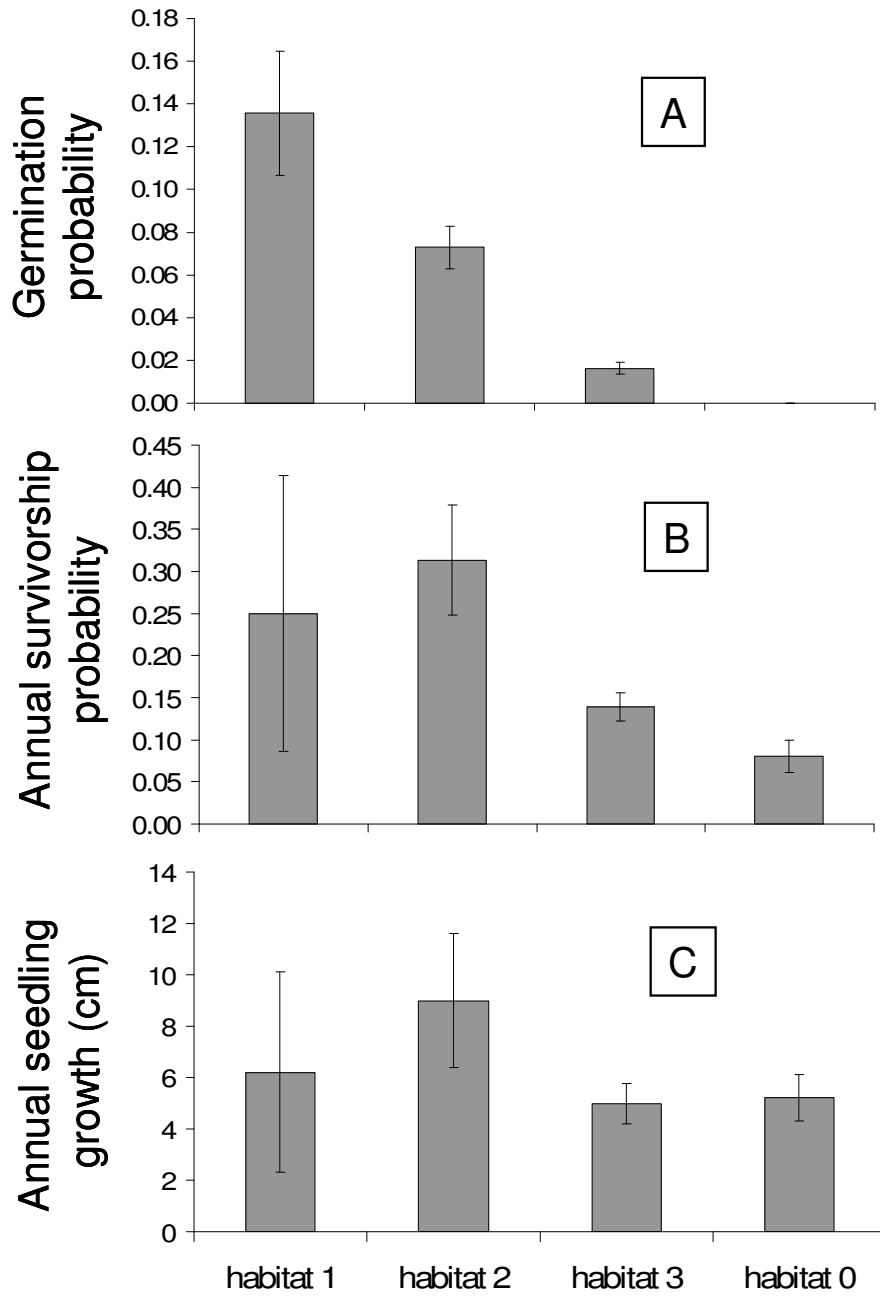


Figure 4.3: Habitat-specific *C. axillaris* population growth rate (with 95% bootstrap confidence intervals).

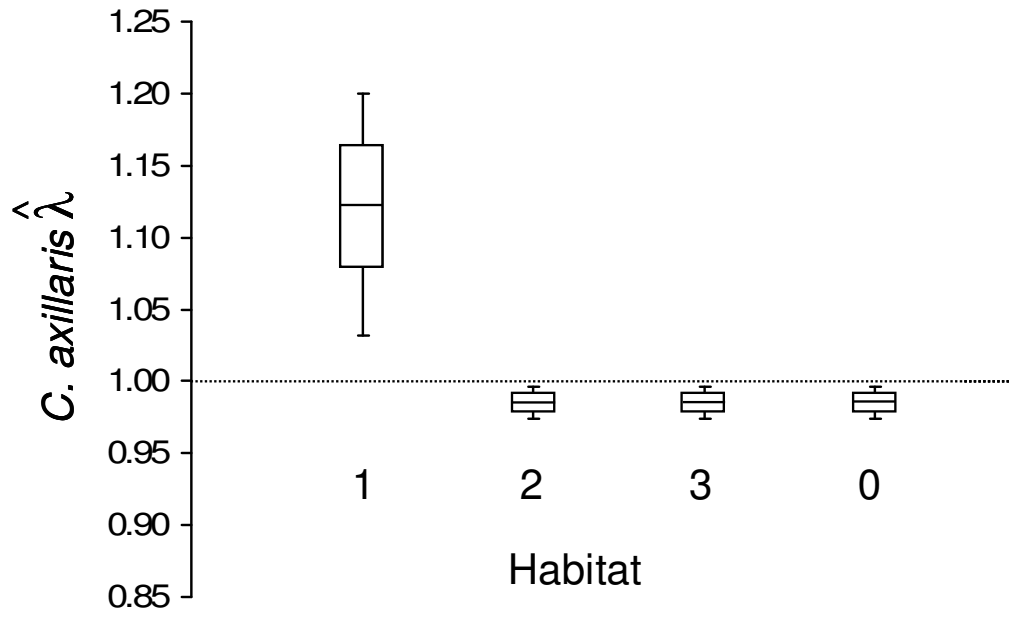
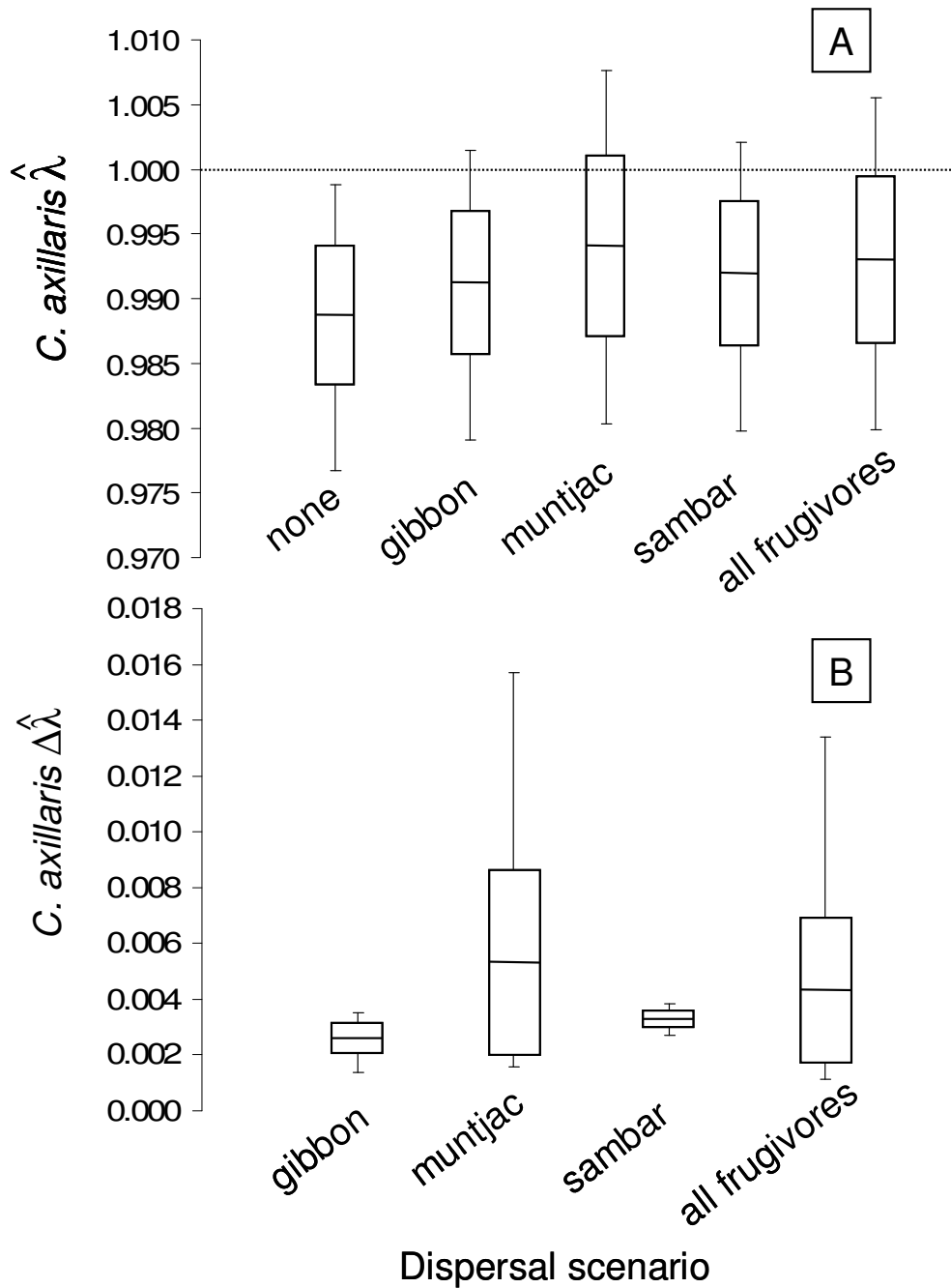


Figure 4.4: A) *C. axillaris* population growth rate attributable to each frugivore alone and in combination; B) difference in *C. axillaris*  $\hat{\lambda}$  between dispersal by each frugivore and no dispersal. Boxes represent mean  $\pm 1$ SD, bars represent 95% bootstrap confidence intervals.



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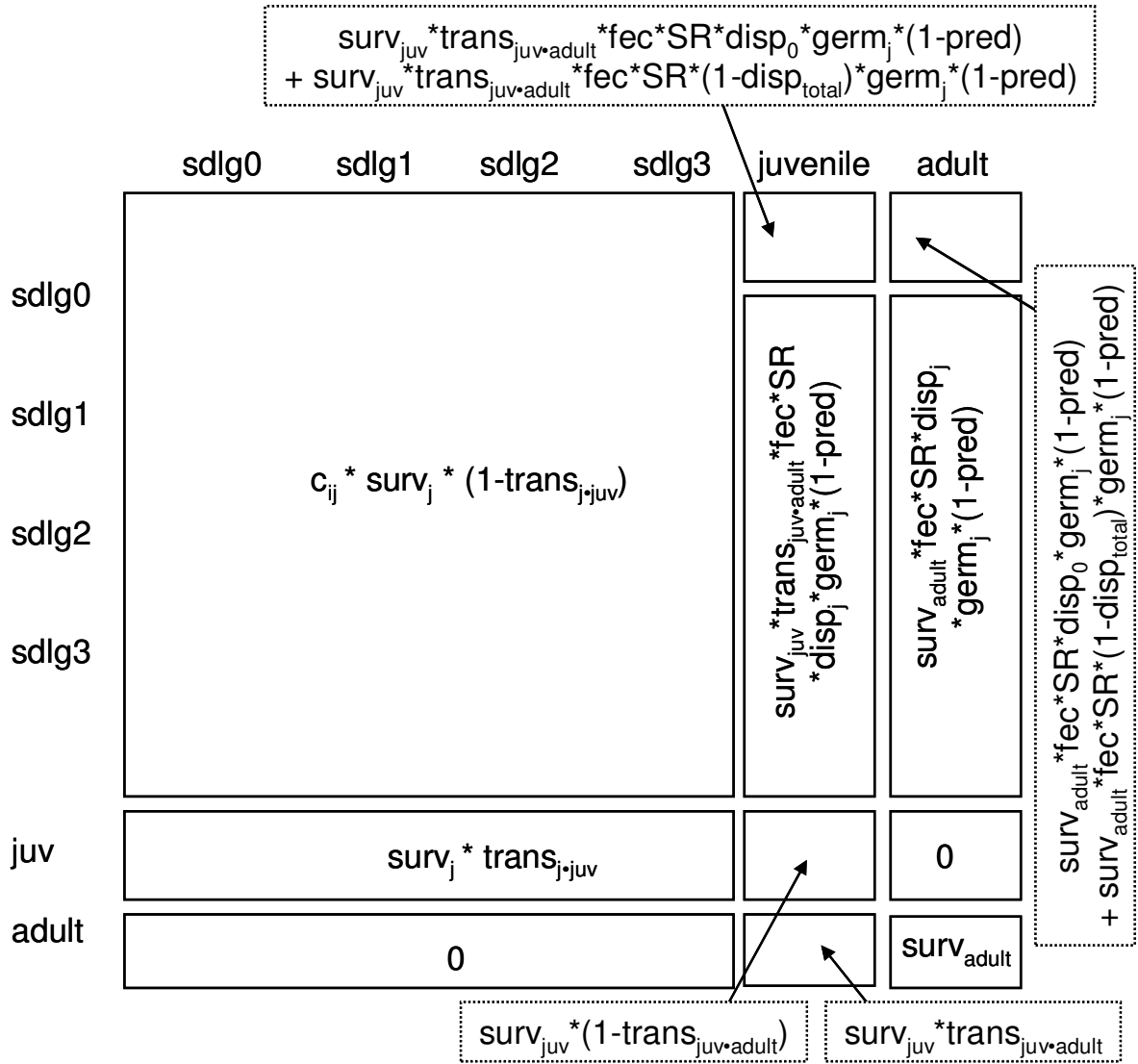
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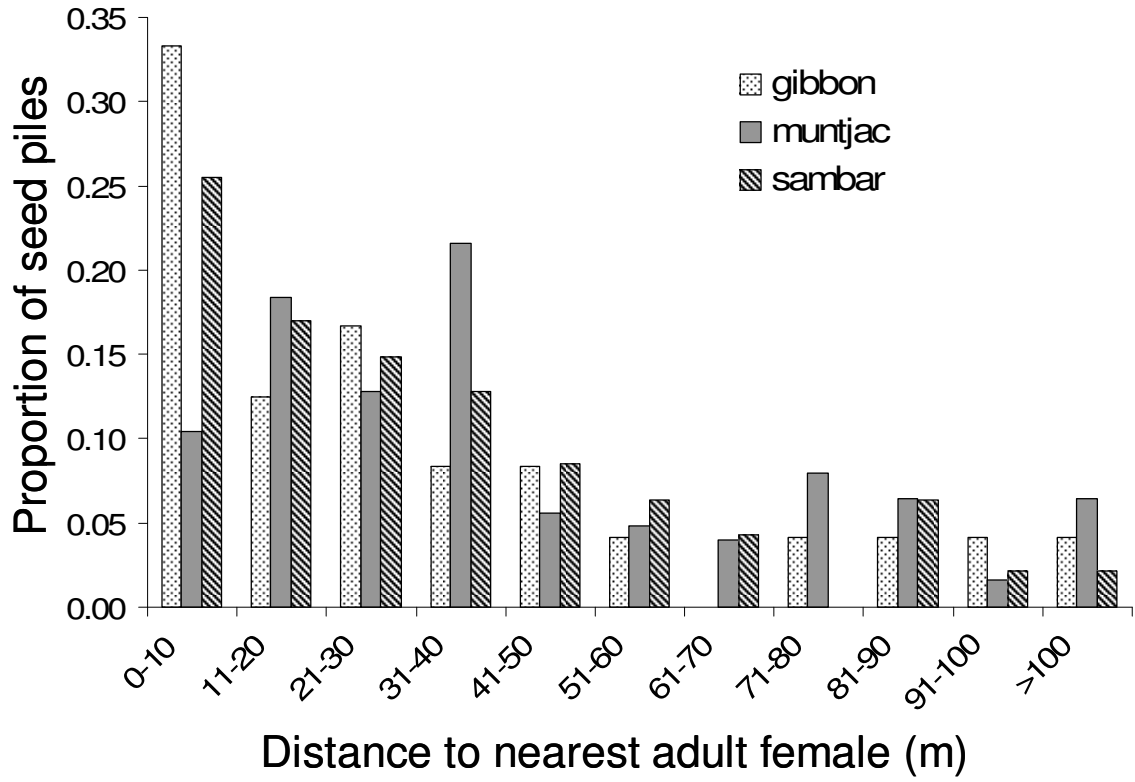
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Appendix A: Structure of *C. axillaris* population projection matrix: “surv” = survivorship, “trans” = stage transition, “germ” = germination, “disp” = dispersal, “fec” = fecundity, “SR” = sex ratio, “pred” = seed predation (habitat independent), “ $c_{ij}$ ” = transition from habitat  $i$  to  $j$ .



Appendix B: Distance from dispersed seed piles to the nearest adult female *C. axillaris*.



Appendix C: Mean habitat transition matrix

	Habitat 0	Habitat 1	Habitat 2	Habitat 3
Habitat 0	0.9922	0.0000	0.0000	0.0000
Habitat 1	0.0000	0.8135	0.0352	0.0031
Habitat 2	0.0058	0.0934	0.5650	0.1064
Habitat 3	0.0019	0.0931	0.3997	0.8904

Appendix D: Mean *C. axillaris* projection matrices for each dispersal scenario. Sdlg<sub>*i*</sub> refers to seedlings in habitat *i*.

No dispersal

	Sdlg <sub>0</sub>	Sdlg <sub>1</sub>	Sdlg <sub>2</sub>	Sdlg <sub>3</sub>	Juvenile	Adult
Sdlg <sub>0</sub>	0.0796	0	0	0	0.1255	5.1982
Sdlg <sub>1</sub>	0	0.5823	0.0257	0.0024	0	0
Sdlg <sub>2</sub>	0.0022	0.0380	0.2146	0.0406	0	0
Sdlg <sub>3</sub>	0.0002	0.0127	0.0508	0.1129	0	0
Juv	0	0.0078	0.0003	0	0.9549	0
Adult	0	0	0	0	0.0238	0.9851

Gibbon dispersal

	Sdlg <sub>0</sub>	Sdlg <sub>1</sub>	Sdlg <sub>2</sub>	Sdlg <sub>3</sub>	Juvenile	Adult
Sdlg <sub>0</sub>	0.0796	0	0	0	0.1523	6.3078
Sdlg <sub>1</sub>	0	0.5823	0.0257	0.0024	0	0
Sdlg <sub>2</sub>	0.0022	0.0380	0.2146	0.0406	0	0
Sdlg <sub>3</sub>	0.0002	0.0127	0.0508	0.1129	0.0154	0.6368
Juv	0	0.0078	0.0003	0	0.9549	0
Adult	0	0	0	0	0.0238	0.9851

Appendix D (continued)

Muntjac dispersal

	Sdlg <sub>0</sub>	Sdlg <sub>1</sub>	Sdlg <sub>2</sub>	Sdlg <sub>3</sub>	Juvenile	Adult
Sdlg <sub>0</sub>	0.0796	0	0	0	0.0994	4.1147
Sdlg <sub>1</sub>	0	0.5823	0.0257	0.0024	0.0052	0.2141
Sdlg <sub>2</sub>	0.0022	0.0380	0.2146	0.0406	0.0032	0.1319
Sdlg <sub>3</sub>	0.0002	0.0127	0.0508	0.1129	0.0048	1.8547
Juv	0	0.0078	0.0003	0	0.9549	0
Adult	0	0	0	0	0.0238	0.9851

Sambar dispersal

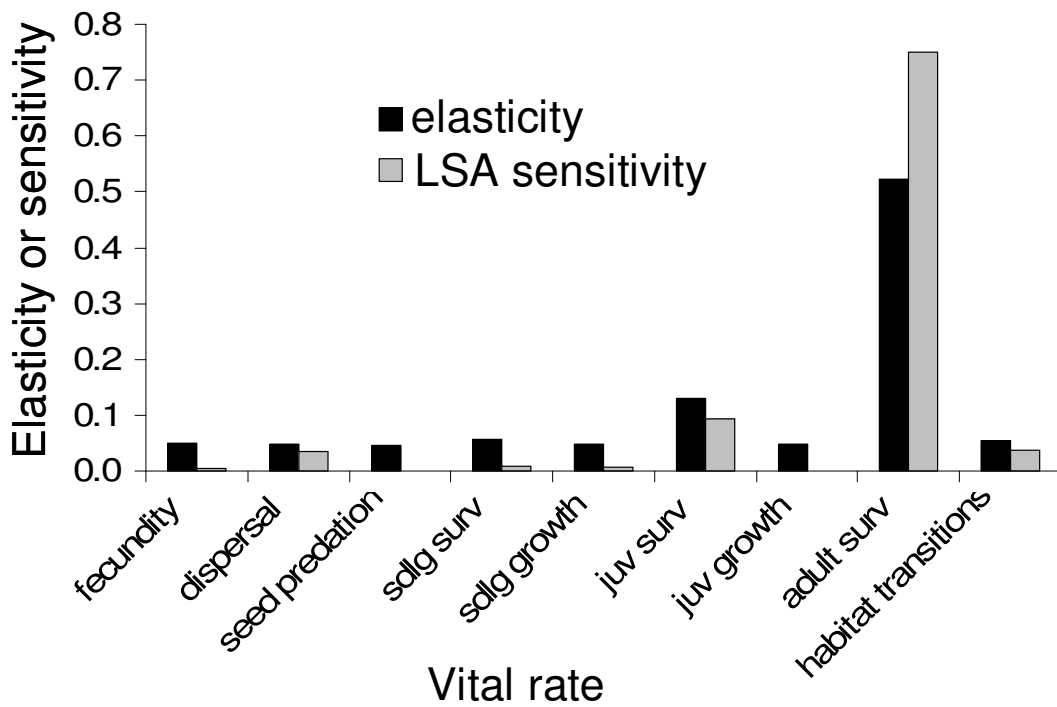
	Sdlg <sub>0</sub>	Sdlg <sub>1</sub>	Sdlg <sub>2</sub>	Sdlg <sub>3</sub>	Juvenile	Adult
Sdlg <sub>0</sub>	0.0796	0	0	0	0.1628	6.7400
Sdlg <sub>1</sub>	0	0.5823	0.0257	0.0024	0	0
Sdlg <sub>2</sub>	0.0022	0.0380	0.2146	0.0406	0	0
Sdlg <sub>3</sub>	0.0002	0.0127	0.0508	0.1129	0.0170	0.7042
Juv	0	0.0078	0.0003	0	0.9549	0
Adult	0	0	0	0	0.0238	0.9851

Appendix D (continued)

Total dispersal (all frugivores combined)

	Sdlg <sub>0</sub>	Sdlg <sub>1</sub>	Sdlg <sub>2</sub>	Sdlg <sub>3</sub>	Juvenile	Adult
Sdlg <sub>0</sub>	0.0796	0	0	0	0.0545	5.1982
Sdlg <sub>1</sub>	0	0.5823	0.0257	0.0024	0.0041	0.1706
Sdlg <sub>2</sub>	0.0022	0.0380	0.2146	0.0406	0.0025	0.1051
Sdlg <sub>3</sub>	0.0002	0.0127	0.0508	0.1129	0.0781	3.2350
Juv	0	0.0078	0.0003	0	0.9549	0
Adult	0	0	0	0	0.0238	0.9851

Appendix E: We estimated the sensitivity of the *C. axillaris* population growth rate (for all disperser species combined) to vital rates using both analytical elasticity analysis (Caswell 2001) and Life-stage Simulation Analysis ("LSA"; Wisdom et al. 2000). The latter accounts for both the ability of infinitesimal changes in each vital rate to affect population growth (analytical elasticity) and the range of variability of the vital rates. For each of 1000 iterations we randomly chose vital rates from uniform distributions bounded by their upper and lower 95% bootstrap confidence limits, constructed projection matrices, and calculated  $\lambda$ . We then performed simple linear regressions of vital rates values versus  $\lambda$ . The  $R^2$  value of each regression (rescaled so that the total summed to 1) was a measure of the sensitivity of  $\lambda$  to each vital rate.



Appendix F: *C. axillaris* population growth rate attributable to each frugivore alone and in combination, A) accounting for storms every 10 years that drive 50% of the forest to habitat 1 (0.11-0.3 proportion canopy cover), and B) with no habitat transitions (no storms and no  $C_{ij}$  matrix) accounted for. Boxes show mean  $\pm 1SD$ , bars represent 95% bootstrap confidence intervals.

