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The Spatial and Temporal Ecology of Seed Dispersal by Gorillas in Lopé National Park, Gabon: Linking Patterns of Disperser Behavior and Recruitment in an Afrotropical Forest

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The Spatial and Temporal Ecology of Seed Dispersal by Gorillas in Lopé National Park, Gabon:
Linking Patterns of Disperser Behavior and Recruitment in an Afrotropical Forest

by

Marc Steven Fourier

A dissertation presented to the
Graduate School of Arts and Sciences
of Washington University in
partial fulfillment of the
requirements for the degree
of Doctor of Philosophy

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LIST OF ABBREVIATIONS

AIC	Akaike's Information Criterion
CA	Correspondence Analysis
CSR	Complete Spatial Randomness
CV	Coefficient of Variation
DBH	Diameter at Breast Height
DEM	Digital Elevation Model
MPLE	Maximum Pseudolikelihood Estimation
MRT	Mean Retention Time
NP	National Park
SA	Subadult (gorilla)
SB	Silverback (gorilla)
SEGC	Station d'Etude des Gorilles et Chimpanzés
IUCN	International Union for Conservation of Nature

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To my loving parents

ABSTRACT OF THE DISSERTATION

The Spatial and Temporal Ecology of Seed Dispersal by Gorillas in Lopé National Park, Gabon:
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By

Marc Steven Fourier

Doctor of Philosophy in Anthropology

Washington University in St. Louis, 2013

Professor Robert W. Sussman, Chairperson

Western lowland gorillas (*Gorilla g. gorilla*) consume large quantities of fruit and disperse a great number of seeds. The majority these seeds are dispersed intact and viable in the dung. Dung is often deposited around the rim of a night nest or at a nest-site. Gorillas often construct nests in areas that have a sparse canopy, flattening the ground vegetation. These locations can be beneficial to the growth and survival of the seed species they disperse. Thus, not only are gorillas effective in terms of depositing seeds great distances from parent plants, away from the highest seed rain densities, they are also effective in directing seeds to potentially beneficial microsites.

The objective of this research was to develop an understanding of the spatial and temporal patterns in fruit availability, seed deposition, and adult plants, and to test whether these patterns relate to the ecology of seed dispersal by gorillas.

Results suggest that gorilla foraging and nesting behavior in particular, impose both spatial and temporal limitations to the distribution of dispersed seeds. In addition, temporal variation in the gorilla diet and factors that affect defecation rates and locations promote variation in the combinations (composition and abundance) of the seed species dispersed to different microsites.

The clustered distribution of nest-sites leads to clumped and spatially restricted seed deposition patterns. Recruitment in gorilla-dispersed seed species corresponds with the aggregated (clumped) distribution of nest-sites. Gorillas have a long-lasting effect on the spatial structure and floristic composition of the forests they inhabit, particularly in large-seeded species.

CHAPTER I

INTRODUCTION

“Plants and animals, most remote in the scale of nature,
are bound together by a web of complex relations,”
The Origin of Species (Darwin, 1859, p. 73).

By the end of the 20th century, logging, human settlement, and disease in west-central Africa had considerably reduced the range and population of western lowland gorillas (*Gorilla gorilla gorilla* Savage and Wyman, 1847; Huijbregts et al., 2003; Walsh et al., 2003). Recently all gorilla populations regardless of taxonomic classification were given a critically endangered status in the 2008 IUCN Red List (Oates et al., 2008; Robbins and Williamson, 2008; Walsh et al., 2008). In addition to the extraordinary loss to the planet's natural heritage that the extinction of such an animal would mean, the extirpation of gorillas throughout their range may have grossly underestimated costs to the structure, composition, and integrity of central African tropical plant communities. “Understanding plant-animal interactions requires a multi-disciplinary approach and can contribute to understanding plant and animal biogeography and to conserving tropical rain forest,” (Tutin, 1998:227).

SEED DISPERSAL: AN OVERVIEW

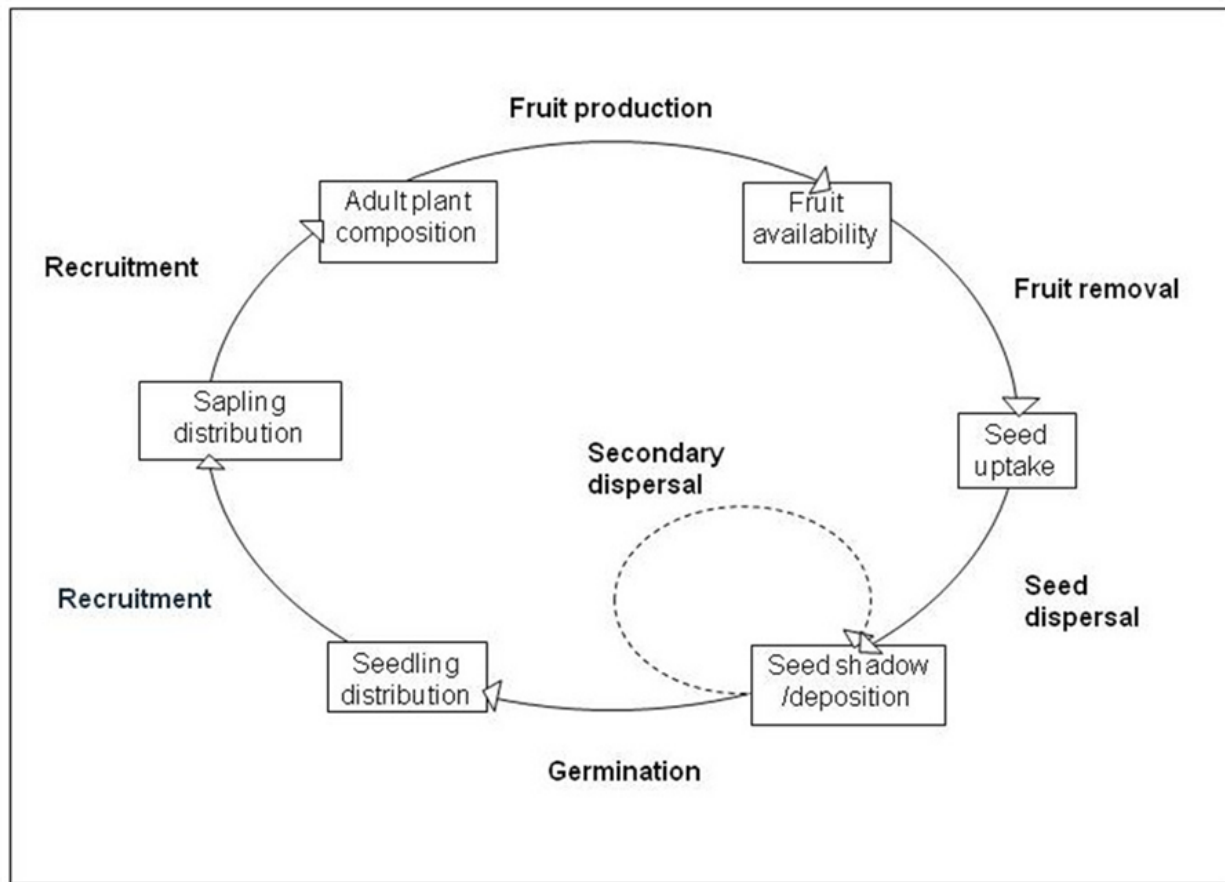
‘Frugivores’ are animals that eat fruits, and play the role of dispersal agents when they move viable propagules or seeds away from the parent plants (Howe, 1986). Effective animal-mediated seed dispersal therefore requires the synthesis of the behavioral ecologies of frugivores with the reproductive ecologies of plants. Though scientists as early as Darwin (1859) saw the importance of seed dispersal, the field did not gain momentum until the 1960s. Since then researchers have recognized that frugivores provide critical ecosystem services to plant communities and select for plant life-history traits, including fruit/seed characteristics and phenological rhythms in plant reproductive events, that increase a plant's ability to be dispersed (Hladik and Hladik, 1969; Gilbert and Raven, 1975; McKey, 1975; Sussman and Raven, 1978; Snow and Snow, 1988). The services that frugivores provide are especially important in tropical plant communities, where zoochory is present in 64% of gymnosperm and 27% of angiosperm

lineages (Herrera and Pellmyr, 2002), and 70-90 percent of all woody species (Fleming et al., 1987; Jordano, 1992, 2000).

The earliest studies of seed dispersal stemmed from research on fruit-eating animals and emphasized the animal behavior side of the interaction, including rates of fruit tree visitation, fruit removal, and fruit handling behavior (Snow, 1971; McKey, 1975, Graham et al., 1995). Insight into the benefits to plant species was, to some degree, secondary to understanding the feeding ecology of the disperser. Then in the 1980's, researchers began to study fruit traits, germination rates, the fates of dispersed seeds, and regeneration strategies, including the growth and survival of seedlings in gap-areas of natural disturbances (Hubble and Foster, 1986), marking the beginning of dispersal ecology from the plant's perspective.

Understanding these two interacting groups (animals and plants) progressed along separate lines of research, independent of each other. Missing from a complete picture of seed dispersal theory however was a demonstrated correlation between an animal's handling of a fruit or seed and the growth and survival of seedlings and subsequently, adults. Researchers today seek to bridge the gap between disperser behavior and plant demography by investigating the complete fate of dispersed seeds, including germination, establishment, and recruitment of seedlings to the adult stage (Wang and Smith, 2002). In Figure 1.1, I show the connection that seed dispersal has with the complete life-history cycle in plants. Being but one of many processes involved in this cycle, seed dispersal is a 'demographic bridge' that connects reproduction in adult plants with the establishment of their progeny (Wang and Smith, 2002). For animal-mediated seed dispersal to have important ecological and evolutionary consequences in plant communities, the growth, survival, and recruitment patterns in seedlings that germinate from animal-dispersed seeds should be retained in the adult distributions of plants (Schupp and Fuentes, 1995; Wang and Smith, 2002).

Figure 1.1. The complete life-history of plants showing seed dispersal as one of many processes. Seed dispersal acts as the 'demographic bridge' between plant reproduction and establishment (adapted from Box 1, Wang and Smith, 2002).



Growth of the field

Disentangling the seed dispersal process from the various fates of seeds is an inherently difficult task, and one characterized by a succession of many processes, each imparting an effect on plant survivorship. Complexities across space and time, coupled with high mortality of seeds (i.e., most dispersed seeds die before completing their life-history cycle), limit the scope of inferences that are available to any one study. Often researchers are forced to study only one or two processes in the seed dispersal cycle and establish a link by interpolating missing processes (Wang and Smith, 2002). Strong inferences typically demand large sample sizes (and, over many years) to estimate accurately the often inherently small, though non-zero, effects of seed dispersal on plant demography (De Steven, 1994).

Complexities notwithstanding, the explosion of literature since the 1980's reflects the impressive development of ideas in the study of seed dispersal. Frugivory and seed dispersal have now been the subject of five international symposium-workshops (1985-2010), producing four edited volumes (Estrada and Fleming, 1986; Fleming and Estrada, 1993; Levey et al., 2002; Dennis et al., 2007), and a special issue of *Acta Oecologia* (Forget et al., 2011). Responding to the trend of increased degradation in natural ecosystems, an increasing number of peer-reviewed articles reflect the growing interest in the consequences that disperser extinctions will have on tropical ecosystems. For example, a special section in the journal *Biotropica* ("Pervasive consequences of hunting for tropical forests", 2007) highlighted the consequences of hunting and disperser loss. These are all examples of the research that is underway on the importance of seed dispersers in maintaining the integrity of complex tropical ecosystems.

To quantify the growth in the study of frugivory and seed dispersal during the last twenty-five years, I searched the published literature using ISI Web of Knowledge ([®]Thomson Reuters). Representing research in animal-mediated seed dispersal, I used 'frugivor* AND seed_dispersal' as a key term; to quantify research in primate-mediated seed dispersal, I used 'primat* AND seed_dispersal'. Further, within primate studies, I separated studies on fruit removal from those on seed fate. I searched all databases from 1970-2011 and used the 'topic' search field. Results, presented in Figure 1.2, show a dramatic increase over the last three decades, with the number of published items on primates increasing to twenty articles in 2011. Though more gradual an increase than in the general 'frugivory and seed dispersal' publications, these results demonstrated an expanding and flourishing field in primate-mediated seed dispersal.

In order to quantify the geographic bias in seed dispersal research, I performed a second search using 'neotropic*', 'africa*', 'asia*', and 'australia*' AND 'seed_dispersal'. Results indicate that the Neotropics have led the other regions in the number of publications after nearly three decades (Fig. 1.3). Africa, Australia, and Asia have followed closely behind, keeping pace with the Neotropics.

Figure 1.2. Number of published items published in each year on “Seed Dispersal” and “Frugivory” or “Frugivores”, and items published on “Seed Dispersal” and “Primate” or “Primate” [Topic=(frugivor*) AND Topic=(seed_dispersal), and Topic=(primat*) AND Topic=(seed_dispersal)]; referenced by ISI Web of Knowledge (®THOMSON REUTERS) between 1985 and 2011 (no indexed references before 1985, updated 19 January 2012)].

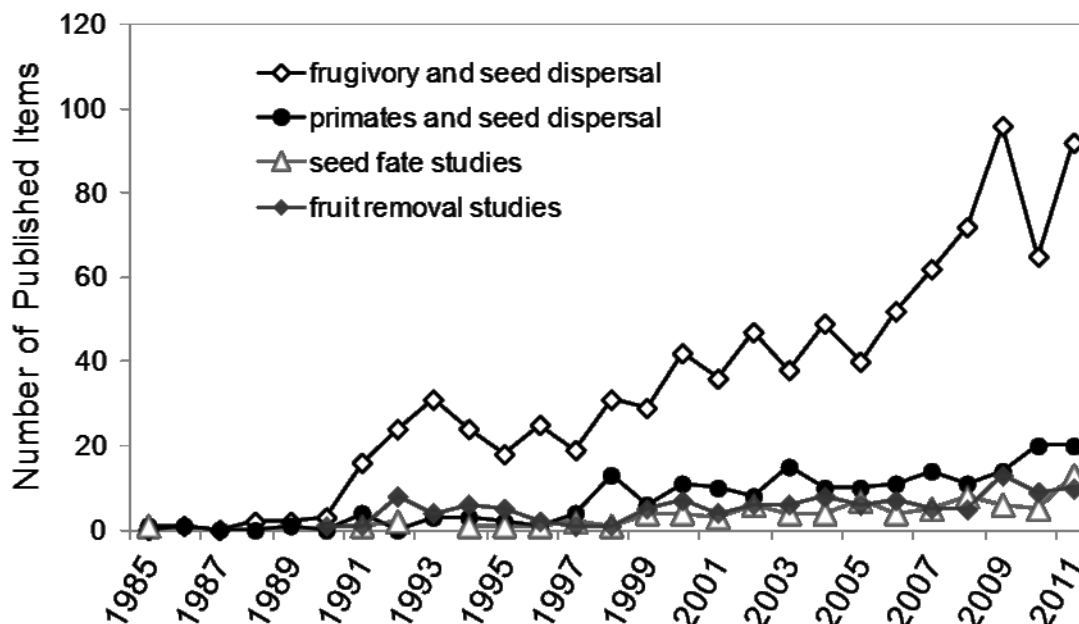
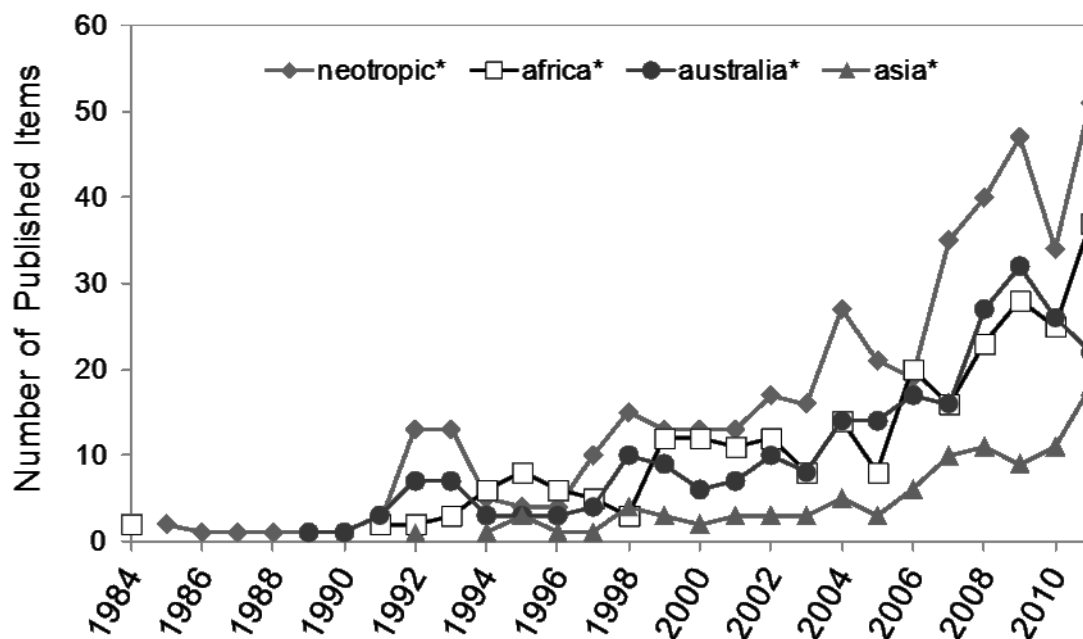


Figure 1.3. Number of published items published in each year across continental regions on “Seed Dispersal” and “Neotropic*”, “Africa*”, “Asia*”, and “Australia*” [referenced by ISI Web of Knowledge (®THOMSON REUTERS) between 1984 and 2011 (no indexed reference before 1984, updated 24 January 2012)].



Diffuse dispersal syndromes

From its onset, the study of frugivory and seed dispersal has been tightly linked to the idea of coevolution (Ehrlich and Raven, 1964; Sussman and Raven, 1978; Futuyma and Slatkin, 1983; Gómez and Verdú, 2012; Sussman et al., 2013). Biologists recognized that frugivores were critical to plant dynamics, providing potentially strong selection pressures on plant life-history traits (Snow, 1965, 1981; Janzen, 1969, 1970; McKey, 1975; Howe and vande Kerckhove, 1980). Subsequently, researchers gradually modified the earlier claims of a “tight” coevolutionary relationship between frugivores and the plants they disperse, acknowledging that persistent, long-term evolutionary relationships between plants and particular dispersal agents are uncommon (Janzen, 1980), and have opted instead for the term “diffuse” coevolution (Herrera, 1985). There are a number of reasons for this. For example, extremely high post-dispersal seed and seedling mortality (> 95%), coupled with redundancies in seed dispersal services among multiple dispersal agents for the same fruit species (Howe et al., 1985; Chapman and Chapman, 1996), limit the possible selective pressures that any one frugivore can exert on a plant. Additionally, a truly non-diffuse, species-to-species coevolution should be contingent upon a congruency of species turnover rates between woody plants and vertebrate dispersers, a congruency that is generally unsupported by the geological record, with woody plant species being significantly longer-lived relative to dispersers (Herrera, 1985). In reference to the presumed ‘strong’ coevolution between primates and the plants they disperse, Fischer and Chapman (1993) concluded there was little known to support claims that nonhuman primates have selectively shaped fruit, seed, and phenological adaptations of the species they exploit.

Ecologically speaking, however, the multiple effects of primate fruit-eating behaviors on the demographics, floristic composition, and distributions of tropical tree communities are undeniable. “Frugivore feeding activities may influence the availability of food to other consumers, the shape of a plant species’ seed shadow, the likelihood of seed survivorship and germination, and the recruitment of seeds and seedlings into the next generation of forest trees” (Lambert and Garber, 1998:10). Thus, a tight coevolutionary interaction notwithstanding, in almost all cases, important diffuse coevolutionary relationships between plants and frugivorous primates do emerge from non-random patterns of seed

dissemination, seed viabilities, and ecologically beneficial conditions that are found in the locations that seeds are deposited by effective seed dispersers.

The ecology of vertebrate-mediated seed dispersal

Seed dispersal is “the one mobile stage in an otherwise rooted existence” (Voysey, 1995:2). Although plants typically have two critical life-history stages where mobility is necessary, i.e., sexual reproduction and offspring dispersal, offspring dispersal is the only stage that typically requires the movement of propagules to spaces *not* already occupied by a conspecific individual. Seed-bearing organs (fruits) that increase the likelihood of seed transfer evolve due to the selective advantage bestowed upon those individual plants that effectively disperse their seeds.

Strategies for achieving this advantage include harnessing wind, water, or the exterior of animals to disperse seeds away from mother trees (van der Pijl, 1982). Alternatively, many tropical plants produce fleshy fruits of various shapes, flavors, and textures to ensure ‘acquisition’ by animals (Stiles, 1992), thereby maximizing their chances of seed transport away from the parent. This strategy is most common in the humid tropics, where 70-90% of woody plant species use animal dispersal (Willson et al., 1989; Jordano, 1992; Mabberley, 1992).

Advantages of seed dispersal strategies

In plant communities, it can generally be assumed that when a tree dies, another takes its place. Why then should it be important to disperse seeds away from the canopy? Considering the high physiological costs to the plant in producing seed-bearing structures that are often brightly colored or large (Cipollini and Levey, 1991) in order to attract potential consumers, there must be a considerable advantage to dispersal (Howe and Smallwood, 1982). Dropping seeds directly below the parent plant, it turns out, has its drawbacks, and the advantages to spreading seeds far and wide have three general forms.

The landscape surrounding a plant can be viewed as containing a limited number of suitable and vacant sites for a future seedling. Under this view, rare and ephemeral vacancies may open unpredictably due to stochastic disturbances, such as a treefall that creates a gap in the canopy. Plants that can

effectively blanket the landscape with seeds that remain dormant, or germinate and then 'lie in waiting' in suppressed growth, will be in an advantageous position when such stochastic vacancies open up. Plants using this strategy are often gap specialists that can grow rapidly in the increased light in of a canopy gap. Thus, under the "colonization" strategy", spreading seeds as widely as possible around the parent stem maximizes the likelihood that a seed will be in location to take advantage of unpredictable vacancies when they occur (Wenny, 2001).

In the "escape" strategy, seeds experience a release from mortality factors the farther they are dispersed from adult conspecifics (Howe and Smallwood, 1982). Central to this hypothesis is the pioneering work of Janzen (1969, 1970) and Connell (1971) who described density- and distance-dependencies in seed and seedling predation by both invertebrates and vertebrates. As a simple function of radial geometry, surface area increases geometrically as distance from any one location increases. Thus, the process of dispersing seeds farther away from a plant naturally results in decreasing seed densities. Predators, especially specialist predators, may be sensitive to differences in seed/seedling densities or distances from conspecific adults. When this occurs, mortality factors are expected to correlate negatively with increasing distances away from conspecifics and positively with seed or seedling densities.

In certain cases, dispersers disproportionately deposit seeds to sites favorable for germination and growth. When non-random disperser behaviors result in seeds arriving predictably to sites associated with a higher per-seed survivorship, the plant is said to benefit from "directed" dispersal (Howe and Smallwood, 1982; Wenny, 2001). For directed dispersal to occur, plants either have characteristics that target acquisition by a particular disperser over others, or a particular morphology that ensures that seeds have a greater than chance arrival to favorable habitats.

A possible fourth advantage of dispersal is enhanced germination of some seed species after passage through the vertebrate gut (Hladik and Hladik, 1969; Lieberman et al., 1979; Estrada and Coates-Estrada, 1986; Idani, 1986). However, given that germination-test results are often mixed and unclear, this advantage is arguably not an advantage of dispersal *per se*. Distinguishing between the

above strategies is not always straightforward, and nothing inherently prevents any single plant from benefitting from all three, especially given the polychorous nature of many seed dispersal systems.

The seed dispersal cycle

As stated above, the seed dispersal process is only one of many processes completing a plant's life history (Wang and Smith, 2002). The effective consequence of seed dispersal depends on processes that occur during all the stages in a plant's life history, including flower and fruit production, removal of fruits, seed deposition, germination, establishment, and seedling growth and survival. The following is a brief overview of some of the key factors in the plant's life history that affect disperser effectiveness.

The adult tree

The factor that most limits tree growth is light availability in tropical rain forests, with performance most often well below the potential maximum due to the effects of shading. For example, in a long-term study of six species at La Selva, Costa Rica, Clark and Clark (1994) found large interannual variation in diameter increments, with increases in diameter at breast height (DBH) negatively correlated with rainfall. They concluded that wet years were cloudier and had substantially lower photosynthetically active radiation than dry years.

Adult stature takes on a number of different forms in tropical forests. Lieberman et al. (1985) simulated maximum potential lifespan and maximum growth rate from 13 years of data at La Selva, and classified tropical forest plants into four species groups:

- Understory species of small stature that mature slowly, are shade-tolerant, respond minimally to increased light irradiance, and have a relatively high mortality.
- Sub-canopy species are shade-tolerant, have a low mortality rate, and can be long-lived.
- Canopy species are the largest trees in the forest, usually with high juvenile survival, and respond to high light with a dramatic increase in growth.
- Pioneer species are fast-growing, short-lived, species that exhibit high mortality rates in juvenile stages and shady locations.

Most trees reproduce over many years, producing a seemingly innumerable number of diaspores in their lifetime. The first major contributor to dispersal limitation is source limitation, or fecundity (Schupp

et al., 2002). A vertebrate-dispersed tree must acquire the interest of a would-be effective disperser, and the bigger the display of fruit the better. As expected, there is a strong correlation between fruit crop size and rates of disperser visitation and fruit/seed removal, a clear example of the diffuse relationship between plant traits and disperser behavior.

Some species produce large fruits that offer a greater reward per fruit to dispersers. Additionally, producing larger seeds appears to be advantageous because a larger seed produces a larger seedling that has a greater amount of reserves to meet the requirements of chemical and physical defense, repair of damage, and periods of resource shortages (Kitajima, 1996). Producing larger fruits and seeds, however, comes at the expense of producing fewer fruits and seeds, due to an evolutionary tradeoff between fruit size and fruit number (fecundity). Over the course of a plant's lifetime, however, this tradeoff may not be as direct as it seems, since the longer lifespan of large stature, large-fruited plants, allows for a much longer period of reproductive output. Over a plant's lifetime, therefore, producing many small fruits over fewer reproductive events may balance against producing fewer large fruits over many more events (Turner, 2001).

Pollination

Tropical plants exhibit a wide range of temporal patterns and potential strategies in reproduction. For example, Newstrom et al. (1994) found that 7% of species flowered continuously, 55% sub-annually, 29% annually, and 9% supra-annually. While many theories on the selective advantage of mass flowering and fruiting exist, particularly regarding synchronous supra-annual flowering (masting) and predator-satiation (Kelly, 1994), most theories on synchronized phenology point to increases in the likelihood of successful pollination. One should expect to see higher rates of pollination events, cross-pollinations, and flower-to-fruit/seed sets, in individuals that synchronize their flowering behavior over those that flower outside of peak times (Augspurger, 1981). Many plants rely on the unwitting animal to deliver pollen between individual plants. Bawa (1990) estimated up to 99% of tropical rain forest plants are animal-pollinated, with the most important agents being insects, birds, and mammals. Common convergent features in floral design within guilds of trees pollinated by the same type of animal have allowed researchers to recognize pollination syndromes and predict the likely pollinator from the floral traits.

However, as we shall see with disperser syndromes, caution is necessary as pollinators often visit flowers that are not 'typical' for them, and careful studies are required to determine the effective pollinators from pollen predators in species that are visited by a wide range of animals (Turner, 2001).

Fruit production and seed dispersal

Although various modes of dispersal exist, including gravity, wind, water, and animals, I will only focus on animal-mediated seed dispersal (zoochory) in this dissertation. In addition, by focusing on primary seed dispersal here, I do not intend to downplay the role that secondary seed dispersal has in the seed dispersal process. Secondary dispersal by ground-dwelling mammals (i.e., rodents, tapirs, and forest antelopes), and insects such as ants and dung beetles, repositions seeds to other locations (Wang and Smith, 2002) and can have a major effect on the distributions of seed shadows and mortalities.

Plants have very little control over what happens to the seed once the ripe fruit is ready for removal. Adaptations in fruit structures and nutritional content, constrained by the degree of plasticity allowed by the tree's evolutionary history, affect the "choice" over who removes a fruit. The final deposition site of a seed is a function of a frugivore's feeding and ranging behaviors, as well as its digestive physiology. While not fitting exactly into discrete categories, the range of variations in fruit structures in vertebrate-dispersed species are broken into disperser syndromes (van de Pijl, 1982) for "acquisition by animals" (Stiles, 1992).

Plant traits that are often used to define dispersal syndromes include the size of the fruit and seed, the thickness and flexibility of the husk, whether the husk dehisces upon ripening, the sweetness and amount of water in the pulp, the amount of fiber, the seediness of the fruit, and the color at the time of ripeness (Howe and Smallwood, 1982; Gautier-Hion et al., 1985; Janson, 1992). For example, bird-dispersed fruits tend to be brightly colored in red, orange, purple or black; are often more than one color; contain many small seeds embedded in pulp; and have thin or dehiscent husks that take very little manipulation to process. Pulp may be thin, firm, watery, dry, or oily.

Primate-dispersed fruits, on the other hand, typically are larger; can be either brightly or dull colored; have thin indehiscent husks; few to many seeds; and contain sugary pulps and various amounts of fiber. Seeds may be of a substantial size, though they are usually less than 1cm in diameter, especially

in species dispersed by small to medium-sized primates. Fruit handling and processing requirements are often greater in primate-dispersed than bird-dispersed fruits.

As with pollination syndromes, caution is warranted in overemphasizing disperser syndromes, since obvious adaptations for dispersal do not always predict the actual process of dispersal (Howe and Smallwood, 1982). Selection pressures for primate dispersal syndromes are expected to be weaker than for suites of traits that are intended to entice bird-dispersal. From the plant perspective, it is far more difficult to exclude primates over birds from feeding on a particular fruit, since primates are better able to manipulate even dramatically mechanically protected fruits. Indeed, the ability to manipulate and consume fallback foods of differing mechanical properties during periods of fruit scarcity is likely related to the primate order's successful radiation into a diverse set of separate and sympatric niches (Chapman and Russo, 2007).

Fruits offer various rewards to would-be dispersers, and the nutritional composition of fruit pulp varies substantially. Jordano (1995), in an meta-analysis of published data on fruit flesh, found three main nodes of variation in the nutritional content of fruits: (1) high lipid, low fiber, and low non-structural carbohydrate (NSC); (2) low lipid, high NSC, and low fiber; and (3) medium lipid, medium NSC, and high fiber. Fruits tend to contain low amounts of protein in general, though protein and water contents vary independently from the above nodes.

Seed deposition patterns

A wide range of hypothetical seed shadows exist depending on disperser traits. Once a fruit is detached from the plant, and if it is not processed on location with seeds dropping to the ground under parent canopies, seeds are dispersed in two general ways. In scatter-dispersal (Howe, 1989), seeds are spat out singly as the fruit is processed by the disperser, usually in a nearby crown. This process leaves a characteristic distribution of seeds, with peak seed densities occurring near the parent canopy, and rapidly, monotonically decreasing densities occurring as distance from the tree increases (Fig. 1.4-A). This type of seed shadow is often distance-restricted as large numbers of seeds are dispersed only short distances. Under distance-restricted deposition patterns, an individual seed has a very small chance of reaching a suitable recruitment site far from the parent plant.

Alternatively, seeds that are swallowed by a disperser may be regurgitated or defecated over time, and in “clumps” of varying densities (aggregations) and distances away from the parent tree. This type of dispersal leads to spatially contagious (*sensu* Schupp et al., 2002) seed shadows. The spatial distribution of seeds in this type of dispersal depends on the behaviors of the individual dispersers involved in the transport. In Figure 4-B, the occurrence of a peak near a tree is due to a combination of distance-restricted dispersal of kin-seeds, and dispersal of non-kin seeds by frugivores that had previously fed at other trees. Many processes can produce the other peaks. For example, seeds that are transported away from the parent tree, via defecation or regurgitation dispersal, may be focused at roosting or fruit processing sites (Julliot, 1996), or around tree foci such as the fruiting crowns of conspecific or heterospecific trees (Clark et al., 2004). Seeds may also be defecated or dropped, en route (“in-transit”) during the course of disperser movements. Lastly, seeds may accumulate in dung left around a sleeping site, such as the contagious deposition of seeds around a gorilla nest-site. As with distance-restricted dispersal, many of the available establishment sites in defecation (contagious) dispersal fail to receive any seeds, although the pattern of seed dissemination, and consequently recruitment, differs greatly between the two.

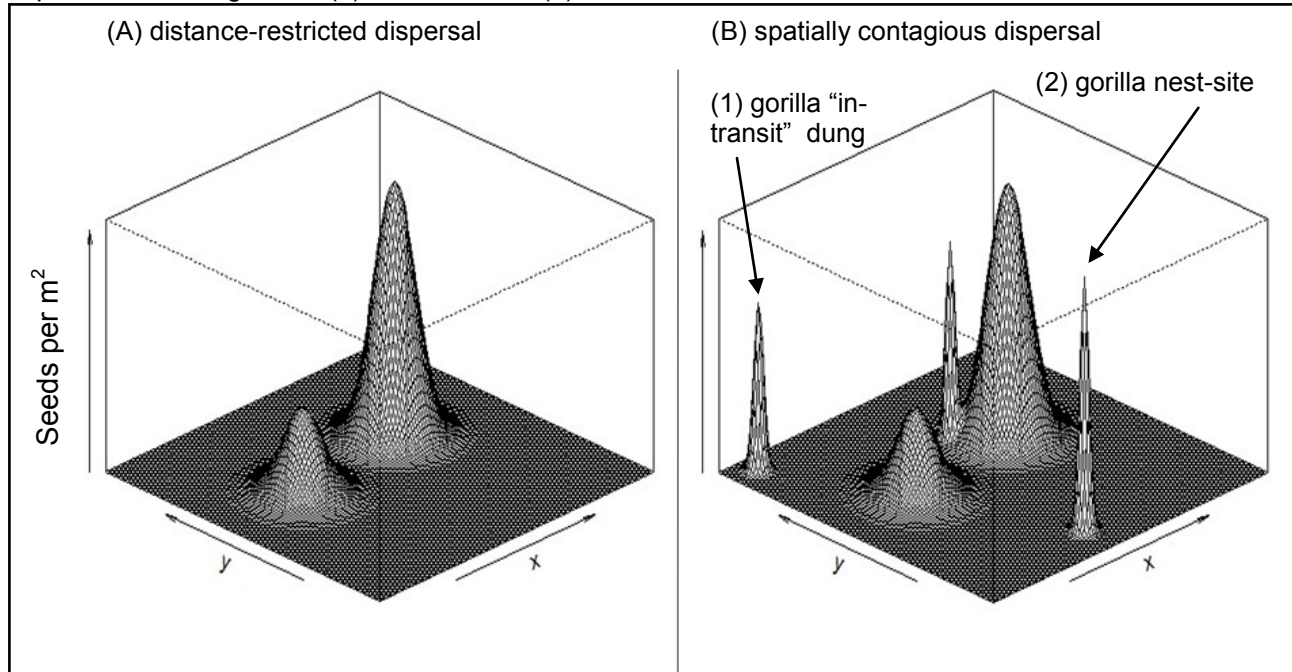
Seed rain is the combined (sum-total) of the individual seed shadows created by the entire frugivore assemblage, and across simultaneously fruiting species in a community. The spatial distribution of seeds in seed rain is dependent on the sizes and foraging behaviors of the frugivorous vertebrates that mobilize a large amount of seeds across the landscape. Small vertebrates, including small passeriform birds, rodents, or lizards, will typically create distance-restricted shadows. Medium to large-sized vertebrates will create complex seed rain patterns, consisting of “clumps” of co-dispersed seeds that typically contain seeds from several maternal trees and species (Garcia and Grivet, 2011).

Seed and seedling growth and survival

Seeds and seedlings are susceptible to attack from a wide range of predatory organisms. These include a large number of both vertebrate and invertebrate seed predators (Janzen, 1971), as well as bacteria and fungi that destroy seeds under favorable conditions. Evolved seed defenses include hard or tough seed coats (Grubb et al., 1998), and chemicals that are toxic to would-be predators. Predators that

forage across the forest floor are more likely to find aggregations of seeds than seeds that are scattered widely, giving rise to the advantages I have already outlined in the “escape” strategy above.

Figure 1.4. Seed shadows around two hypothetical parent trees (the center of peaks) where seeds are scattered by dispersers near to the tree (A). This pattern describes distance-restricted dispersal. (B) Seeds may also be dispersed in spatial “contagions”. Defecation dispersal of seed by gorillas visiting multiple trees during the course the day focuses seeds in both spatial and taxonomic contagions to deposition sites, e.g., trails (1) and nest-sites (2).



Mortality rates are generally higher in the seedling stages of tropical plants than during any other time. Cohorts of germinants decline in a log-linear fashion (Turner, 2001), meaning that a straight line of negative slope may be drawn when numbers of seedlings is drawn on a logarithmic scale against linearly-plotted time. It appears that even in species with abundant seedlings, seedling survival is low, and survivorship increases only as seedlings get larger. Mortality factors on the forest floor include the following: damage due to fallen debris or trampling by large animals, predators of seedlings, pathogens and disease, drought, too much shade, and competition among conspecific and heterospecific seedlings.

Seed dispersal modeling

Nathan and Muller-Landau (2000) reviewed the advances made in modeling seed dispersal. The inverse-modeling approach is the most often used approach in the dispersal literature. It takes advantage

of observed densities of seeds arriving to a sampled site (i.e., seed trap) and determines the parametric dispersal kernel model that best fits the data. These analyses typically result in a function that describes the seed shadow around a hypothetical, mapped parent tree. However, best-fit inverse models seldom lead to a better understanding of the underlying disperser behavior behind the seed shadows they describe, since parameters are not necessarily ecologically interpretable. Additionally, such an approach has limitations in describing seed dispersal by animals that (1) range widely, (2) disperse seeds in clumps, and (3) have behaviors or anatomies that lead to directed dispersal (Chapman and Russo, 2007). In short, they are ill-equipped to handle processes that deposit seeds anisotropically, where seed densities may not simply be a function of distance from the parent tree (Fig. 1.4-B). Hence, the effect of clumping and directed dispersal is commonly underestimated in primate-dispersed kernels estimated using the inverse-modeling approach.

Mechanistic models, on the other hand, predict patterns that result from processes built directly from the empirically observed, ecological traits of dispersers. An example of this is Russo (2003), who directly measured the effects of spider monkey behavior on the locations of dispersed seeds and found “the shape of the seed-dispersal curve was a direct consequence of primate dispersal processes, highlighting the need to incorporate primate behavior directly in seed-dispersal models” (Chapman and Russo, 2007:515).

FRUIT EATING IN PRIMATES AND SEED DISPERSAL

Up to 95% of all tropical seeds are moved by fruit-eating animal species (Terborgh et al., 2002) with certain vertebrate groups, including bats, birds, and primates, being particularly important because they eat large quantities of fruit, and defecate, spit, or regurgitate large numbers of viable seeds. Among mammals, phylogenetic clustering of frugivory has only occurred in the primate order (Fleming and Kress, 2011), with most primate families being frugivorous. Primates are also the only group where strict frugivory is common (Turner, 2001). In terms of biomass, most of the vertebrate community in many tropical forests is supported by fleshy fruit (Fleming et al., 1987), with primates constituting between twenty-five and forty-five percent (Chapman, 1995) of tropical frugivore communities, reaching ca. 3000 kg/km² in some areas of Kibale Forest in Uganda (Struhsaker, 1975, 1997). In contrast, tropical forests

dominated by one or two plant families have been found to sustain only low primate biomasses, between ca. 204 kg/km² in Makandé, Gabon (Brugiere et al., 2002) and ca. 700 kg/km² in the Ituri Forest, DRC (Thomas, 1991). As a rule, however, primates are the most important arboreal frugivore in botanically diverse tropical forests in central Africa, southeast Asia, and South America (Struhsaker and Leland, 1979; Emmons et al., 1983; Galat and Galat-Luong, 1985; Tutin, 1998).

Evidence of effective primate-mediated seed dispersal comes from direct observations of high rates of fruit removal, the regular and repeated exploitation of particular trees, the presence of intact seeds in dung, and successful germination of seeds, often in greenhouse settings (Traveset et al., 2007). The fact that germination studies are typically undertaken *ex situ* is important, since results from these studies are likely to misrepresent the germination advantage of endozoochory (and defecation dispersal in particular) in light of research demonstrating that many agricultural plants may allelochemically alter the ground around their bases, thereby stunting or retarding the germination of other individuals (Traveset et al., 2007). Additional evidence of effective dispersal comes from research on the fate of seeds, demonstrating that seeds dispersed to suitable recruitment sites become an important fraction of the seedling cohort. Finally, in a few cases, researchers have demonstrated a direct relationship between patterns of adult tree distributions and primate-generated seed shadows (Russo, 2003; Russo and Augspurger, 2004).

Fruit-eating in primates is characterized by the arboreal processing of fruit, resulting in either the mastication or dropping of seeds under the parent tree, or the spitting/defecation of seeds some distance away from the parent tree (Lambert, 1997). The traditional classification of primate species into seed dispersers or predators is uninformative from the perspective of seed dispersal, since the majority of primate species act as both predators and dispersers (spit, swallow, or wadged seeds) in their lifetimes (Gautier-Hion et al., 1993; Kaplin and Moermond, 1998; Kaplin et al., 1998; Norconk et al., 1998; Lambert, 1999). Indeed, most primates use some combination of seed-handling behaviors, depending on the species of plant consumed, the age or sex of the animal, and the season (Gautier-Hion, 1980; Chapman, 1988; Corlett and Lucas, 1990).

Despite the seeming numerous possible consequences of primate seed handling behaviors, non-random, long-distance, directed dispersal of seeds appears to be a common trademark of primate-mediated seed dispersal systems. For example, mantled howler monkeys (*Alouatta palliata*) on Barro Colorado Island, Panama, defecated one-half of all ingested seeds in leaf-source trees in the morning and again after prolonged rests throughout the day (Milton, 1980). Since leaf-source trees were exploited non-uniformly throughout the day, and often as sleeping or resting sites, dispersed seeds were clumped in both space and time beneath them. Milton (1980) goes on to state:

“It would seem that over a long period of time howlers might shape the forest to some extent, but chance would take a heavy toll here, since the number of seeds that germinate and survive out of the virtually millions that are produced per species per annum in a tropical forest must be extremely low. Still, in time, clusters of howler food trees (fruit and leaf) might be found to be in significantly closer proximity to one another than species not eaten by howlers.” (p 119-120)

Dispersal consequences of medium-bodied primates

The distribution of seeds left by an effective disperser lays the template upon which all subsequent dispersal, predation, and recruitment processes act. To date, few studies have completely quantified primate-generated seed shadows, though exceptions include Garber (1986), Lieberman and Lieberman (1986), Wrangham et al. (1994), and Russo and Augspurger (2004). Variation in primate feeding behaviors creates a great diversity of seed shadow shapes.

For example, both qualitative and quantitative differences are expected between shadows left by spit- versus defecation-dispersal agents, with the former being associated with scattered and distance-restricted patterns, and the latter contagious ones. Clumped deposition patterns are typically expected from large-bodied primates that defecate the bulk of ingested seeds in associated aggregations. These differences are associated with distance and density-dependent mortality factors that can modify, and sometimes may even obscure, the patterns of seed rain left by primates (Russo and Augspurger, 2004).

Guenons (genus *Cercopithecus*) typically handle seeds in a limited number of ways. They can spit or drop seeds after removing the pulp, swallow seeds whole and defecate them, or place fruits in their cheek pouches and remove them later to consume the pulp and spit or swallow the seeds (Kaplin and Moermond, 1998; Lambert, 1999). These behaviors differ qualitatively in the types of the seed rain they

produce. When fruits are handled within the canopies of the parent plant, guenons commonly drop seeds directly below. These seeds contribute nothing to the coterie of dispersed seeds. Alternatively, guenons can defecate both large and small seeds intact. Dung composition studies have found substantial variation between species and sites. In Nyungwe National Park, Rwanda, all mountain monkey (*Cercopithecus lhoesti*) dung (N= 58), and 94% of blue monkey (*Cercopithecus mitis*) dung (N= 50) contained intact seeds, dispersing an average of 2.3 and 6.4 seeds (> 0.2 cm in diameter) per dung sample, respectively, and a maximum of 105 seeds (Kaplin and Moermond, 1998).

Similarly, Fairgreaves (1995) found a mean of 6.12 seeds (N= 147, SD= 12.76, range= 0-92) and a maximum of 92 seeds (> 0.2 cm) of a single species in the dung of blue monkeys in the Budongo Forest, Uganda. Eighty-five percent of dung contained intact seeds. In Kibale, Uganda, Lambert (1999) found 54% of redbellied monkey (*Cercopithecus ascanius*) dung (N= 135) to contain seeds, though nearly 84% of these were very small *Ficus* spp. (< 0.2 cm). Blue monkey dung had seeds (> 0.5 cm) in only 16% of samples (N= 63, range= 5-16, mean= 9.3), and 16% of these contained only destroyed seeds, while 83.7% contained only intact seeds (Lambert, 1999). Therefore, though dispersal of seeds via defecation has the potential to distribute seeds widely, and to a great distance, this type of dispersal by guenons is likely to be limited to seeds of less than 0.5 cm in diameter.

Of all guenon behaviors, none contributes more to the seed rain than their habit of placing fruits in their cheek pouches (Corlett and Lucas, 1990; Rowell and Mitchell, 1991; Ham, 1994; Lambert, 1999; pers. obs.). Fairgreaves (1995) documented 14 tree species whose seeds were spat from blue-monkey cheek pouches after the pulp had been removed (seed size range: 0.3-3.0 cm). In Kibale NP, seed spitting was the most common pattern of seed handling year round, and spat seeds were typically stored in cheek pouches (Lambert, 1999). While the majority (83.3%) of seeds stored in cheek pouches was dropped under the parent tree, some seeds (16.7%) were spat as far as 100 m from the parent tree. Dispersal of large-seeded species by guenons is thus characterized by cheek-pouching (followed by spitting) behaviors, occurs at only a moderate rate and in only a small percentage of a tree's crop, and to distances that are generally limited to less than 100 m.

Ham (1994) intensively studied the ecology of the resident grey-cheeked mangabey (*Cercocebus albigena*) at Lopé. Seeds too small to be separated from pulp (e.g., *Ficus* spp. and *Nauclea diderrichii*), were commonly ingested with the fruit. Mangabeys appeared to use their cheek pouches more often than sympatric *Cercopithecus* monkeys, though sample sizes were too small to test this (Ham, 1994). Some seeds were spit-dispersed by mangabeys, though dispersal distances were typically less than 100 m.

Seed dispersal in the great apes

In Africa and parts of Asia, the largest arboreal frugivores are the great apes (Pongidae). Because of their seed handling behaviors and body size, the great apes are increasingly recognized as effective seed dispersers (Idani, 1986; Wrangham et al., 1994; Gross-Camp and Kaplin, 2005, 2011). The combination of consistently ingesting a great number of seeds, numerous intact seeds in dung, long daily path-lengths, slow digesta passage rates, and the ability to handle the largest fruits that other frugivores cannot manipulate, sets the great apes apart from other primates in terms of their abilities to disperse large-seeded species. They have been shown to play a significant role in the initial distribution of seeds (Lambert, 1999; Voysey et al., 1999a; Gross-Camp and Kaplin, 2005), and in the fate of large-seeded plant species (Voysey, 1999b; Gross-Camp and Kaplin, 2011).

Seed removal by great apes

The great apes remove a great many seeds and to potentially great distances. Whole seeds, for example, were observed in 44% (Rijksen, 1978) and 94% (Galdikas, 1982) of orang-utan (*Pongo abelii* and *P. pygmaeus*) dung in Sumatra and Kalimantan, respectively. In Kalimantan, dung had a median of 111 seeds (Galdikas, 1982), and seeds could be expected to travel relatively far from parent plants since orang-utans traveled an average of 968 meters per day (Harrison, 2009), and have a mean gut retention time of 73.7 hours (Caton, 1999).

Chimpanzees (*Pan troglodytes schweinfurthii*) in Kibale, Uganda, dispersed seeds in 98.5% of dung, ranging in size from 0.1 to 2.7 cm in diameter, and at a rate of 369 very large seeds (> 2 cm) per square kilometer per day (Wrangham et al., 1994). In the same forest, the average number of large seeds per dung sample was 149, with hundreds of small seeds dispersed far from parent trees (Lambert, 1999).

Large seeds (> 0.5 cm) from 37 species were dispersed in 35% of chimpanzee dung samples in the montane forests of Nyungwe National Park, Rwanda (Gross-Camp and Kaplin, 2005, 2011; Gross-Camp et al., 2009), contrasting with only eleven dispersed species by the sympatric and semi-terrestrial monkey, l'Hoesti's monkey (*Cercopithecus lhoesti*). Some species, e.g., *Syzygium guineense* (~ 1.4 cm in diameter), were only dispersed (in both wadges and feces) by chimpanzees (Gross-Camp and Kaplin, 2005). In Dja National Park, Cameroon, chimpanzee dung (*P. t. troglodytes*) contained an average of 41 seeds (> 2 cm; Poulsen et al., 2001). Chimpanzees have a smaller swallowing threshold than gorillas, and disperse fewer seeds. They add, however, a unique (pre-ingestion) processing behavior called "wadging". Fruit is kept in their lower lips and unwanted material is spit out (i.e., seeds, skins and fiber). In terms of the quality of seed dispersal, "wadging" may ultimately limit the chimpanzee's effectiveness (Gross-Camp and Kaplin, 2011), since it limits the distance a seed is transported and leaves some pulp attached to the seed, which promotes fungal attack.

In Dja National Park, Cameroon, a total of 45 seed species (plus an additional 42 unidentified species) were dispersed by gorillas (*Gorilla g. gorilla*), averaging 3.9 species per dung pile (Petre et al., 2011). Dung contained a mean of 18 very large seeds (> 2 cm), and 67 seeds (of any size) per 100 grams (Poulsen et al., 2001; Petre et al., 2011).

Seed arrival benefits of great ape-mediated seed dispersal

Nielsen et al. (2001) studied the germination effects in seeds dispersed by orang-utans and found high rates of viability and germination speed. In bonobos (*Pan paniscus*), thirteen out of seventeen species from dung germinated, and six of these germinated at greater rates than control seeds (Idani, 1986). Increased seed germination viabilities and velocities have also been found in seeds from chimpanzee dung in both Tanzania and Uganda (Takasaki, 1983; Takasaki and Uehara, 1984; Wrangham et al., 1994). In Nyungwe NP, seed germination and survival varied, depending on elevation and slope (Gross-Camp and Kaplin, 2005, 2011). In Dja NP, eight out of ten, and four out of four, species tested from chimpanzee dung and gorilla dung, respectively, were viable (Poulsen et al., 2001).

In addition to germination effects, benefits to seeds stem from behaviors that may increase a seed's chances of arriving to sites with a high probability of survival (i.e., directed dispersal). In Rwanda,

Gross-Camp and Kaplin (2011) found that some seeds were deposited in feces and others in wadges, and both types could be distinguished from singly spit seeds in terms of seed fate. Differences in the handling of large seeds (> 0.5 cm) between l'Hoest's monkeys and chimpanzees could predict the spatial arrangement of dispersed seeds, with defecated and spit seeds having little spatial overlap. Although they experienced poorer rates of establishment, defecated seeds were deposited farther from adult conspecifics than spit seeds (Gross-Camp and Kaplin, 2011). In experimentally placed seeds, open forest sites experienced the highest germination rates. Thus, habitat type was the most important factor in determining seed fate, suggesting that dispersers that occupy different niches pose different limitations to dispersal. There may be less of a compensatory role between apes and monkeys in terms of seed dispersal quality.

Gorillas are defecation seed dispersers, wasting and dropping very little of the fruit as they feed. In Lopé National Park, defecations along gorilla feeding trails contained fewer seeds than those deposited at nest-sites (Rogers et al., 1998), and while higher seed densities at nest-sites were associated with lower survival rates, no reduction in germination resulting from crowding was observed (Voysey, 1995). In fact, though seed/seedling mortality was high at nest-sites, the greater number of initial seeds in dung increased the probability that at least one seedling would survive over time (Voysey, 1995). Nest-sites and seed aggregations varied depending on habitat type in Dja NP (Petre et al., 2011), with 65% of seed preferentially deposited into open canopy sites, which might increase the survival of shade-intolerant plant species.

Because lowland gorillas foraged on multiple fruit species in a day, their dung typically contained more than one seed species (Voysey, 1995), generating different combinations of seeds at deposition sites, where the probability of individual survival (Kwit et al., 2004) may depend on the context of co-dispersed seeds (Loiselle, 1990; Schupp et al., 2002; Kwit et al., 2004; Blendinger et al., 2011).

In summary, gorilla-mediated seed dispersal is characterized by the arrival of seeds to deposition sites in high-density, heterospecific aggregations. Unlike monkey- (but see Clark et al., 2004) or bird-dispersed seeds, gorilla-dispersed seeds are not typically associated with fruiting trees. Since gorillas aggregate a large number of seeds from different plants and species in their dung, the act of dispersal

deposits polyspecific associations of seeds to certain deposition sites at the expense of others. The exact nature of spatial clumping in the gorilla-mediated component of the seed rain is expected to be a complex function of their social behavior, foraging and defecation patterns, gut capacity and passage rates, and the gorilla's propensity to construct a new sleeping site each night.

RATIONALE FOR THIS STUDY

Fruit is more important in the diets of lowland gorillas (*G. g. gorilla* and *G. beringei graueri*) than in the mountain subspecies (*G. beringei beringei*) (Schaller, 1963; Jones and Sabater Pi, 1971; Calvert, 1985; Tutin and Fernandez, 1985, 1993a; Williamson et al., 1990; Nishihara, 1992, 1995; Remis, 1994; Kuroda et al., 1996; Tutin, 1996). In all locations where lowland gorillas have been studied, the number of fruit species in their diets far surpasses those of their montane congeners, presumably due to the lower densities of fruiting tree species in high altitude habitats (Hladik, 1988; Williamson, 1988; Watts, 1990). The western gorilla diet is therefore defined as eclectic, including up to 230 items across 180 species, with fruit species being the most diverse component (Rogers et al., 2004).

During the course of foraging, western lowland gorillas can make multiple regular visits to the same tree and remove hundreds of fruits per visit, often spending more than an hour feeding continuously in a single tree (Williamson et al., 1990; Voysey, 1995). In most cases, the fruit is swallowed whole and ripe seeds are passed through the gut undigested (Williamson et al., 1990; Tutin et al., 1991a; Tutin and Fernandez, 1993a, Nishihara, 1995).

The typically undamaged seeds are deposited in dung, and at great distances from the parent plant, often to locations that are beneficial for germination, growth, and survival. Benefits, in part, stem from the fact that nightly nest-sites are foci for much of the dung (Williamson, 1988), the majority of which are constructed on the ground and in light gaps (Schaller, 1963; Williamson, 1988; Tutin and Fernandez, 1993a; Tutin et al., 1995; Rogers et al. 1998). The combination of a large gut capacity, variable gut passage time, and large day-ranges (extending for several kilometers), make lowland gorillas unique among seed dispersers in terms of the quantity and quality of services (*sensu* Schupp, 1993) they provide to seeds.

Effective seed dispersal by gorillas has been studied extensively in only one location in west-central Africa, the Station d'Etude des Gorilles et Chimpanzés (SEGC) in Lopé National Park, Gabon (Voysey, 1995; Rogers et al., 1998; Voysey et al., 1999a,b). Despite these works, gaps in our understanding of the spatial and temporal consequences of gorilla-mediated dispersal of large-seeded species remain. In the present study, I intend to address and fill some of these gaps. The objectives of this dissertation are:

- to describe quantitatively, the temporal patterns in the availability of fruit resources consumed by gorillas (and the greater primate community) at the Station d'Etude des Gorilles et Chimpanzés (SEGC) in Gabon, and identify the environmental covariates to these patterns.
- to describe qualitatively, the aggregations of co-dispersed seeds, by evaluating the combinations of seeds dispersed in gorilla dung across high and low fruit seasons and across deposition sites.
- to analyze the spatial ecology of gorilla nesting behavior, a factor found to be of significant importance to seed and seedling establishment. By determining the spatio-temporal environmental covariates that underlie the behavioral ecology of nest-site choice in gorillas, I intend to provide insight into a key component of their effectiveness as a seed disperser.
- to describe the spatial distributions of extant, adult trees across different disperser guilds, and assess the consequences of gorilla-mediated seed dispersal to the demographic ecology and diversity of tree species in a tropical forest ecosystem.

CHAPTER II

MATERIALS AND METHODS

THE STUDY SITE: LOPÉ NATIONAL PARK

The Republic of Gabon straddles the equator on the west central coast of Africa. It is bordered by Equatorial Guinea and Cameroon to the north, the Republic of the Congo to the east and south, and 885 km of Atlantic Ocean coastline to the west. Its surface area of 267,667 km², is divided into three topographical zones: a narrow coastal alluvial plain; an extensive, hilly inland plateau; and several low-elevation mountain zones (max. 1575 m) (Lee et al., 2006).

Central Africa's tropical moist forests cover 1.8 million km², making it the second largest contiguous block in the world after Amazonia. Gabon is an important part of that block, with roughly 75% of the country covered by moist tropical forest (Myers, 1991). The predominant forest types are 'mixed moist semi-evergreen Guineo-Congolian rain forest' and 'hygrophilous coastal evergreen Guineo-Congolian rain forest' in the UNESCO classification by White (1983). According to the JRC TREES project (Tropical Resources and Environment Monitoring by Satellites project of the Joint Research Center), Gabon's forest covered ~210,000 km² in 1995, suggesting that 20 percent of the original forest cover has already been converted to cropland or other land use (Mayaux et al., 1997). Gabon's forest serves as a huge carbon reservoir, sequestering between 0.94 and 5.24 gigatons of carbon (Olson et al., 1983).

Lowland forest diversity in Gabon is among the richest in Africa (Breteler, 1996). High biological diversity, and an abundance of globally rare species, such as sea turtles, forest elephants, humpback whales, and great apes, makes Gabon a valuable region for conservation at an international level (Kamdem-Toham et al., 2003). Human influence on this forest system is relatively recent (White, 2001). Agriculturalist Bantu tribes immigrated to the area only in the past 5,000 years, however the presence of hunter-gatherers in the middle Ogooué region of Gabon is known from the Early Stone Age (ca. 400,000-120,000 years BP) (Oslisly, 2001). An era of resource exportation to international markets began in the

1470s with the arrival of European explorers, missionaries, and traders seeking timber, forest products, ivory, and slaves. Gabon was part of French Congo, then French Equatorial Africa until 1920, and eventually gained independence in 1960.

Since independence, timber, oil, manganese, and uranium exports have supported Gabon's 1.5 million inhabitants ("World statistics pocketbook 2011", 2012). Although vast areas remain uninhabited and ecologically intact, Gabon's valuable resources are under threat as the territory and offshore are gazetted for commercial extraction (Collomb et al., 2000; Walsh et al., 2003; Laurance et al., 2006). As oil revenues have declined during the past two decades, demands for the country's forest resources have increased, with Gabon's total concession area increasing seven-fold between 1957 and 1999, from 16,000 km² to 119,000 km² (Collomb et al., 2000).

In August 2002, a National Park System was created by Presidential decree to protect Gabon's natural heritage and develop an ecotourism industry. In this landmark decision, an area of 28,900 km² (10.8% of the national territory) was granted full protection (Anonymous, 2002).

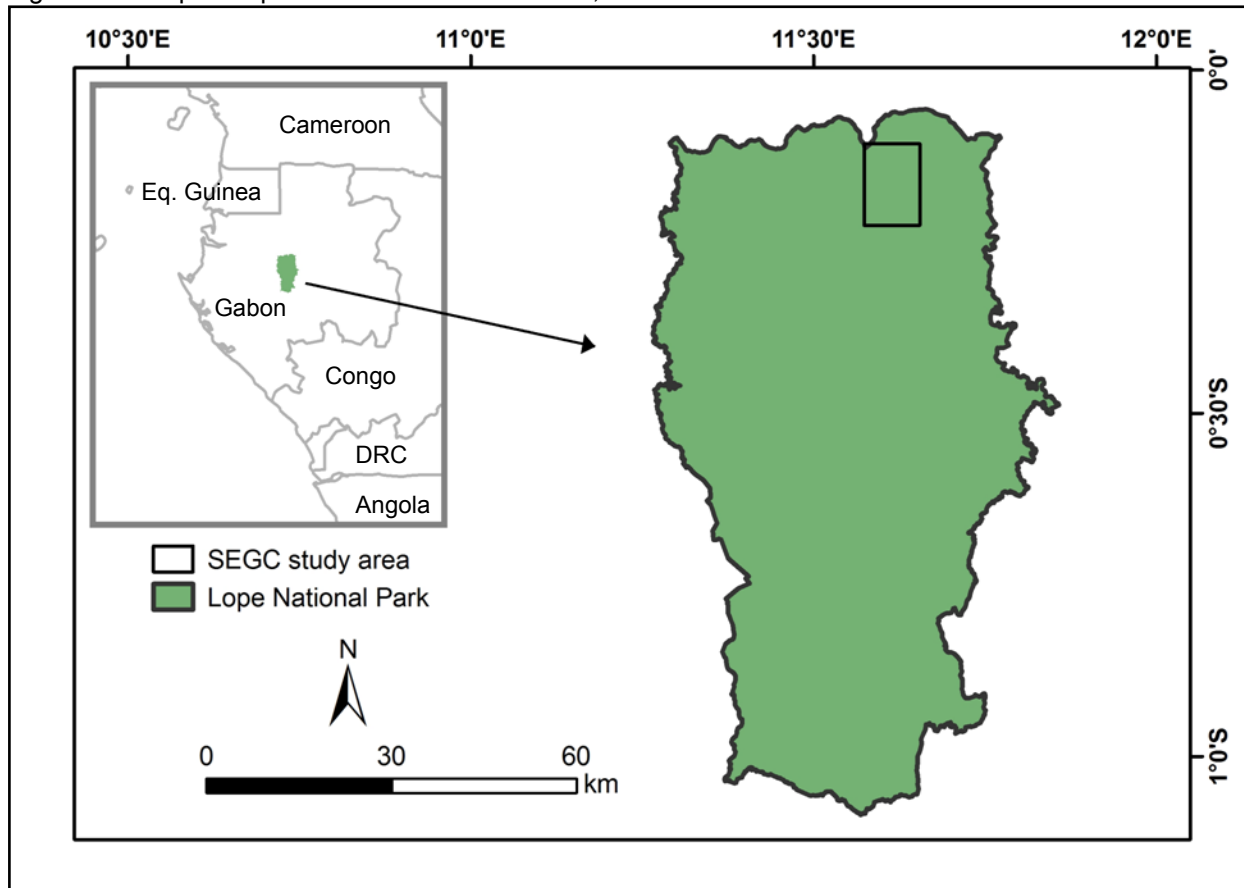
Study location and climate

The study area is located in Lopé National Park, which is situated in central Gabon (Fig. 2.1). A wildlife reserve since 1946 and a national park since 2002, Lopé NP covers an area of 4948 km² and was inscribed on UNESCO's World Heritage List in August 2007. Rainfall is lower in the Lopé region than the rest of Gabon due to a rain shadow effect from the Massif du Chaillu mountains southwest of the national park, as well as a low band of rainfall associated with the Ogooué river along the northern border of the park (White, 2007). The core area of research for this dissertation was the Station d'Etude des Gorilles et Chimpanzés (SEGC), located in a 50 km² sector of forest along the north-eastern limit of the park (0°10' S 11°37'E).

The mean annual rainfall at SEGC is 1474 mm (SE ±44.8, from 1984 to 2004) (Palla et al., 2011). Monthly rainfall is shown in Figure 2.2. The distribution of rainfall is seasonal, with a long dry season between mid-June and mid-September, and a shorter one in January and February. The severity and duration of these dry seasons varies between years. Temperatures vary little throughout the year, with quotidian range often equaling the annual range. Temperatures recorded by a logger at the SEGC

research station gave a mean daily temperature of 25.9°C (SE ± 0.06 , from January 2003 to December 2004), ranging from 17.5° - 38.8°C (Palla et al., 2011).

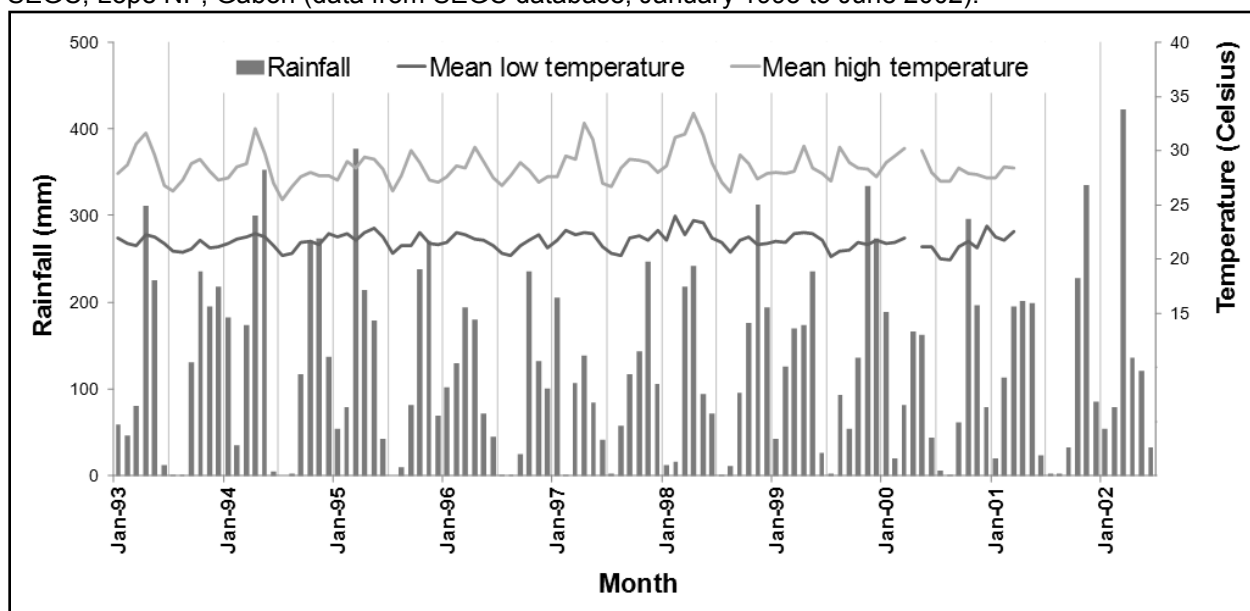
Figure 2.1. Map of Lopé National Park and SEGC, Gabon.



Physical characteristics

Topographic relief in Lopé is characterized by a chain of convex, rolling hills dominated by the Okanda chain (450-850 m above sea level) to the south of the research station. To the north of the station is a former lake basin that was drained when the Ogooué river went through the Okanda chain. The vegetation is varied and contains several ecological plant associations, including gallery forests and “bosquets” (French, “wood, grove”), forest-savanna mosaic, young forests, and mature forests (White, 1992; Tutin et al., 1994).

Figure 2.2. Monthly rainfall, monthly mean low temperature, and monthly mean high temperature at SEGC, Lopé NP, Gabon (data from SEGC database; January 1993 to June 2002).



Research history

SEGC was established in 1983 following a nationwide census of great apes (Tutin and Fernandez, 1984), and research on the ecology of gorillas and chimpanzees has been underway since that time. Attempts to habituate apes to close human presence at SEGC have ultimately been unsuccessful, and research efforts have concentrated on great ape feeding ecology, including diet (Tutin and Fernandez, 1985; Williamson, 1988; Williamson et al., 1990; Tutin and Fernandez, 1993a; Rogers et al., 1994), and food chemistry (Rogers et al., 1990, 1992). The nesting behavior of gorillas (Tutin et al., 1995) and the phenological patterns of their food plants (Tutin and Fernandez, 1993b; White, 1994a; Tutin and White, 1998) are well understood. Few forested sites in Africa have been studied as extensively as Lopé, and much is known of its vegetation history (Rogers and Williamson, 1987; White, 1992; Williamson, 1993; Tutin et al., 1994; White et al., 1995; Palla et al., 2011), and the effects of selective logging (White, 1992, 1994b). The mammal community (White, 1994c), and the ecologies of elephants (White et al., 1993, 1994; White, 1994d), sympatric monkeys (Ham, 1994), mandrills (White et al., 2010), and an introduced ant species (Mikissa et al., 2008), are just a few of the research topics that have been undertaken at Lopé.

Plant-animal interactions have always been a component of the research at SEGC. Tutin and colleagues undertook a preliminary study of seed dispersal by gorillas (Tutin et al., 1991a), which was followed by a pilot study of frugivory for nine months involving a concerted observational effort to investigate gorilla feeding on the fruit of four tree species (Rogers and Parnell, 1991). In the most comprehensive study to date on gorilla-mediated seed dispersal, Voysey (1995) investigated fruit removal and seedling fate in four gorilla-dispersed species. Some of the results of the above research are considered in the sections below.

Vegetation

Although forest structure and composition in Lopé National Park is heterogeneous, the two principal forest types are described as “Marantaceae forest” (after Letouzey, 1968) and “mixed closed canopy forest” (Williamson, 1988; White, 1992; Tutin et al., 1994; White et al., 1995). White (1992) identified twenty vegetation associations, including forest that is actively colonizing savanna, rocky forest, marshes, gallery forest, and different forest types related to the degree of transition from Marantaceae forest to mixed closed canopy forest. See Figure 2.3 for a map of vegetation types in the SEGC study area.

Marantaceae forest in Lopé NP colonized savannas relatively recently (Tutin et al., 1994; White, 2001), eventually giving rise to closed canopy forest. Marantaceae forest contains fewer tree species, and a lower stem density and basal area than closed canopy forest. The majority of plants are adapted for animal dispersal, and White (1994a) found that 75% of the fruit species (N= 195) on fruitfall transects are dispersed by animals.

Marantaceae forest dominates the vegetation in the study area at SEGC, which Letouzey (1968) described as “forêt clairsemées à strate inférieure de Marantacés”. This forest type is characterized by an uneven and broken canopy, typically 25-35 m high, a sparse understory (10-20 m), and a dense undergrowth of herbaceous vegetation consisting principally of plants in the Marantaceae (arrowroot) and Zingiberaceae (gingers) families. The dominant tree species in Marantaceae forest, in terms of basal area, are *Aucoumea klaineana* (Burseraceae) and *Cola lizae* (Malvaceae), and relatively common species include *Lophira alata* (Ochnaceae), *Xylopia* spp. (Annonaceae), *Diospyros* spp. (Ebenaceae),

Pentaclethra spp. (Fabaceae), and *Pycnanthus angolensis* (Myristicaceae) (Tutin et al., 1994; White et al., 1995). The “top ten” species account for 69% of the tree stems above 10 cm DBH and 76% of the total basal area (White, 1992). Marantaceae forest is important to gorillas and elephants, providing a major source of food (Tutin et al., 1994; White et al., 1995), as well as ample nest construction materials for gorillas (Tutin et al., 1995).

Closed canopy forest corresponds to the “mixed moist semi-evergreen Guineo-Congolian rain forest” of White (1983) and has a more continuous and speciose canopy, and a much denser understory than Marantaceae forest (Tutin et al., 1994; White 2001). It generally lacks the dense herbaceous floor vegetation found in earlier successional forest types. The major tree species are *Dacryodes buettneri* (Burseraceae), *Aucoumea klaineana*, *Scyphocephalum ocochoa* (Myristicaceae) and *Coula edulis* (Olacaceae).

Fruit production at Lopé is highly seasonal, with the highest fruit abundance occurring from November-February and fruit scarcity occurring during the dry season (White, 1994a; Tutin and White, 1998). Underlying this general pattern, however, a wide range of flowering and fruiting patterns exist among species. These include (1) asynchronous fruiting species, (2) species with long fruiting periods and sequential ripening, (3) species with short, sharply peaked fruiting, (4) species that produce fruit every 2 or 3 years (alternate-bearing), and (5) mast-fruiting species, in which occasional years see a major fruit crop. Between years, considerable variation exists in the amount of fruit that is available to frugivores. Tutin and Fernandez (1994) described “good” and “bad” years of community-wide fruit production depending in part on factors related to climate, pollination success, and predispersal predation.

Selective logging occurred in some of the study area in the 1960s, principally for one species, okoumé (*Aucoumea klaineana*), and extraction rates were about 1-2 trees per hectare. According to White (1994b), an estimated 10% of the canopy has been lost due to extraction, although 50% of the canopy may have been disturbed or changed in some areas.

The vertebrate community

Little is known on nocturnal primates and carnivores at Lopé, though one notable exception is a study on leopard feeding ecology (Henschel et al., 2005). As for the other large mammals that occur in Lopé, White (1992, 1994c) surveyed mammals along a transect in Marantaceae forest to the south of the research station and his results are shown in Figure 2.4 and Appendix A. He reported that Lopé supported the highest mammalian biomass of any rain forest studied, with elephants comprising the majority of the total biomass (89%) (White, 1992). Primates accounted for only 10 percent. Due to their greater size, the biomass of gorillas (~1 individual per km²) is nearly three times that of chimpanzees (0.7 individuals per km²). Since these results come from an area that is predominantly Marantaceae forest, a vegetation type favored by both elephants and gorillas, the biomasses of these species are higher relative to those found in the mature closed forests found in other regions of Lopé NP (White 1992, 1994c).

Gorillas are one of eight species of diurnal primates that occur at Lopé. Despite their low percentage of overall mammalian biomass (White, 1994c), primates are still the most important arboreal consumers. Fruit dominates the diets of seven of these, with seeds being the dominant food in the eighth species, the black colobus (*Colobus satanus*) (Tutin et al., 1991a).

A field guide (Christy and Clarke, 1994) covers the extensive avifauna found in Lopé. The major frugivorous groups include the hornbills (Bucerotidae), touracos (Musophagidae), pigeons (Columbidae), barbets (Capitonidae), bulbuls (Pycnonotidae) and starlings (Sturnidae).

Figure 2.3. Vegetation types in the SEGC study area. The crosshaired circle in the center indicates the location of the research station.

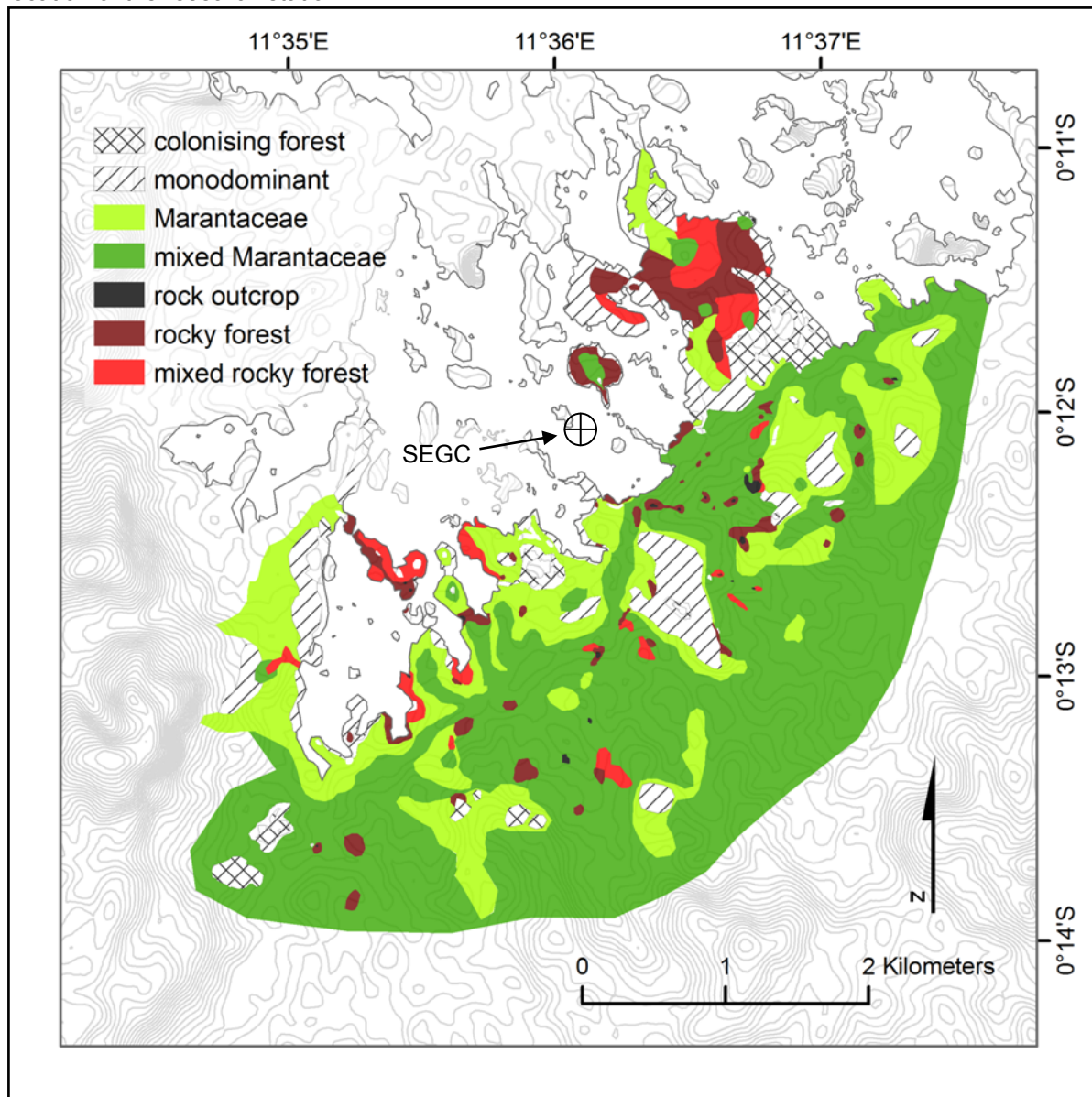
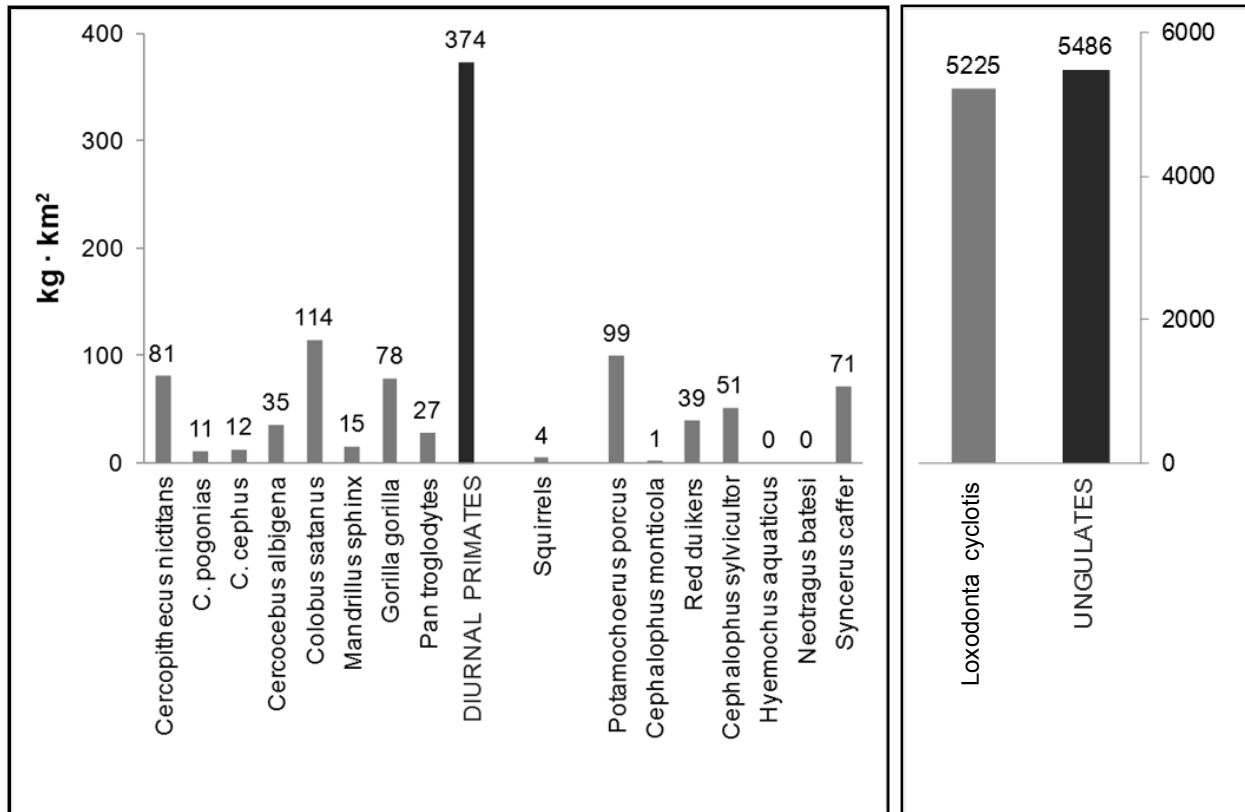


Figure 2.4. Biomasses in kilograms * kilometer⁻² of mammals at SEGC. Data were collected by White (1994c), along "transect 1", which falls within the major habitat type in the northeastern sector of the park, Marantaceae forest.



THE STUDY ANIMALS

Until recently, gorillas were considered a single species, with three subspecies: the western lowland gorilla (*Gorilla gorilla gorilla* Savage and Wyman, 1987), the eastern lowland gorilla (*Gorilla g. graueri*), and the mountain gorilla (*Gorilla g. beringei*). Considerable genetic differences exist between the western and eastern subspecies, as well as between populations (Ruvolo et al., 1994), and the consensus today is that two species of gorillas exist, each with two subspecies. The western gorilla is comprised of the western lowland gorilla (*Gorilla gorilla gorilla*) and the Cross River gorilla (*G. g. diehli*), and the eastern gorilla is comprised of the mountain gorilla (*Gorilla beringei beringei*) and the eastern lowland gorilla (*G. b. graueri*) (Groves, 2003). For this study, the important distinction is that mountain gorillas have a largely foliaceous diet and eat little fleshy fruit, while all other taxa regularly incorporate fruit in their diets. The current distribution of *Gorilla g. gorilla* (hereafter 'gorilla') is discontinuous,

occurring in southern Cameroon, Gabon, Equatorial Guinea, southwestern Central African Republic, and the Republic of Congo.

Gorillas are considerably sexually dimorphic, with female gorillas typically 42% of the mean weight of adult male gorillas (170 kg, N= 13; Smith and Jungers, 1997). A prominent sagittal crest on top of the skull provides for the attachment of powerful temporal muscles (Dixson, 1981) and large molars are set in huge jaws. A long, voluminous hindgut facilitates the processing of plant foods (Chivers and Hladik, 1984), and contains cellulose-digesting ciliates (Collet et al., 1984). Chivers (1989) notes the lack of gut specialization, and places the gorilla firmly in the class of frugivores rather than folivores among “caecocolic fermenters”.

Gorillas at Lopé live in relatively stable family groups usually led by one adult, silverback male. Groups range between four and fifteen individuals (median= 9; Tutin et al., 1992). Ranging patterns are difficult to assess in unhabituated gorillas. In one study at Lopé, only 11% of night nest-sites were found due to difficulties associated with maintaining gorillas trails through dense vegetation (Tutin et al., 1992). Mean daily path length at Lopé was 1172 m (N= 30; range= 320-2600 m), and minimum home range sizes were 4-14 km² (Tutin et al., 1992). These estimates are likely to be conservative.

Effective gorilla-mediated seed dispersal

Frugivory in lowland gorillas is well documented at Lopé (Tutin and Fernandez, 1985; Williamson et al., 1990; Tutin and Fernandez, 1993a) and other sites in west-central Africa (Rogers et al., 2004). At Lopé, gorillas consume at least 100 species of fruit, dispersing the seeds of the majority of these (Tutin, 1998). In a 7-year study, fruit species represented 55% of plants in the diet, and fruit remains were in 96% of 4301 dung samples (Tutin and Fernandez, 1993a).

The number of reported fruit species consumed by gorillas at Lopé continues to increase, as more data is collected since research began in 1984, with 75 succulent fruits reported in 1991, and 100 species in 1998 (Tutin et al., 1991b; Tutin, 1998). With more than 1,300 plant species from which to choose in the study area (Tutin, 1998), gorillas are considerably selective in their foraging. Similarly, Williamson (1988) found that gorillas at SEGC consumed only 36% of the 138 species of trees found along vegetation transects.

Jordano (2000) outlined the criteria that determine effective seed dispersal by a frugivore. These include (1) reliable visitation to a fruiting tree, (2) removal of many seeds away from the parent, (3) minimal waste, (4) ingestion of seeds and intact passage through the gut, (5) large body size relative to seed size, (6) gentle treatment of the seed by mouth and gut, and (7) the deposition of seeds in a favorable site.

For the majority of the fruit species they consume, gorillas satisfy the above criteria. They are large-bodied frugivores that provide a gentle gut passage for the numerous seeds they remove. Many fruit species in their diet are consumed whenever they are available. Their reliability as visitors to a particular fruiting tree is a function of multiple factors, including their preference for that species, the abundance and distribution of fruiting trees, its relative importance in the diet, the size of the individual tree and ripe-fruit crop, and the number of simultaneously fruiting foods and their abundance and importance (Voysey, 1995). Each of these factors vary from food species to food species, and from one year to another. Fruits classified as 'important' are those species that "dominate the diet on a regular or irregular basis and influence ranging patterns" (Tutin et al., 1991a,b; Tutin and Fernandez, 1993a). Fifteen such species are listed in these publications. Gorillas at Lopé will stay in one small area if ripe foods are concentrated there (Voysey, 1995), and use uncommon habitats such as gallery forests and swamps whenever fruit is abundant.

Although gorillas maintain a high degree of foliaceous material in their diets, the quantity and diversity of seed species in the dung are impressive. A single dung pile may contain hundreds of seeds of one or more species, thus, gorillas disperse many thousands of seeds of a species during one fruit season (Tutin et al., 1991a). Thus, gorillas remove and disperse considerable quantities of seeds (Voysey, 1995) and waste is generally low. Several of the 'specialist' species they feed on have fruit that are firmly attached to the branches and are not easily knocked down by the activity of gorillas in the crown (e.g., *Gambeya africana*, Sapotaceae; and *Cola lizae*, Malvaceae).

Gorillas deposit seeds in a pile of natural fertilizer (Fig. 2.5-A). With the exception of one study (Todd et al., 2008), precise data on defecation rates are not available for wild gorillas, but 4-5 defecations per day is a reasonable figure albeit conservative (Tutin et al., 1991a). Gorillas frequently defecate in the

evening and again in the morning, leaving much of their daily fecal output at nest-sites (Voysey, 1995). The aggregate effects of seed accumulation are minimized since gorillas often construct fresh nests (Fig. 2.5-B) in a new locality each night. Sixty-four percent of nests are made on the ground (N= 2435 nests, Tutin et al., 1995), but this varies across habitat types. Nest-sites are often found in areas of open canopy, such as natural treefall gaps, and these sites may favor shade-intolerant species over others. Despite the greater abundance of herbaceous material that is sometimes associated with nest-sites, the act of nest building and feeding severely flattens the vegetation and may even kill it (Voysey, 1995). Dung is usually deposited adjacent to the nest, and on a clear patch of ground with few herbaceous stems around it. Dung that is deposited from a tree where a gorilla is feeding tends to break up, thereby scattering the enveloped seeds. Dung is also left as the gorilla moves about the forest floor. Thus, in terms of seed deposition, dung may be separated into two categories, nest-associated and “in-transit”. Support for this distinction comes from site-specific properties related to (1) environmental characteristics at deposition locations, (2) the combinations of seeds they contain, (3) the spatial arrangements among seeds, and (4) the degree of spatial association with other dung piles.

Seed Removal

Voysey (1995) extensively studied fruit removal and seed fate in four tree species important in gorilla diets at Lopé. Gorillas visited 75% of fruiting *Ganophyllum giganteum* (Sapindaceae) trees, removing between 40.7% and 54.8% of fruit crops depending on the year. On average, they removed twice as many seeds as sympatric monkeys (e.g., 54.8% compared to 22.4%), and wasted less than half those of monkeys in some years (Voysey, 1999a). For example, gorillas dropped only 5.3% of *Ganophyllum* fruit crops in 1992 compared to 12.8% in monkeys, and their foraging tended to be ‘goal-directed’ with groups moving from tree to tree (Voysey, 1995).

In *Cola lizae* (Malvaceae), visitation rates were lower, with gorillas feeding from only 32% of groves and 27% of individual trees. This species is the most abundant species in the study area. Despite this, gorillas moved a large number of seeds in dung that often contained little else, with seeds from *Cola* comprising 70-100% of wet dung weights. Consequently, each gorilla in the study area was estimated to

Figure 2.5 (A-B). Plates of gorilla dung pile and ground nest.

A) Dung pile of a silverback gorilla.



B) Gorilla night nest on ground. Expert pisteur (Tracker) Samedi of Mondika, CAR, demonstrates its size and comfort. Credit: Kate Golden.



disperse between 4600 and 7600 seeds over a two to three month period within a typical *Cola* fruiting season. Extrapolating this figure, Voysey (1995) estimated 10,500-17,500 dispersed seeds per gorilla per year, akin to the number reported by Tutin et al. (1991a).

Gorillas removed a relatively small proportion of ripe seeds from the entire *Cola* fruit crop, and a significantly smaller one than monkeys. Of the trees that gorillas did visit, however, they removed 24.6% of crops, a statistic that was not different from monkeys, which removed 31.9% (Voysey, 1995). Waste was higher in monkeys, and when they did carry seeds away from the parent tree, seeds were widely scattered. When mandrills traveled through an area in large groups (> 450 individuals), they fed in *Cola* patches and wasted much of the crop by feeding on unripe fruits.

In the case of *Dialium lopense* (Fabaceae), gorillas visited 100% of focal trees (N= 10 trees), and made multiple visits to all but the smallest trees. They removed on average 78% of the focal crops, compared to 12% for chimpanzees and 7% for monkeys. A great number of fruits in a short period of time may be removed from a *Dialium* tree by a group of gorillas, with 10,000 to 17,000 fruits being removed during an average feeding bout (Rogers and Parnell, 1991; Voysey, 1995). Wasted fruit was exceptionally low in this preferred species, with nearly all frugivores in the forest partaking. Three *Cercopithecus* spp. (*C. nictitans*, *C. cephus*, and *C. pogonias*) fed on the mesocarps, and either swallowed or discarded the seeds. *Mandrillus sphinx*, *Colobus satanas*, and *Cercocebus albigena*, however, ate the seeds and discarded the mesocarps. Fruit quantities consumed by elephants were considered negligible in comparison to apes, presumable since only a small amount of intact fruit ever reaches the forest floor in *D. lopense* (White, 1992; Voysey, 1995).

Fruits of *Uapaca guineensis* (Phyllanthaceae) can take long time to ripen. This can work to decrease ripe-fruit regularity (increased variance around the mean date of bearing ripe fruit), which in turn appears to influence visitation rates by primates (Voysey, 1995). Given its restricted habitat requirements (i.e., gallery forests and forest-savanna edges; Ham, 1994), if peak fruiting should occur later than expected, *Uapaca* trees might compete with different food species for disperser attention. This was presumably the case in 1992, when some focal trees fruited later than expected and were not fed upon, to any extent, by primates (Voysey, 1995).

In the next year (1993), 75% of *Uapaca* patches (N= 14 trees) monitored received gorilla visits, removing on average 17.7% of fruit crops in these trees (30.1% if lone-male visitations were removed). Among all trees monitored (i.e., including those not visited), gorillas removed 11.8% of fruit crops, compared to 22.1% in monkeys and 9% in chimpanzees, with no significant differences between frugivores in pairwise comparisons. Ripe fruits in *Uapaca* are tenuously attached to panicles, with gorillas causing much “knockdown” of fruit as they move about the crown. It is therefore common for a majority of fruit crops to be dropped under the crown in this species. Dropped immature and ripe fruit is readily “hoovered” up and dispersed by elephants (Voysey, 1995). Monkeys only scatter-disperse *Uapaca* seeds from fruit removed in their cheek pouches. Mandrills may be the only monkey that both swallow and spit the seeds of *Uapaca* trees.

Seed deposition sites and the fate of seeds

Voysey (1995) analyzed the density and survival of seed and seedlings in four species dispersed by gorillas. Compared to “in-transit” gorilla dung sites and scatter-dispersed seeds, designed to mimic the spit-dispersal behaviors of cheek-pouch monkeys that singly scatter seeds up to 100 meters from fruiting trees, seedlings at gorilla nest-sites exhibited the best performances in terms of growth and survivorship. These results suggest the potentially disproportionate importance of gorilla nest-sites for establishment in some large-seeded species.

THE FRUITING PLANTS

Plant species used in this study include 48 species, most of which are large-seeded species (i.e., greater than 0.5 cm in length). Table 2.1 shows the list of species considered, and their consumers. Additional characteristics for each species can be found in Appendix B.

Table 2.1. Plant species used in this study.

Family	Species	Habitat ^a	LF ^b	Consumers					
				BRD	MON	CHP	GOR	ELE	UNK
39	Anacardiaceae	<i>Pseudospondias longifolia</i>	Marantaceae forest	mc	1	2	1	1	1
		<i>Pseudospondias microcarpa</i>	water	mc	1	2	1	1	1
		<i>Trichoscypha</i> spp.	forest; closed canopy forest	mc		2	2	2	
	Annonaceae	<i>Annickia chlorantha</i>	forest	mc	1	2		1/2	
		<i>Monanthotaxis congoensis</i>	rocky; forest-savanna	cs	1	2	1	1	1
		<i>Uvariastrium pierreanum</i>	Marantaceae forest	mc		2	2	1	1
		<i>Xylopia aethiopica</i>	Marantaceae forest; forest-savanna; disturbed	mc	1	2			
		<i>Xylopia hypolampra</i>	forest	uc	1				
		<i>Xylopia quintasii</i>	Marantaceae forest	mc	1	2			
	Burseraceae	<i>Dacryodes normandii</i>	forest	mc		2	1	1	1
		<i>Santiria trimera</i>	closed canopy forest	mc		1		1	1
	Calophyllaceae	<i>Mammea africana</i>	forest	uc		2	2	2	1
	Cannabaceae	<i>Celtis tessmannii</i>	forest	uc	2	1	1	1	1
	Clusiaceae	<i>Pentadesma butyracea</i>	forest	mc		2	2	2	1
	Ebenaceae	<i>Diospyros dendo</i>	forest (rocky)	lc		2	1	1	1
		<i>Diospyros mannii</i>	forest	mc		2	2	1/2	1
		<i>Diospyros polystemon</i>	forest	uc		2	1	1	1
		<i>Diospyros zenkeri</i>	rocky	mc			1	1	
	Fabaceae	<i>Detarium macrocarpum</i>	Marantaceae forest	uc		2	2	2	1
		<i>Dialium lopense</i>	forest	mc		2	1	1	1
		<i>Parkia</i> spp.	forest	uc			2	2	1
	Humiriaceae	<i>Sacoglottis gabonensis</i>	forest-savanna	uc				2	1
	Irvingiaceae	<i>Irvingia gabonensis</i>	forest	uc		2	2	2	1
		<i>Irvingia grandifolia</i>	forest	uc		2	2	2	1
		<i>Klainedoxa</i> spp.	forest	uc		2	2	2	1
	Lamiaceae	<i>Vitex doniana</i>	forest-savanna	lc					1
	Lecythidaceae	<i>Scytopetalum</i> sp.	closed canopy forest	lc				1	

Table 2.1, continued.

Family	Species	Habitat ^a	LF ^b	Consumers					
				BIR	MON	CHP	GOR	ELE	UNK
Malvaceae	<i>Cola lizae</i>	Marantaceae forest	mc		2		1		
	<i>Duboscia macrocarpa</i>	forest	mc		1	1	1	1	
Moraceae	<i>Ficus bubu</i>	forest-savanna	ep	1	1	1	1		
	<i>Ficus mucuso</i>	Marantaceae forest	mc	1	1	1	1		
	<i>Ficus recurvata</i>	Marantaceae forest	ep	1	1	1	1		
Myrtaceae	<i>Psidium</i> spp.	savanna	sh	1	1	1	1	1	
Olacaceae	<i>Heisteria parvifolia</i>	forest	mc						1
Phyllanthaceae	<i>Antidesma vogelianum</i>	forest-savanna; water; disturbed	sh	1					
	<i>Uapaca guineensis</i>	forest-savanna; Marantaceae forest (water)	mc	2	2	1	1	1	
	<i>Uapaca</i> spp.	forest	mc	1	2	1	1	1	
Rubiaceae	<i>Nauclea didderichii</i>	forest	uc	1	2	1	1	1	
	<i>Nauclea vanderghuchtii</i>	water	mc	1	2	1	1	1	
	<i>Porterandia cladantha</i>	disturbed; Marantaceae forest	mc	1	2				
	<i>Psychotria</i> spp.	Marantaceae forest; forest-savanna	sh	1	2	1	1	1	
Sapindaceae	<i>Ganophyllum giganteum</i>	Marantaceae forest	uc			1	1		
	<i>Lecaniodiscus cupanoides</i>	Marantaceae forest; rocky (water)	mc						1
Sapotaceae	<i>Gambeya africana</i>	closed canopy forest	mc		2	1	1	1	
	<i>Gambeya subnuda</i>	forest	mc		2	1	1	1	
	<i>Pachystela brevipes</i>	rocky	uc				1	1	
Urticaceae	<i>Myrianthus arboreus</i>	Marantaceae forest; water	lc		2	2	1/2	1	
Vitaceae	<i>Cissus dinklagei</i>	forest	li	2	1	2	2	1	

^a Habitat types: "forest" = both Marantaceae and mixed closed canopy forest; "forest-savanna" = prefers the interface between forest and savanna; other types are self-explanatory.

^b Life form: ep= epiphytic, li= liana, sh= shrub (<7 m height), lc= lower canopy (7 – 15 m), mc= medium canopy (15 – 30 m), uc= upper canopy (>30 m).

¹ Seeds passed without physical damage.

² Seeds dropped from cheek pouches or hands.

SPECIFIC QUESTIONS AND HYPOTHESES

Considering the general themes outlined above, I concentrated on the spatio-temporal aspects of diet and nesting behavior in the western lowland gorilla to characterize the effect of this species on the seed rain in a tropical plant community, in the northeast sector of Lopé National Park, Gabon. This population has already received significant attention with regard to seed dispersal (Tutin et al., 1991a; Voysey, 1995, 1999a,b; Rogers et al., 1998), and nutritional value of some food species in the gorilla diet (Rogers, et al., 1990). In this dissertation, I have attempted to complement that which is already known of gorilla-mediated seed dispersal at Lopé with a complete spatio-temporal perspective, one that considers the entire life history of putatively gorilla-dispersed plant species. Throughout this approach, I have introduced novel methodologies in temporal and spatial modeling. It is my hope that through my descriptions of these methodologies, they will become more accessible to primate ecologists.

My specific objectives in this study were to investigate the following questions:

- What are the primary factors that account for fluctuations in fruit availability in the gorilla diet? In **Chapter Three**, I investigate biotic and climatic correlates that predict the timing and intensity of fruiting in plant species that gorillas consume.
- What are the factors that determine the acquisition and composition of seeds dispersed by gorillas? In **Chapter Four**, I analyze the effect of synchronously fruiting species on the composition and associations of seed species dispersed by gorillas.
- What are the effects of gorilla behavior on the spatial distribution of dispersed seeds, and on plant demographics? In **Chapter Five**, I use spatial point analysis to determine the ecological covariates to gorilla nesting behavior.
- Does the seed-dispersing behavior of gorillas impact the demographic distribution of the trees upon which they feed? In **Chapter Six**, I assess the degree of clumping that exists in seedlings and adults of some gorilla-dispersed species in order to make the link between gorilla behavior and plant demographics.

The strategy for data collection consisted of maintaining long-term datasets on the phenology of Lopé plant species and on the diets of gorillas and chimpanzees from indirect fecal analysis. Because the

objectives of the study were to elucidate processes that occur on a large temporal scale, and because previous studies at the site have shed considerable light on specific aspects of the seed dispersal cycle, I focused on the missing steps in this process, directing much of my fieldwork to vegetative sampling in order to evaluate the factors that relate to the growth and survival of gorilla-dispersed species. As the discovery rate of gorilla feces and nests was limited during my fieldwork, datasets from a particularly productive period of sample collection in gorilla ecology at SEGC (1993-2004) were used to provide information for some of the more general objectives.

I organize this dissertation into four analysis chapters on the topics of fruit and seed source availability, seed contagion in seed rain, gorilla nesting behavior, and the distributions of adult plants at SEGC. In general, the specific methods and analyses used appear in their associated chapter. In Chapter Three, I describe the temporal distribution of fruit availability in gorilla fruit trees in Lopé NP, and determine the abiotic and biotic correlates to this distribution. Results include circular moment statistics that characterize each fruit species analyzed, which in turn, are used in analyses in subsequent chapters. In Chapter Four, I describe factors that affect seed rain (i.e., the numbers of dispersed seeds), and quality (i.e., seed composition and abundance in deposition sites), and make inferences on an important factor in gorilla-mediated seed dispersal; namely, competition among co-dispersed seeds at microsites. In Chapter Five, I analyze the factors that influence the location of gorilla nest-sites, an important microsite for dispersed seeds. Lastly, in Chapter Six, I evaluate the spatial distributions of extant trees across species dispersed by wind, birds, monkeys, and apes. These distributions are compared with those expected from the specific seed shadows in each case. Special consideration is given to the spatial and demographic consequences of dispersal limitation in species that depend on gorillas for long-distance and directed seed dispersal.

CHAPTER III

CORRELATES TO VARIATION IN THE FRUITING PHENOLOGIES OF THE GORILLA DIET: IMPLICATIONS FOR SEED DISPERSAL

INTRODUCTION

The timing and intensity of plant reproductive events can greatly alter the distribution and abundance of fruit resources that are available to the frugivore community in tropical forests. The ability of a frugivore to track these fluctuating resources in space and time is influenced by life-history traits including daily and seasonal foraging behaviors, ranging patterns, territoriality, breeding seasonality, mating systems, social organization, and population densities or biomasses (Clutton-Brock and Harvey, 1977; van Schaik, 1983; Wallace and Painter, 2002).

Conversely, in plants that depend on animals for seed dispersal (zoochory), the spatial distribution of conspecific and heterospecific plants, the size of fruit crops, the timing of fruiting onset, the duration of fruiting seasons, the synchronicity in fruit ripening, the regularity of fruiting cycles, and the nutritional composition and the size of fruits, are all critical plant traits that affect disperser behavior and the effectiveness of the seed dispersal services they provide.

As important as fruit morphology and nutritional composition are to frugivores, fruit selection is greatly influenced by “the timing and duration of fruiting, crop sizes, and neighborhood effects” (Westcott and Fletcher, 2011:652). The study of these recurrent botanical events (phenophases) and their relationship to climatic and biotic environmental factors is phenology (Hudson and Keatley, 2010). In terms of seed dispersal, phenological traits are part of a suite of pre-dispersal traits that also include fruit morphology; and as such, quantifying phenological patterns in dietary foods is an important starting point for evaluating the potential effectiveness of gorilla-mediated seed dispersal in a diverse tropical forest community.

Causality in phenological patterns

The causal factors behind reproductive patterns in tropical plants are important areas of inquiry (Richards, 1952, 1996). The answers are inherently complex, and circularity of causation makes studying them difficult. The onset, duration, and synchronicity of reproductive events in plants are heritable traits (Allard and Hansche, 1964) that will affect all other aspects of life history, including pollination, fruit and seed development, dispersal, germination, and recruitment. Determining which environmental cues trigger, and thus synchronize, reproductive events in tropical plants is never straightforward or certain (Tutin and Fernandez, 1993b), especially since interactions between internal and external factors are likely to confound analyses of the timing of reproductive events (Borchert, 1983). Difficulties notwithstanding, hypotheses do exist.

Biotic hypotheses focus on animal-plant interactions, proposing that simultaneity of flowering, for example, should increase pollination success by increasing the number of potential pollination events and the likelihood of cross-pollination (Frankie et al., 1974; Janzen, 1974; Augspurger, 1981; Turner, 2001). Similarly, synchronous flowering or fruiting might inundate the population of pollen, seed, or seedling predators, ensuring that some diaspores will survive the onslaught (Rathcke and Lacey, 1985; Wheelwright, 1985; Murah and Sukumar, 1993; Curran and Leighton, 2000). Conversely, temporal displacement (i.e., staggering) of flowering or fruiting may reduce competition for a limited set of pollinators or dispersers (Snow, 1965; Smythe, 1970; Stiles, 1977; Devaux and Lande, 2009).

In some cases, fruit ripening may be timed to occur when conditions for dispersal are optimal. Examples include wind-dispersed fruits that mature during dry or windy seasons, or bird-dispersed fruits whose ripening is timed to coincide with the arrival of migratory birds (Leck, 1972; Levy, 1988). The latter case, however, highlights the circularity that is often encountered in biotic explanations, since birds might time their migration to coincide with peaks in ripe fruit (van Schaik et al., 1993).

In summarizing biotic explanations for phenological patterns, pollinators, more than seed dispersers, are expected to exert stronger selective forces on phenological rhythms, since pollinator-flower interactions are, on average, more specialized than those involving frugivores (Wheelwright and Orians, 1982; Gautier-Hion et al., 1985). Since the seeds of most tropical plants are dispersed by more

than one frugivore (polychory), any one disperser is likely to impart only a small selective force on phenological traits. This brings me to the possible climatic factors behind phenological patterns.

In contrast to biotic factors, abiotic influences, including available moisture, solar radiation (insolation), day-length, and temperature, appear to be both more important and pervasive than biotic factors in influencing plant reproductive phenology (Anderson et al., 2005). Rainfall, for example, is an important inducing factor in flowering (e.g., anthesis) in some seasonal tropical forests (Opler et al., 1976). Likewise, peak fruiting is often observed during the wet season in both dry (Ghana: Lieberman, 1982) and moist forests (Foster, 1982; Terborgh, 1983; Heideman, 1989; Tutin et al., 1991a,b; Chapman et al., 1999), presumably because of an increased need for moisture in fleshy-fruit production.

Reproducing early in the wet season might occur if (1) moisture is needed throughout fruit maturation (Lieberman, 1982; Rathcke and Lacey, 1985), or (2) germination requires ever-wet conditions, assuming no seed dormancy. The latter case is supported by results that show that water stress has a negative effect on germination in seasonally dry forests (van Schaik et al., 1993; Justiniano and Fredericksen, 2000).

The effect of rainfall on fruiting phenology is neither clear nor universal, however. For example, no correlation was found between fruit availability and rainfall in the montane forests of Kahuzi-Biega, DRC (Yamagiwa and Basabose, 2006), or Kibale, Uganda (Mitani et al., 2002), and in some forests, fruiting increased throughout the rainy season and even peaked during the dry season (Nyungwe, Rwanda: Sun et al., 1996; Taï, Côte d'Ivoire: Anderson et al., 2005; Kahuzi-Biega, DRC: Yamagiwa and Basabose, 2006).

Adding to the confusion, irrigation experiments on Barro Colorado Island, Panama, failed to demonstrate the importance of water stress as a cue for leaf fall in most species studied, leaving variation in photoperiod, leaf age, canopy structure, relative humidity, or incident radiation as possible constraints on plant phenologies (Wright and Cornejo, 1990). In a comparison of 53 different tropical forests, van Schaik and Pfannes (2005) found that 53% of species flowered within one month of the sunniest month. They argued for an insolation-limitation hypothesis in tropical phenology, stating that flowering (and leaf

flushing) is concentrated during the sunniest times of the year, except when prevented from doing so by water-stress (Van Schaik et al., 1993).

Research results support this theory. For example, synchronous leaf bud break occurred even in the driest months around the spring equinox in brevideciduous and evergreen, spring-flushing species in Costa Rica, Argentina, and Brazil (Rivera et al., 2002). Bud break in these species is therefore determined by variation in day-length (i.e., insolation) and not by seasonality in moisture. Moisture must play a role, however, since spring-flushing species, themselves, are rare in seasonally dry evergreen forests and relatively common in semideciduous tropical forests (Rivera et al., 2002).

Temperature, particularly low temperature, has been shown to be important. Minimum night temperatures in the months leading up to flowering, for example, appears to trigger flowering in eight closely monitored woody plant species at Lopé (Tutin and Fernandez, 1993b). From a ten-year sample, failures in floral induction in these species occurred in years when nighttime lows during the dry season did not fall below 19°C, and aseasonal flowering occurred when unusually low temperatures occurred at other times of the year (Tutin and Fernandez, 1993b). Since many of these species are important in terms of stem densities and frugivore diets, higher than normal temperatures and the subsequent floral failures explained a large part of the variation in amount of fruit available to the frugivore community at Lopé (Tutin and Fernandez, 1993b, Tutin and White, 1998; White, 2001). Similar results have been reported from other regions. For example, a 2°C drop in minimum temperatures over three or more consecutive nights triggers flowering in western peninsular Malaysia (Ashton et al., 1988).

Phenological patterns are complex, and the factors that influence them may be numerous and context-dependent. Any analysis of phenological patterns and their potential causes should be location-dependent, particularly if they are to be useful in (1) assessing the responses of a frugivore community to cyclical variation in fruit availability, and (2) determining the consequences of these responses to seed dispersal services.

A final comment on causality should be made. Despite the pervasive influence of abiotic factors on the timing of tropical plant reproduction (Chapman et al., 2005), evidence of an abiotic environmental trigger does not necessarily preclude an ultimately biotic cause behind reproductive patterns in tropical

plants. “If the timing of a particular phenophases represents an adaptation to pressures exerted by animals, plants are likely to rely on changes in the abiotic environment to provide the trigger” (van Schaik et al., 1993:354).

Variation in the phenological patterns of tropical plants

Despite relatively stable weather patterns, wet tropical tree communities exhibit substantial seasonal and interannual variation in the timing of flowering, fruiting, and leaf flushing (Tutin and Fernandez, 1993b; van Schaik et al., 1993; Anderson, 2001). For example, from long-term data on 173 plant species, Newstrom et al. (1994) graphically described the typical flowering patterns among individuals and populations in Costa Rica. At each organizational level, patterns exhibited a great deal of irregularity and complexity, varying in timing, intensity, and synchronicity.

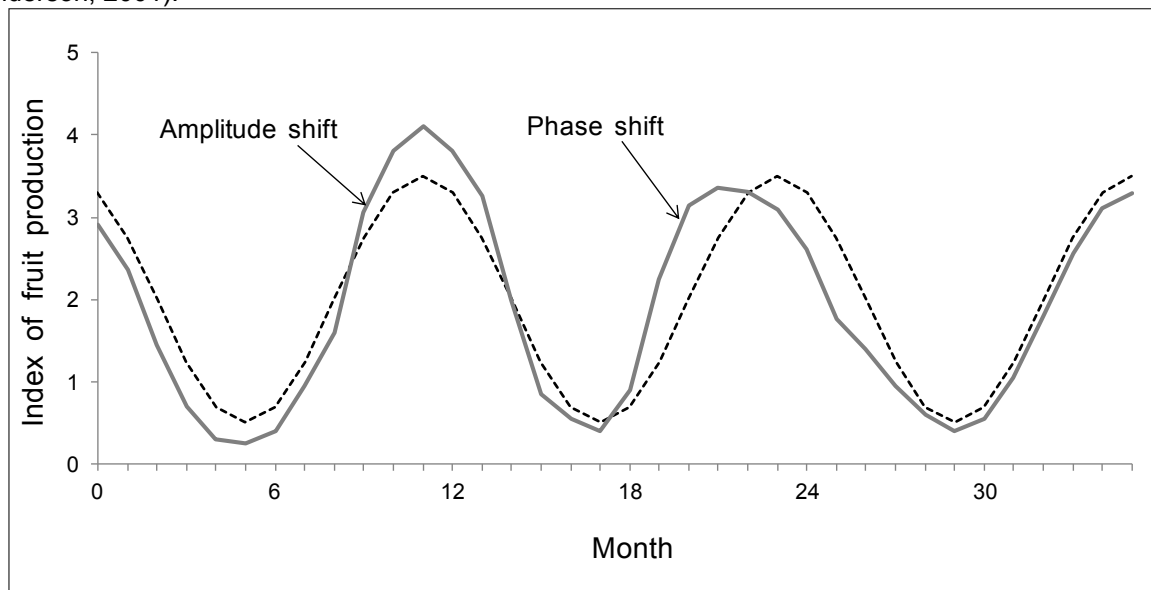
Phenophases generally fell into four frequency categories: continual, sub-annual, annual, and supra-annual. Regularity, which was defined as the variance in cycle length (i.e., one reproductive cycle plus non-reproductive interval) was a secondary descriptor to frequency (Newstrom et al., 1994). Though some species had regular cycles, many species were highly irregular, with sub-annually flowering plants being the most irregular. Regularity, can have a major impact on the abundance of resources available to frugivores, as well as on the seed rain left by dispersers.

Flowering and fruiting schedules that maximize reproductive success over evolutionary time have been adaptively shaped by environmental factors affecting plant growth and reproduction (Anderson, 2001; Anderson et al., 2005). Overlaying these ‘fixed’ schedules is some degree of flexibility in response to short-term changes in the environment. In Figure 3.1, for example, the dashed line is a typical entrained cycle in fruiting activity for a hypothetical plant. The solid line demonstrates the two types of deviations that can occur in response to short-term changes. These include phase and amplitude shifts. Plants can alter the onset (a phase shift), or the intensity and duration (an amplitude shift) of a phenological event (Anderson et al., 2005).

Shifts in amplitude should be more common than phase shifts due to the temporal dependences that exist between consequential phenophases (Anderson et al., 2005). A change in the onset of flowering (a phase shift), for example, should invariably force a change in the timing of fruiting, resulting in

a shift that could undo the selective advantages that have been shaped by the environment with regard to fruit production. A well-adapted plant is more likely to reduce, or abate altogether, a reproductive event under unfavorable environmental conditions, than to delay it until conditions that are more favorable occur. Having outlined the kinds of variations in phenological patterns that exist in a hypothetical tree, I move now to describing the responses of gorillas at Lopé to these variations.

Figure 3.1. Hypothetical entrained (dashed line) and deviated (solid line) patterns in phenology (adapted from Anderson, 2001).



Gorilla responses to variations in fruit availability

Western gorillas always consume, like their mountainous counterparts, large quantities of non-reproductive parts of trees and understory plants (Rogers et al., 2004). These foods, which provide staple nourishment throughout the year, take on particular significance during periods of fruit scarcity wherever gorillas have been studied extensively (Rogers et al., 1988; Williamson et al., 1990; Tutin et al., 1991b; Kuroda et al., 1996; Doran and McNeilage, 1998).

In Lopé, the young leaves and pith of five species belonging to the Marantaceae (arrowroot) and Zingiberaceae (gingers) families are eaten throughout the year by gorillas (Rogers et al., 1990; Williamson et al., 1990; Tutin and Fernandez, 1993a). These include *Aframomum* spp., *Haumania liebrechtsiana*, *Megaphryium velutinum*, *M. macrostachyum*, and *Hypselodelphys violacea*.

In addition to these common food types at Lopé, gorillas exhibit clear preferences for habitats associated with water during the dry season, where they consume large quantities (pith and young leaves) of the aquatic herb, *Marantochloa cordifolia* (Marantaceae) (Tutin et al., 1991b; White et al., 1995). They also consume the leaves and bark (bast) of *Chlorophora excelsa* (Moraceae), a species they generally avoid during other times of the year (Tutin et al., 1991b).

These foods are considered keystone foods, and are distinguished from ‘fallback foods’, in that they are not available year-round. From a nutritional standpoint, gorillas are highly selective in their feeding behavior. They actively select parts that are either the least fibrous and the most proteinous (i.e., leaves), or the most sugary and least tannic (i.e., ripe fruit). When these foods are not available, western gorillas maintain a balanced diet by eating more fibrous and less proteinous leaves and stems, and switching to more fibrous, less succulent fruits that are usually ignored under more bountiful circumstances (Rogers et al., 1988; Nishihara, 1995; Remis et al., 2001; Remis, 2003). At Lopé, for example, gorillas increase their consumption of the fibrous fallback fruit, *Duboscia macrocarpa* (Malvaceae) during ‘bad’ fruiting seasons (Tutin and Fernandez, 1994).

Even during times of high fruit abundance, it is clear that gorillas do not forage as opportunists, adjusting their intakes of a particular food in direct accordance to their abundance in the environment. Rather, they pursue fruit species they prefer, even though they may occur at lower densities and in more specialized or rare habitats than other fruit species, often traveling further and incurring a higher energy cost to obtain them (Williamson, 1988; Doran and McNeillage, 1998). During periods of low fruit, gorillas decrease their day ranges as a direct result of adopting a ‘low-energy’ strategy of eating lower-quality herbaceous foods and fibrous fruits.

Specific research questions

In this chapter, I investigate the climatological and life-history correlates to plant reproductive patterns and community-wide fruit abundances in fruit species that are important in the gorilla diet at SEGC. From eleven years of phenological observations, I model community-level flowering and fruiting in relation to rainfall and temperature. At the species-level, I use circular statistics to calculate within and between-year summary statistics that characterized reproductive phenologies. Gorillas are regular

consumers of all fruit species analyzed, and while some seeds are infrequently predated, not all seed species are swallowed and dispersed to the same degree. Specific questions include the following:

- What are the entrained reproductive patterns in gorilla fruit species at SEGC?
- Do fruit development times, fruit size, or seed size, influence the timing of reproductive events?
- Are the reproductive schedules of species with large fruits and large seeds constrained by environmental conditions, such as moisture availability or insolation?
- Do regeneration strategies and life forms (e.g., canopy strata) in fruit species determine the timing of reproductive events?
- In terms of regularity to entrained phenological cycles, how much shifting in reproductive schedules exists among gorilla fruit species, and is this variation distributed evenly across fruiting seasons, or are there distinct differences between seasons?
- Lastly, at the community-level, what are the climatic predictors of the timing and intensity of flowering and fruiting among gorilla fruit trees?

METHODS

Fruit resource sampling

Sixty-three plant species known to be important resources to sympatric gorillas and chimpanzees have been monitored continually since 1984 in Lopé NP, making it one of the longest, on-going phenology studies in ape ecology. In most cases, phenological data have been collected on at least ten individuals per species. Each month, and for each individual tree in the sample, the relative quantities of new leaves, flowers, unripe fruits, and ripe fruits (from zero to a maximum of four) are recorded by a minimum of two observers using 10 x 40 binoculars. Data collection occurs during the first week of each month, and always over a period of four to seven days (Tutin and White, 1998).

Since longitudinal data are needed to characterize phenological patterns, species were selected for analysis only if they had a minimum of five consecutive years of observations between the years of 1994 and 2004. I chose to analyze this period because it coincides with a period of particularly high sampling effort of gorilla feces at SEGC (see Chapter Four). These data are comprised of 399 trees, from

48 species in 22 families, and across 132 months, representing approximately 49% of the fruit species and 31% of plant species consumed by gorillas at Lopé. In a few cases, two or more closely related species are pooled as morphospecies during data collection due to difficulties in identifying them to species. For example, the group "*Psychotria* spp." includes both *P. peduncularis* and *P. vogeliana*. I refer to all morphospecies as "species" for simplicity in this dissertation.

The number of trees monitored in any month per species varies ($N = 48$ species, $\mu = 7.9$ individuals/species, $\sigma = 2.81$, range = 2-11). Trees that died during the study were replaced with new individuals; thus, the number of trees monitored for a given species in the entire dataset can be slightly greater than the number of trees sampled on any given date.

Taxonomic classification to Family and Order follows that of The Angiosperm Phylogeny Group (APG, 2003), and botanical synonyms are according to Tropicos.org (2012) or the African Flowering Plants Database (2012). Data were not available for July and August of 2000; thus, I have omitted the entire year of 2000 from analyses requiring information from complete years.

Plant species traits

I collected morphological and ecological characteristics for each plant species in the analysis in a variety of ways. In addition to taking measurements in the field, information on species traits are from existing SEGC databases, the published literature, dissertations, guidebooks, floras, and herbaria. Primary sources include White and Abernethy (1997), Flore du Gabon Editorial Committee (1961-2012), Sosef et al. (2006), Tailfer (1990), and Poorter et al. (2004). I assigned traits to species according to a geographical prioritization; namely, (1) local vegetative transect data, (2) field measurements, (3) expert-authored local guides, and lastly, (4) regional floras and herbaria specimens located in the Missouri Botanical Garden in St. Louis, Missouri. I checked for consistency between references in order to obtain reliable data.

Tree species are classified into different life forms based on their maximum height (shrubs $\leq 7\text{m}$, $7\text{m} < \text{small trees} \leq 15\text{m}$, $15\text{m} < \text{medium trees} \leq 30\text{m}$, and large trees $> 30\text{m}$). I also note the maximum diameter at breast height (DBH, in centimeters), broad-scale floristic associations, densities, and basal areas of plant species from White (1992), Ham (1994), and Tutin et al. (1994).

In the species-rich forests of the tropics, several morphological features are closely associated with regeneration guilds and seedling development, the so-called “seedling syndromes”. Regeneration guilds are classified in the literature according to a species’ ability to establish itself under various shade conditions (see Hawthorne, 1995), and a species’ tolerance for shade is positively correlated to adult wood density (Augspurger, 1984; Turner, 2001; van Gelder et al., 2006). I use wood density as a proxy for shade tolerance along the pioneer ↔ shade-tolerant spectrum of Hawthorne (1995). Wood densities (i.e., wood-specific gravities: the ratio between oven-dry weight and green volume) were available for many of the tree species considered here (N= 21) from Gourlet-Fleury et al. (2011). In the absence of species-level wood densities, I assigned densities from information on genus, family, order, or global levels, following the rules described in Gourlet-Fleury et al. (2011).

Following Gautier-Hion et al. (1985), I classified fruit and seed characters with regard to whether they hindered or facilitated consumption as a whole and without regard to their botanical origins of fruit parts. For each species in the analysis, I recorded ripe-fruit morphology, size, structural protection, and color. Fruit morphological types were classified as: CA = capsule (dry dehiscent fruit consisting of more than one carpel, follicle is one carpel), BE = berry (or berry-like, i.e., the many-seeded tomato), APO = apocarp (coming from one pistil/carpel, i.e., indehiscent mericarps in Annonaceae), DR = drupe, PI = indehiscent pod (husk), PO = dehiscent pod, and SY = syncarpic forms (multiple carpellate origin and aggregates).

I classified fruit sizes as small ($S < 0.5$ cm), medium ($0.5 \text{ cm} < M \leq 3$ cm), large ($3 \text{ cm} < L \leq 10$ cm), and very large ($VL > 10$ cm). I recorded the color of the outer skin (exocarp or pericarp) if the fruit was indehiscent and had to be processed prior to consumption, ignoring the color of the actual tissue eaten. In the case of “dehiscent” fruit, such as the arillate fruit in the Annonaceae family, the colors of both the inner wall of the capsule or follicle, and that of the contrasting arillate tissue were reported.

I measured seed lengths along the longest axis and widths along the second longest axis whenever available. Categories of seed sizes were: $A < 0.5$ cm, $0.5 \text{ cm} < B \leq 2$ cm, $2 \text{ cm} < C \leq 4$ cm, and $D > 4$ cm.

Data analyses

Species-level analysis

I use circular vector algebra (Batschelet, 1981) to characterize flowering and fruiting patterns in forty-eight gorilla fruit species. Though used infrequently in the primate literature, the analysis of temporal, recurrent events, as well as directional data on the movements of animals, converge in the field of circular statistics. Circular statistics “is an area of statistics not very much used by ecologists, nor by other researchers from the biological sciences, and indeed not much visited, till recently in statistical science” (Morellato et al., 2010:339).

In an early application of circular statistics to phenology, Milton et al. (1982) tested for asynchronous fruiting in two species of *Ficus*, a genus that is commonly referred to as ‘asynchronous’ (Janzen, 1979). Surprisingly, they found that fruiting, though not entirely synchronous, exhibited consistent ‘fruiting peaks’, and neither species fruited randomly with respect to time or season. Results such as these, would have been difficult to obtain without the use of circular statistics.

Within primate ecology, this tool has been gaining in strength. For example, circular statistics have been used to examine female reproductive seasonality in Neotropical primates (Di Bitetti and Janson, 2000), the Madagascan red-bellied lemur (*Eulemur rubriventer*: Tecot, 2010), red-shanked douc langurs (*Pygathrix nemaeus*) in Lao PDR (Phiapalath et al., 2011), and mandrills (*Mandrillus sphinx*: Setchell and Wickings, 2004). Notable multi-site studies on the seasonality of resource abundance and primate births include van Schaik and Pfannes (2005) and Janson and Verdolin (2005), respectively.

The Rayleigh test is the most commonly used circular tool. It tests for deviations from randomness in mean directions. For example, Joly and Zimmermann (2007) used it to test against uniformity in the directions that Malagasy gray mouse lemurs (*Microcebus murinus*) left their sleeping sites, and Carnegie et al. (2011) used it to investigate the degree of seasonality in fruit abundance and reproductive events in capuchins (*Cebus capucinus*) in Costa Rica. Kamilar (2009) used the length of the circular mean vector, r , as a proxy for rain seasonality in a meta-analysis of the environmental correlates to taxonomic structure of primate communities. Lastly, in a non-primate example of how circular statistics

can be used on a daily scale, circular summaries were used to assess the nightly activities of pacas (*Cuniculus paca*) in southern Brazil (Michalski and Norris, 2011).

Circular statistics: The need for an appropriate statistic

The structures of many ecological datasets are nonlinear. On a linear scale, the difference between an event occurring in the 10th month one year and one in the 2nd month of the next year is recognized as eight months, not four, as it should be. In reality, however, there is no natural start or end to the year (or the day), and measurements that cycle over circular timeframes should be analyzed as 'circular' variables (Jammalamadaka and SenGupta, 2001). The circle can be used to represent one cycle, and the interest of analysis may lie in the timing, duration, or intensity of any event within this cycle.

Calculations

I use circular vector algebra calculations, following Zar (2010), to calculate statistics representing the mean date, duration, and regularity of flowering and fruiting events for each species and year of the study. Each month is converted into an angle between 0° and 360°, corresponding to the midpoint of the first week (i.e., median date of phenology data collection) of each month from the series $a_i = (3.75^\circ, 33.75^\circ, \dots, 333.75^\circ)$, with month $i = (\text{Jan, Feb, ..., Dec})$. The raw data consist of species-level monthly sums of relative scores among individuals in a phenophase, $p_i = (\text{flowering, fruiting, and ripe fruit})$.

The 'core' circular calculations are little more than some simple trigonometry. For example, the mean date (called the angle of central tendency), μ_p , of a flowering or fruiting event for a species in an event-year is calculated as:

$$\mu_p = \arctan\left(\frac{y}{x}\right) \text{ (if } x > 0) \quad \text{or} \quad \mu_p = 180 + \arctan\left(\frac{y}{x}\right) \text{ (if } x < 0)$$

with

$$x = \frac{1}{n} \sum_{i=1}^n (p_i \cos a_i) \quad \text{and} \quad y = \frac{1}{n} \sum_{i=1}^n (p_i \sin a_i)$$

where n is the number of groups (i.e., 12 monthly samples) and a_i is the angle in degrees for month i . The temporal dispersion, or concentration, r_p , of fruiting or flowering around the mean date is:

$$r_p = \sqrt{x^2 + y^2}$$

From the series a_i above, I group data collection dates around the mid-point of the first week in each sampled month. Grouping of angular data occurs when the circle is divided into arcs of equal length, as is the case of phenological data collected k times per cycle. In the case of monthly samples, $k = 12$, and the arc length (λ) = $360^\circ/k = 30^\circ$. While grouping does not affect the mean angle, μ , it does result in a vector length, r , which is too small. I correct for the effect of grouping by applying a correction factor, c , as proposed Batschelet (1981), such that the corrected vector length, r_c , is:

$$r_c = cr_p = \frac{\lambda/2}{\sin \lambda/2} \times r_p = \frac{15^\circ}{\sin 15^\circ} \times r_p$$

Together, μ_p and r_c constitute the two parameters necessary to describe the mean vector of any phenophase, for any species, and in any given event-year; namely (analogous to the location and scale of a probability distribution). The angle of the mean vector, μ_p , indicates the mean date of flowering or fruiting on a circular scale with 0° representing January 1. The length of the mean vector, r_c , is linear and varies between zero and one. It describes the concentration of a phenophase around the mean angle. The length of r_c may also be interpreted as the inverse approximation of the duration of an event; equaling zero when flowering (or fruiting) is uniformly distributed over all months of a year, and one when it occurs in a single month.

For each species, therefore, the matrix of first-order vectors, (μ_{pj}, r_{pj}) , fully characterized the entire phenology dataset, with values indexed on flowering or fruiting, $p(=fl \text{ or } fr)$, and year, $j(=1994, 1995, \dots, 2004)$. In Figure 3.2, I demonstrate the circular distributions for two hypothetical plant species, the first exhibiting an annual cycle in fruiting, the second an asynchronous pattern.

Having characterized the within-year phenology patterns for each species, I next summarize these patterns across years. For example, the average duration of a phenophase for a species across all

sampled years, \bar{r}_p , is calculated as the arithmetic mean of all r_{pj} 's from above. The average central tendency (e.g., the average date of flowering across years) in a species is:

$$\bar{\mu}_p = \arctan\left(\frac{\bar{y}}{\bar{x}}\right) \text{ (if } \bar{x} > 0) \quad \text{or} \quad \bar{\mu}_p = 180 + \arctan\left(\frac{\bar{y}}{\bar{x}}\right) \text{ (if } \bar{x} < 0)$$

where

$$\bar{x} = \frac{1}{N(j)} \sum_{j=1994}^{2004} (\cos \mu_{pj}) \quad \text{and} \quad \bar{y} = \frac{1}{N(j)} \sum_{j=1994}^{2004} (\sin \mu_{pj})$$

and $N(j)$ is the number of years sampled in the calculation.

To characterize the distribution of mean phenophase dates around the overall average date for a species, I calculate circular deviations, defined here as within-year regularity. Since the information contained in the first-order vectors, (μ_{pj}, r_{pj}) , confounds regularity and duration, I calculate regularity, $r_{p,reg}$, for a given phenophase (p), using only the angles, μ_{pj} , as inputs (effectively giving each vector a length of one):

$$r_{p,reg} = \sqrt{\bar{x}^2 + \bar{y}^2}$$

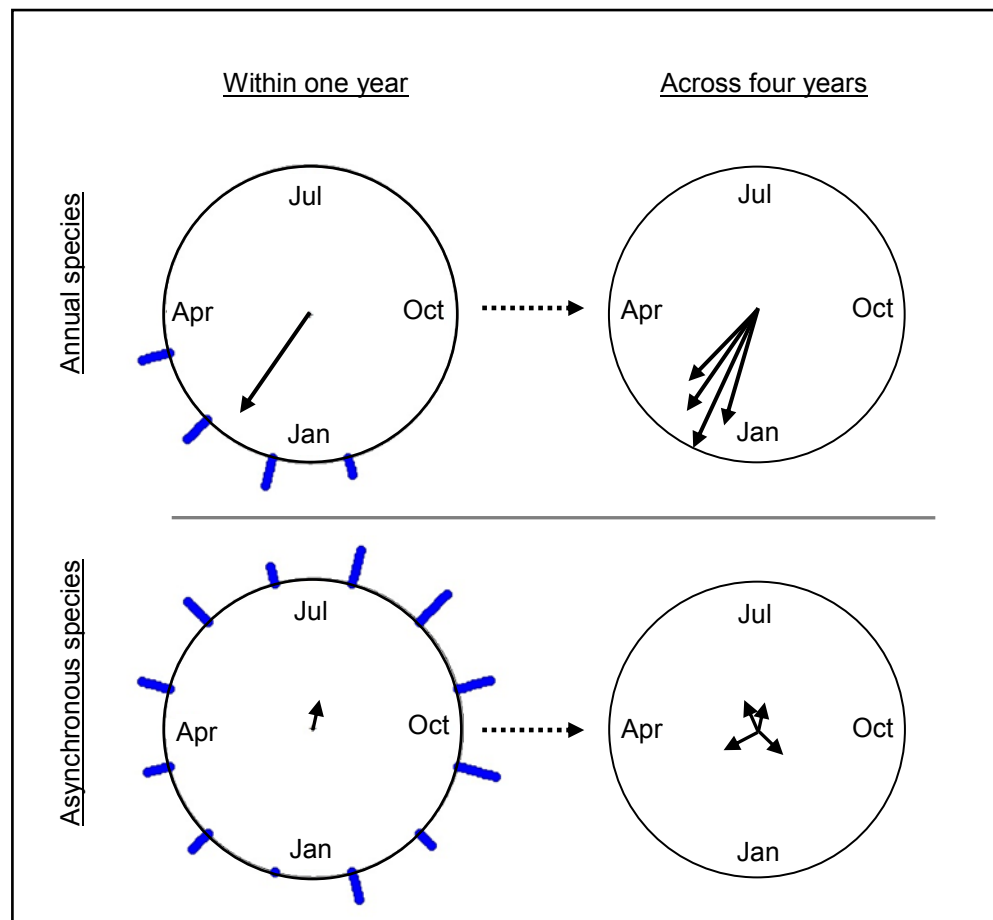
The length of $r_{p,reg}$ represents the regularity in the timing of a phenophase within a species' reproductive cycle. It does not represent the "frequency" with which a species reproduces. For this, I calculate the CV (= standard deviation of cycle lengths / mean cycle length) over the entire 11-year sample. Cycle lengths are defined as the difference in time (i.e., degrees) between consecutive mean flowering or ripe-fruit dates.

For each species and for each phenophase (flowering and fruiting), therefore, the second-order statistics ($\bar{\mu}_p$, \bar{r}_p , and $r_{p,reg}$) represent the mean date of a phenophase, the mean duration of that phenophase, and the variance (i.e., regularity) around the mean date. The CV for each species represents the variation in the frequency that a species reproduced.

In species that reproduce more than once per year, I calculate all of the above statistics using a six-month "year" that uniquely captures an entire flowering or fruiting event. Phenology records were

missing from the dry season months of July and August of 2000. Since a few species do exhibit reproductive activity during these months, I exclude 2000 in second-order statistics since not doing so would have introduced error. Analysis across of the entire dataset (1994-2004), therefore contained ten, not eleven, years.

Figure 3.2. Two example circular distributions of the number of individuals bearing fruit. The upper diagram demonstrates a hypothetical species with an annual reproductive cycle, the lower a species with an asynchronous one. Stacked dots outside the circles are the number of individuals bearing fruit. The direction of the arrows represents the mean date of fruiting, while the length represents the concentration of individuals around the mean date. The longer the arrow is, the shorter the duration of fruit bearing, with an arrow of unit length (1) meaning all individuals bear fruit during the same unique month. In the right-hand set of diagrams, the mean dates and fruiting durations across four years (i.e., four arrows) are shown.



Statistical analyses

I use circular statistics to classify gorilla fruit species into frequency categories (i.e., annual, supra-annual, irregular, and continuous reproducers), and test for significant relationships between

phenological schedules and season: 1st wet (January – May), dry (June – August), 2nd wet (September – December). I use Spearman's rank correlation tests, Watson's two sample U² test for homogeneity, and Kruskal-Wallis χ^2 tests to test for relationships between timing, duration, and regularity, of phenological events in gorilla fruit species and species-level traits (e.g., canopy level, wood density, fruit and seed size). All statistics are performed in the R programming language (R Core Team, 2012), and circular analyses were done using the “circular” package (Agostinelli and Lund, 2011).

Community-level analysis

To analyze dependencies of phenological events in gorilla fruit species on climatic variables, I use generalized least squares models (GLS) to fit variables to a dataset consisting of 40 species x 89 months (from January 1994 to May 2001).

Generalized least squares model

Generalized least squares models (GLS) are applied when either the variances of the observations are unequal (i.e. heteroscedastic), or there is a certain degree of correlation between the response observations. Both of these conditions apply to phenological data where sample values are bound by zero (i.e., count data) and clustered, with strong correlations between samples of high temporal proximity (temporal autocorrelation). In these cases ordinary least squares can be statistically inefficient and give misleading inferences. GLS models are mixed-effect models that, as used here, incorporate a random temporal correlation term, producing more realistic estimates of standard errors and type-I errors in the presence of temporally correlated residuals (Ver Hoef et al., 2001; Dormann et al., 2007).

Response variables

My response variables consist of the monthly number of species flowering and fruiting (= fl, fr), $Sp_{fl,t}$ and $Sp_{fr,t}$, for t (= 1, 2, ..., 89 months). In addition, I calculate an index of monthly ripe fruit abundance, $A_{rf,t}$, among gorilla fruits as a proxy to the availability of ripe fruit to gorillas in the study area. I calculate the fruit abundance index as follows (modified from Anderson et al., 2005):

$$A_{rf,t} = \sum_{k=1}^{89} D_k P_{k,t} I_{k,t} \bar{B}_k M_k$$

where D_k is the density of species k (individuals per km^2) in the study area, $P_{k,t}$ is the proportion of individuals having ripe fruit in species k at time t , $I_{k,t}$ is the average intensity score of all “in-phase” individuals for species k at time t ranging between 0 and 1, \bar{B}_k is the mean basal area of species k (m^2 per km^2), and M_k is a dioecious index equaling 0.5 if male and female organs are on distinct individuals and 1.0 if all individuals have female organs.

The units associated with the fruit abundance index are individuals * square meter of basal area in a standardized square kilometer. A value of $A_t (= 0.1)$ is the equivalent of one monoecious tree per km^2 , bearing maximal ripe fruit and having an average tree basal area of 0.1 m^2 . Playing with the possible variable combinations in the formula, a value of $A_t (= 1.0)$ could be the equivalent of (1) ten individuals having the same parameters as above, (2) twenty dioecious individuals, (3) forty individuals each bearing only one-half maximal ripe fruit, or (4) two monoecious trees each of a large, 0.5 m^2 basal area.

Tree density information in the study area was available for 24 of 40 species (White, 1992; Williamson, 1988); therefore, I fit models to ripe fruit availability based on only these 24 species.

Models

To determine the periodicity of community-wide reproduction in gorilla fruit species, I fit GLS models that include the first Fourier series (the sum of sine and cosine wave functions) as predictors to each of the response variables. Following Anderson et al. (2005), three varying frequency wave lengths are tested, λ (= 6, 12, or 24 months). Predictor variables, $X_{\sin,\lambda}$ and $X_{\cos,\lambda}$, are vectors of length 89 (months), and calculated as:

$$X_{\sin,\lambda} = \left(\sin\left(\frac{2\pi \cdot t}{\lambda}\right), \sin\left(\frac{2\pi \cdot (t+1)}{\lambda}\right), \dots, \sin\left(\frac{2\pi \cdot 89}{\lambda}\right) \right)$$

$$X_{\cos,\lambda} = \left(\cos\left(\frac{2\pi \cdot t}{\lambda}\right), \cos\left(\frac{2\pi \cdot (t+1)}{\lambda}\right), \dots, \cos\left(\frac{2\pi \cdot 89}{\lambda}\right) \right)$$

where t (= 1, 2, ..., 89) is the month of observation, corresponding to the months between January 1994 and May 2001. Once the best-fitting periodicity (6, 12, or 24 months) is determined for each response

variable, I retain the appropriate frequency wavelength in the model and proceed to add additional climatic variables. As is standard practice in fitting Fourier frequencies to time series data, both sine and cosine variables are always entered or removed as a pair, regardless of whether their fitted coefficients are significant.

To determine the effects of climatic predictors on community-wide reproduction, I not only consider their effects in the current month, but also in the 12 preceding months. For example, if T_t^m is the mean minimum temperature in the current month, and T_{t-1}^m the mean minimum for the preceding month, I fit thirteen separate models, regressing each response variable on each of thirteen ($T_t^m, T_{t-1}^m, \dots, T_{t-12}^m$) predictor variables. Whenever a month is found to be significant, I expand the number of months that enter the model around the significant month. For example, if mean low temperature in the third month prior is significant in a model that predicts the number of species fruiting, then two-month blocks (i.e., summed monthly temperatures) that surround the third month prior, i.e., $T_{t-2,t-3}^m$ and $T_{t-3,t-4}^m$, are also tested. If either of these are significant, I then test three-month blocks, and so on. In this way, the predictive qualities of sets of months over singular months can be determined.

In addition to varying the dimensions of the time blocks used, combinations of predictor variables are entered in models, with notation following: T^m = monthly mean low temperature, T^x = monthly mean high temperature, and R = monthly rainfall in millimeters. Notation in response variables follow: SP_{fl} = number of species in flower, Sp_{fr} = number of species in fruit, and A_{rf} = ripe fruit abundance. A typical GLS model is:

$$Sp_{fr,t} \sim \sin\left(\frac{2\pi \cdot t}{12}\right) + \cos\left(\frac{2\pi \cdot t}{12}\right) + T_{t-2,t-3}^m + R_{t-5,t-6,t-7}$$

The number of possible models initially fit to each response variable are numerous. Thirty-nine models have one predictor variable (i.e., 3 variables times 13 time frames each), 507 models have two predictor variables (3 variables times 13 time frames each, taken two at a time), and 2197 models have three predictor variables (3 variables times 13 time frames each, taken three at a time), for a total of 2743

initial models. From these, I choose the best fit models (see model selection and diagnostics section below) and expand the time blocks surrounding the predictors as described above.

An important assumption in least squares regression is that the error terms for observations are independent of each other. As I previously mentioned, autocorrelation of errors exists when measurements taken at adjacent times are more highly correlated than measurements taken several time-points apart (Ting et al., 2008). The presence of autocorrelated errors results in reduced variance estimates of fixed effects, thereby increasing the possibility of type I errors in applying significance to coefficients. To overcome this, I incorporate an autoregressive order-1 covariance structure into the each model. In these so-called AR(1) models, the correlation parameter, ϕ , represents the lag-1 correlation that considers response variable observations one time unit apart, i.e., between $t - 1$ and $t + 1$ (Pinheiro and Bates, 2000).

Model selection and diagnostics

I use Akaike's Information Criterion (AIC) to choose the best-fit candidate models from the initial model sets, as well as to arbitrate between subsequent "expanded" models. AIC is an objective measure to find the predictor variables that explain most of the variation of the dependent variable in relation to the number of variables included in the model (Quinn and Keough, 2002). In cases where model AIC's are similar (i.e., within 4 AIC units), I use a combination of graphical representations of residuals to arbitrate among non-nested models (Pinheiro and Bates, 2000), and likelihood ratio tests among nested ones. I consider a model appropriate when the assumption of normality of residuals is satisfactorily met by visual inspection (Minder, 2012).

In the case of likelihood ratio tests, models must first be refit using maximum likelihood estimates, since fitted AR(1) models use restricted maximum likelihood (REML) in order to produce unbiased estimates of the random variance component. In running these tests, I "fixed" the correlation parameter (ϕ) of the more general model to that of the more specific model, as suggested by Pinheiro and Bates (2000).

Once the final best-fit model to each response variable is determined, I could test for the significance of the Fourier series by removing it and observing the behavior of its residuals and AIC.

Similarly, I test for the significance of the correlation structure using the likelihood ratio test on REML estimated models, with and without the AR-1 term.

I report the final fitted coefficients from the best-fit models using maximum likelihood and Type-III sum of squares. Type-III estimates provide the most conservative confidence intervals for fixed effects since coefficients are estimated only after all other predictor coefficients have already entered the model.

Prior to running models, I transform variables to approximate normality. Monthly rainfall data are Poisson-distributed (in addition to being slightly zero-inflated), and are transformed using the square-root of $R_t + 1$. All response variables and remaining climatic (predictor) data have log-normal distributions and are Ln-transformed. Model regressions and goodness-of-fit tests are performed in the R programming language (R Core Team, 2012). I fit GLS models using the “nlme” package (Pinheiro et al., 2012).

RESULTS

Species-level patterns

Circular variables and some general descriptions

For a list of the 10-year averages of circular variables for the forty-eight species, see Table 3.1. The mean vector lengths for fruiting and flowering (\bar{r}_{fl} and \bar{r}_{fr}) are strongly correlated with actual phase durations in months ($y = -12.912 \bar{r}_c + 14.341$, $R^2 = 0.883$); thus, vector lengths can be converted into months. Characteristics of the plant species in this analysis, including life-form, densities, biomasses, maximum DBH, fruit size and color, seed size, seed fate, and importance in the gorilla diet are in Appendix B.

Using the statistics from Table 3.1, I classify gorilla fruits into thirty-five annual, five asynchronous, five sub-annual, one staggered, and two supra-annual producers. In terms of fruit types, thirty-four are succulent drupes or berries (including two “berry-like” apocarpic forms from the Annonaceae family), five are capsules (including three “indehiscent capsules” that have sugary arils, again from the Annonaceae family), three are indehiscent, leguminous pods (considered to be “drupaceous” with fleshy pulp), and six are syncarpic-aggregate forms. Figure 3.3 shows fruit types

distributed across their average dates of ripe fruit. From this figure, it is clear that the most common types of fruit consumed by gorillas are drupes and berries, and ripe fruit is least common during the months corresponding to the severe dry season (June-August).

In order to categorize species according to phase durations, I define extended fruiting or flowering as ≥ 6 months, short as < 2 months, and long as 2 – 6 months. Species with long periods of ripe fruit availability occur during any month of the year (Fig. 3.4), while short duration species (< 2 months) are never centered during the severe dry season between June-August.

Regularity occurs on two levels, either as variance in within-year mean date ($\overline{r_{reg}}$), or as variance in cycle lengths (measured as the coefficient of variation of fruiting-to-fruiting intervals). I divide within-year regularity into four classes: very regular ($\sigma \leq 15$ days), regular ($15 < \sigma \leq 30$ days), irregular ($30 < \sigma \leq 60$ days), and very irregular ($\sigma > 60$ days). Between-year regularity of a reproductive event is defined as regular ($CV < 0.1$), irregular ($0.1 < CV \leq 0.5$), and very irregular ($0.5 < CV \leq 1.0$).

Table 3.1. Circular variables in forty-eight species consumed by gorillas at Lopé. Mean dates are converted from degrees to days and months. Only ripe fruit regularity, the distribution of mean ripe fruiting dates around the global average, are provided. Species in bold are those that are also analyzed in the community-level regression analyses.

Species	frequency	Mean date				Mean duration		
		$\bar{\mu}_{fl}$	$\bar{\mu}_{fr}$	$\bar{\mu}_{rf}$	$\sigma_{rf,reg}$ (days)	\bar{r}_{fl} (m o n t h s)	r_{fr}	\bar{r}_{rf}
<i>Antidesma vogelianum</i>	sub-annual	2-May	18-May	2-Apr	12	4.3	6.1	2.5
<i>Pseudospondias longifolia</i>	sub-annual	20-Feb	14-May	15-Jul	42	2.4	3.9	2.1
<i>Pseudospondias microcarpa</i>	sub-annual	18-Mar	2-May	15-May	29	3.2	4.7	1.6
<i>Psidium guineensis</i>	sub-annual	3-May	31-May	19-Jul	56	3.5	6.1	4.2
<i>Psychotria</i> spp.	sub-annual	28-Apr	23-Apr	28-Apr	8	2.7	4.3	1.5
<i>Antidesma vogelianum</i>	sub-annual	26-Oct	18-Nov	16-Oct	16	5.6	6.2	3.1
<i>Pseudospondias longifolia</i>	sub-annual	5-Nov	7-Dec	na	na	1.7	3.0	na
<i>Pseudospondias microcarpa</i>	sub-annual	8-Sep	17-Oct	9-Dec	26	3.2	5.0	3.2
<i>Psidium guineensis</i>	sub-annual	3-Oct	9-Dec	23-Feb	10	5.1	5.6	3.8
<i>Psychotria</i> spp.	sub-annual	17-Oct	15-Dec	23-Nov	42	3.9	4.8	2.9
<i>Annickia chlorantha</i>	annual	17-Oct	5-Dec	14-Dec	12	3.1	2.9	2.4
<i>Celtis tessmannii</i>	annual	30-Oct	22-Dec	4-Feb	19	2.9	2.7	1.7
<i>Cissus dinklagei</i>	annual	25-Mar	30-Jun	25-Sep	34	9.8	9.4	4.6
<i>Cola lizae</i>	annual	28-Sep	23-Jan	18-Feb	13	3.9	3.9	2.2
<i>Dacryodes normandii</i>	supra-annual	4-Oct	2-Dec	12-Jan	6	1.4	3.0	1.6
<i>Detarium macrocarpum</i>	annual	2-Oct	13-Apr	11-Aug	31	6.0	12.5	4.9
<i>Dialium lopense</i>	supra-annual ¹	28-Oct	27-Feb	7-Apr	58	3.2	4.7	2.6
<i>Diospyros dendo</i>	annual	19-Oct	5-Feb	12-Apr	19	2.4	5.3	1.8
<i>Diospyros mannii</i>	annual	20-Jul	13-Nov	22-Jan	18	3.9	7.5	2.7
<i>Diospyros polystemon</i>	annual	6-Nov	8-Feb	23-Apr	57	2.0	5.5	1.9

¹ *Dialium lopense*: reproduced each year at the level of species; individuals, however, did not reproduce yearly.

Table 3.1, continued.

Species	frequency	Mean date				Mean duration		
		$\bar{\mu}_{fl}$	$\bar{\mu}_{fr}$	$\bar{\mu}_{rf}$	$\sigma_{rf,reg}$ (days)	\bar{r}_{fl}	r_{fr}	\bar{r}_{rf} (m o n t h s)
<i>Diospyros zenkeri</i>	annual	28-Oct	17-Jan	23-Feb	16	1.9	3.3	1.7
<i>Duboscia macrocarpa</i>	asynchronous	7-May	4-Nov	10-Nov	59	11.7	12.4	10.4
<i>Ficus bubu</i>	asynchronous	3-Sep	4-Sep	5-Jun	94	1.4	5.4	3.6
<i>Ficus mucoso</i>	asynchronous	31-Mar	12-Mar	5-Mar	42	5.0	9.8	7.2
<i>Ficus recurvata</i>	asynchronous	18-Sep	28-Nov	4-Dec	102	2.5	8.9	8.1
<i>Gambeya africana</i>	annual	28-Jan	17-Aug	23-Oct	18	3.8	5.4	2.1
<i>Gambeya subnuda</i>	annual	28-Aug	15-Dec	9-Jan	14	2.6	2.6	1.7
<i>Ganophyllum giganteum</i>	annual	29-Oct	20-Dec	8-Jan	6	1.8	2.2	1.5
<i>Heisteria parvifolia</i>	annual	4-Oct	19-Dec	12-Jan	14	3.6	3.3	2.1
<i>Irvingia gabonensis</i>	annual	22-Sep	30-Nov	6-Jan	42	1.8	3.4	3.3
<i>Irvingia grandifolia</i>	annual	13-Sep	17-Nov	26-Dec	13	2.0	2.7	1.6
<i>Klainedoxa</i> spp.	annual	18-Apr	17-Sep	28-Oct	42	4.2	8.9	6.3
<i>Lecaniodiscus cupanoides</i>	annual	6-Oct	14-Nov	26-Dec	11	1.5	2.5	1.5
<i>Mammea africana</i>	annual	30-Sep	10-Jan	24-Feb	16	1.5	3.5	1.9
<i>Monanthotaxis congoensis</i>	annual	9-Dec	21-Mar	13-May	42	6.8	7.3	5.7
<i>Myrianthus arboreus</i>	annual	29-Oct	24-Mar	20-Mar	86	5.7	12.6	5.6
<i>Nauclea didderichii</i>	annual	7-May	18-Aug	18-Oct	27	3.5	6.3	1.9
<i>Nauclea vanderghuchtii</i>	annual	3-May	17-Aug	26-Oct	22	3.1	7.6	3.7
<i>Pachystela brevipes</i>	annual	16-Jul	4-Nov	26-Jan	82	5.0	7.0	5.9
<i>Parkia</i> spp.	annual	22-Dec	6-Feb	15-Feb	15	5.2	4.1	3.4

Table 3.1, continued.

Species	frequency	Mean date				Mean duration		
		$\bar{\mu}_{fl}$	$\bar{\mu}_{fr}$	$\bar{\mu}_{rf}$	$\sigma_{rf,reg}$ (days)	\bar{r}_{fl}	r_{fr}	\bar{r}_{rf} (m o n t h s)
<i>Pentadesma butyracea</i>	annual	1-Jun	3-Oct	3-Dec	21	7.6	9.1	4.5
<i>Porterandia cladantha</i>	annual	3-Jan	13-Jun	2-Oct	14	3.3	11.5	3.8
<i>Sacoglottis gabonensis</i>	annual	11-Jan	28-Jun	21-Sep	21	6.0	9.7	4.2
<i>Santiria trimera</i>	annual	18-Oct	14-Dec	7-Jan	10	2.7	2.8	1.6
<i>Scytopetalum</i> sp.	annual	6-Jan	22-Jun	14-Aug	56	5.0	4.1	2.3
<i>Trichoscypha</i> spp.	annual	14-Sep	9-Oct	21-Nov	56	2.9	5.0	3.3
<i>Uapaca guineensis</i>	annual	19-Feb	2-Jul	23-Oct	60	5.9	9.9	5.5
<i>Uapaca</i> spp.	annual	9-Feb	21-Jul	24-Oct	19	4.0	12.0	5.3
<i>Uvariastrum pierreanum</i>	annual	2-Sep	25-Dec	17-Feb	18	5.5	7.4	3.4
<i>Vitex doniana</i>	annual	6-Apr	25-Jul	21-Sep	16	2.6	6.2	3.3
<i>Xylopia aethiopica</i>	staggered	5-Oct	12-Jun	7-Aug	63	8.9	9.2	5.3
<i>Xylopia hypolampra</i>	asynchronous	22-Feb	31-Jul	30-Aug	70	9.6	12.6	11.5
<i>Xylopia quintasii</i>	annual	2-Feb	11-Jul	28-Aug	29	4.5	6.7	4.1

Figure 3.3. Fruit types of all species distributed according to their ripe-fruit central tendencies. Sub-annual (bimodal) species are represented twice (N= 52). Data on the 2nd fruiting season in *Pseudospondias longifolia* were insufficient to include in the figure.

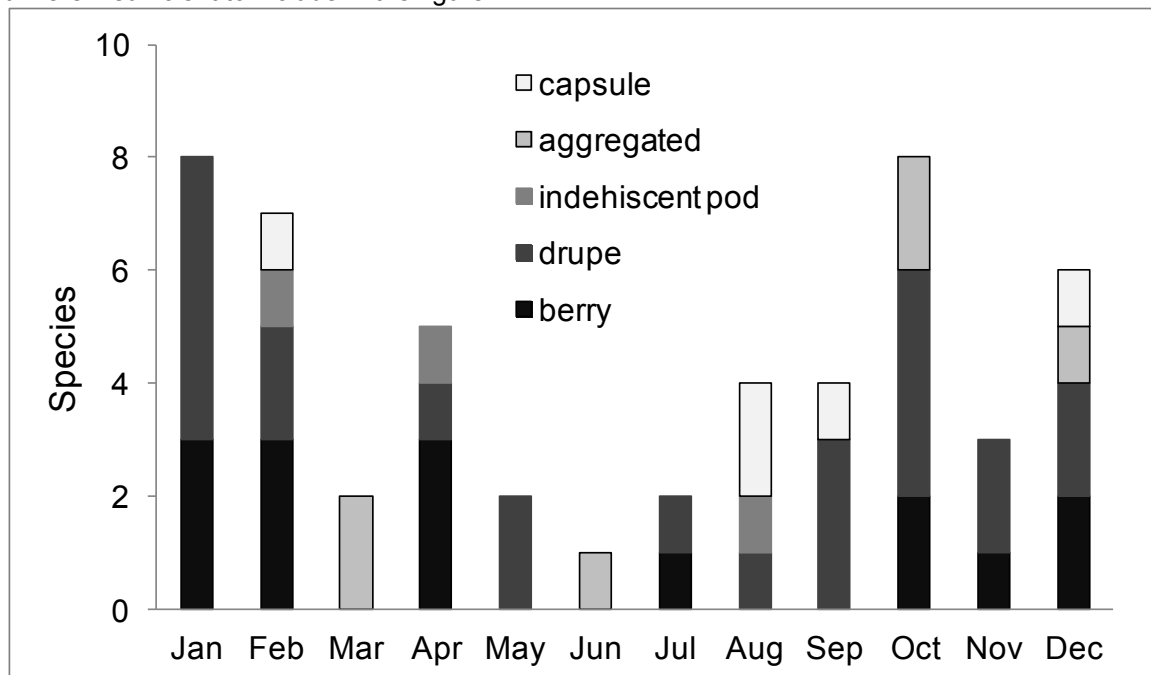
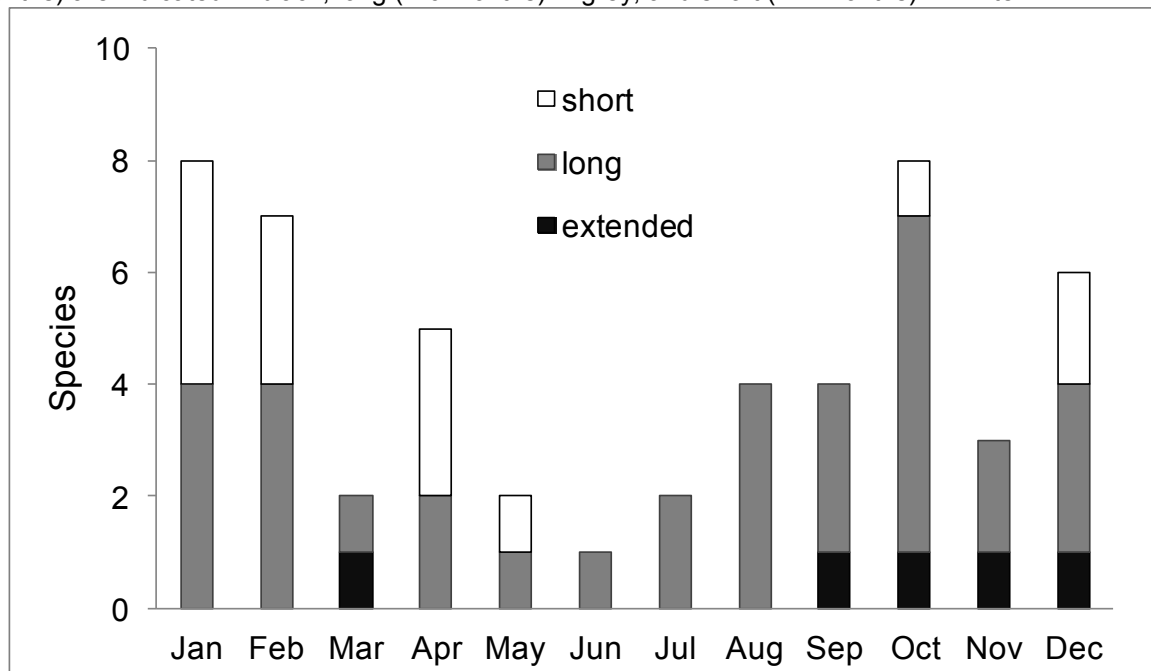


Figure 3.4. Distribution of species according to their ripe-fruit mean dates and phase durations. Extended (> 6 months) are indicated in black, long (2-6 months) in grey, and short (< 2 months) in white.

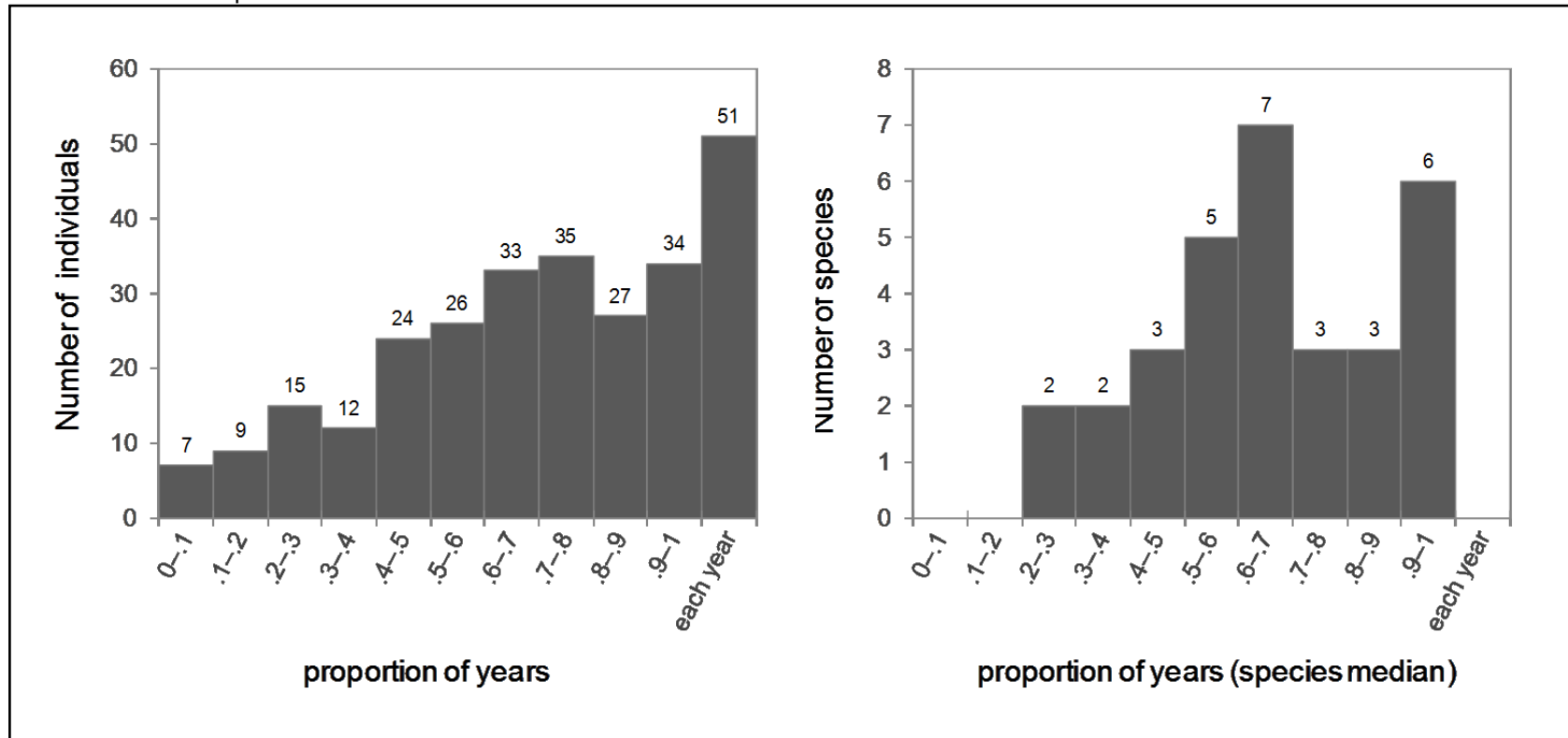


Excluding sub-annual species and one species with insufficient data (N= 42), 38% of species have within-year flowering schedules that are very regular, 31% are regular, 17% are irregular, and 14% are very irregular. In terms of fruiting (N= 43), 19% are very regular, 46% are regular, 21% are irregular, and 14% are very irregular. And, in terms of ripe fruit availability (N=43), 26% of species are very regular, 32% of species are regular, 28% are irregular, and 14% are very irregular. Within-year regularity in flowering is strongly correlated with between-year regularity ($\overline{r_{reg}}$ correlated with CV_{fl} , Spearman's $\rho=0.5980$, $p<0.0001$, $N=42$); the same was true for ripe fruit ($\overline{r_{reg}}$ correlated with CV_{rf} , Spearman's $\rho=0.4214$, $p=0.0054$, $N=42$).

Most species have at least one individual reproducing in each year. In species having at least 5 routinely sampled individuals, 89% flowered in greater than 90% of years (Fig. 3.5). Supra-annual reproducers are notably rare in the gorilla diet. Exceptions include *Dacryodes normandii*, which reproduce at intervals greater than one year, and *Dialium lopesense*, which produce large crops only once every two to three years.

Individually, however, plants do not reproduce frequently, nor do they every year (see Fig. 3.5). Among two-hundred seventy-three individuals across thirty-one annually reproducing species, only 19% of individuals flowered in each year, and 2.6% of individuals either never flowered, or flowered in less than 10% of years. While constraints controlling reproductive rates may be operating at the individual level, species may also differ in this trait. Using the median proportion of years that individuals within a species reproduced, only 29% of annual species reproduced in greater than 80% of years, 48% reproduced in 50-80% of years, and 23% in less than 50% of years. Reproduction is not frequent, therefore, at either the individual or the species levels.

Figure 3.5. Proportion of years that individuals of annually-reproducing species reproduced based on flowering phenology ($N_{\text{years}} = 11$, $N_{\text{ind}} = 273$, $N_{\text{species}} = 31$). Left: Frequency distribution of the proportion of years that an individual tree flowered. Right: The median value across individuals within a species.



Phenology patterns in gorilla fruit species

Based on species mean dates, flowering is evenly distributed between the two wet seasons, with twenty species (thirteen annual, five sub-annual, and two asynchronous) in the 1st wet season (January-May), and twenty-three species (sixteen annual, four sub-annual, two supra-annual, and one asynchronous *Ficus* sp.) in the 2nd rainy season (September-December). Few species (six annual, one sub-annual, and one asynchronous *Ficus* sp.) flower during the long dry-season (mid-June to mid-September; Fig. 3.6-A).

Nearly continuous flowering patterns were observed in *Duboscia macrocarpa*, and extended flowering (6-9 months in duration) occurred in *Monanthotaxis congoensis*, *Pentadesma butyracea*, *Xylopia aethiopica*, *Xylopia hypolampra*, and *Cissus dinklagei*. A substantial cluster of short duration species exists around the onset of the rains in September and October, a period that coincides with the southerly passing of the sun. Flowering at other times appears more uniformly distributed in terms of mean dates and durations. However, there is a notable absence in flowering from mid-May to mid-August, and mid-November to December, periods that correspond to drier conditions.

In all species, fruit development lasts longer than two months duration. Excluding extended species, the number of species with mean dates in the 2nd rainy season is fifteen (ten annual and five sub-annual) compared to only ten in the 1st rainy season (six annuals, three sub-annuals, and one supra-annual; Fig. 3.6-B). During the severe dry-season, species with long development times (between 2 and 6 months) number only two annuals (*Gambeya africana*, and *Scytoperalum* sp.) and one asynchronous species (*Ficus bubu*). A notable cluster of 13 species are in mid-development immediately prior to the minor dry season in January-February, corresponding well to the cluster in flowering at the beginning of the 2nd wet season.

Fifty percent of species (N= 24/48) have extended fruiting durations (i.e., > 6 months), and twelve are greater than 9 months. *Antidesma vogelianum* and *Psidium* spp. have bi-annual fruiting schedules and fruiting durations of approximately six months; thus, individuals in these species are at some stage of fruit development year-round.

Ripe fruits (Fig. 3.6-C,D) are visually more ephemeral in terms of duration than either flowers or fruit development, but appear less evenly distributed over the year. Of those species with short periods of availability (N=14), all but one species (*Diospyros polystemon*) have regular or very regular mean dates (ten annuals, one supra-annual, and two sub-annuals), and all of these occur between mid-October and mid-May, outside the severe dry season. Ripe fruit mean dates in eight species (19%) occur during the severe dry-season (*Detarium macrocarpum*, *Scytopetalum* sp., *Xylopia quintasii*, *X. hypolampra*, *X. quintasii*, *Psidium* spp., *Pseudospondias longifolia*, and *Ficus bubu*); however, in terms of predictability, each of these are either irregular or very-irregular with mean dates that moved in and out of the dry season, depending on the year. Extended availability of ripe fruit (> 6 months) occurs in five species (12%), suggesting their importance as fallback species within the frugivore community. Of these species, *Duboscia macrocarpa*, two *Ficus* spp., *Klainedoxa* spp., and *Xylopia hypolampra*, are considered as keystone species at Lopé (Rogers et al., 2004).

Figure 3.6 (A-B). Mean dates (central tendencies) and durations of phenological events in gorilla fruit species at SEGC, Lopé National Park (N= 48 species). Months are denoted by capital letters outside the circles, and species are plotted according to their mean vector ($\bar{\mu}_p, \bar{r}_p$). Concentric circles indicate phase duration in months. Symbols: annuals = open circles, supra-annuals = closed circles, sub-annual = cross-hatches, asynchronous or staggered = open triangles. The shaded sector indicates the severe dry season (mid-June to mid-September).

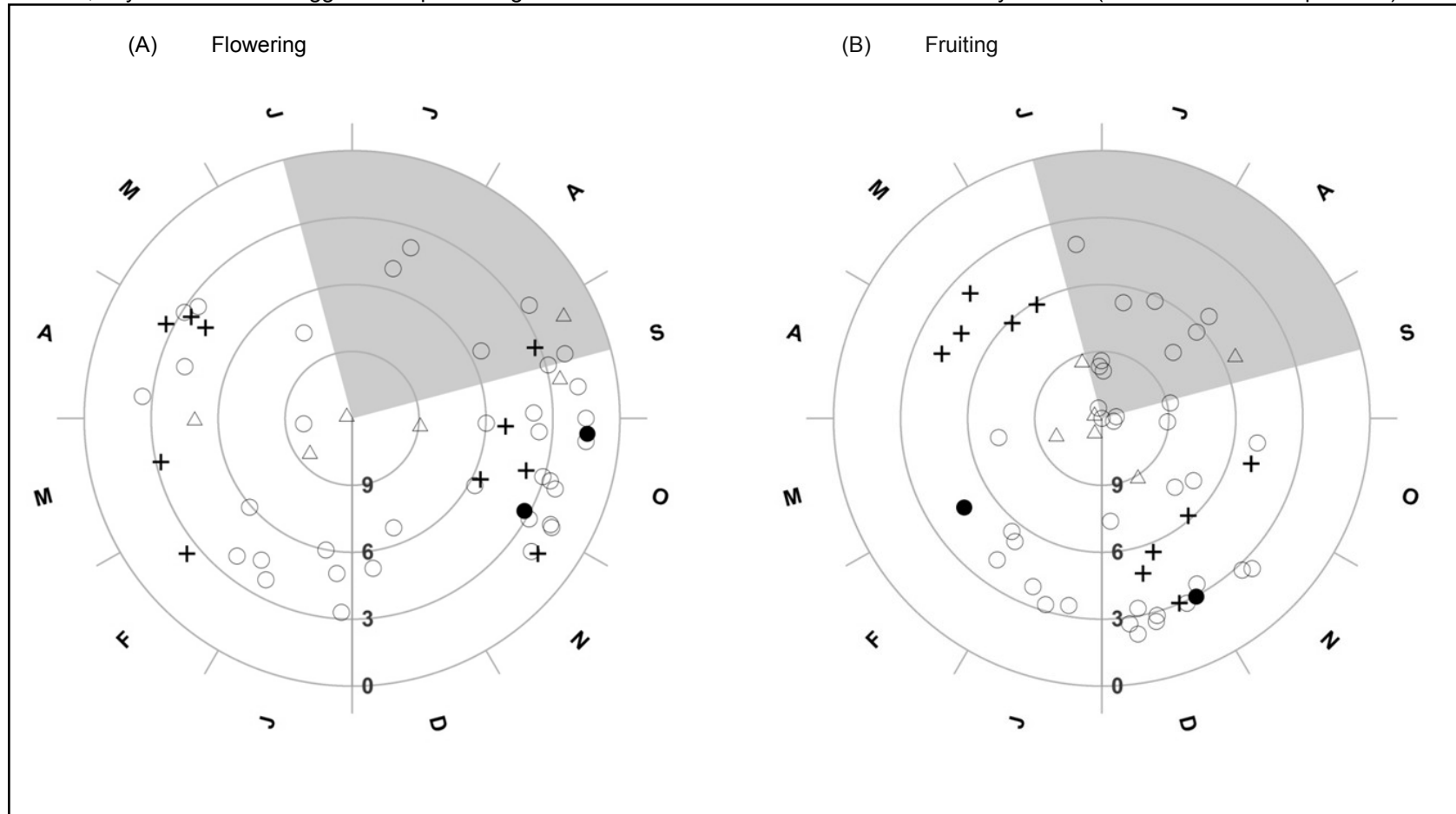
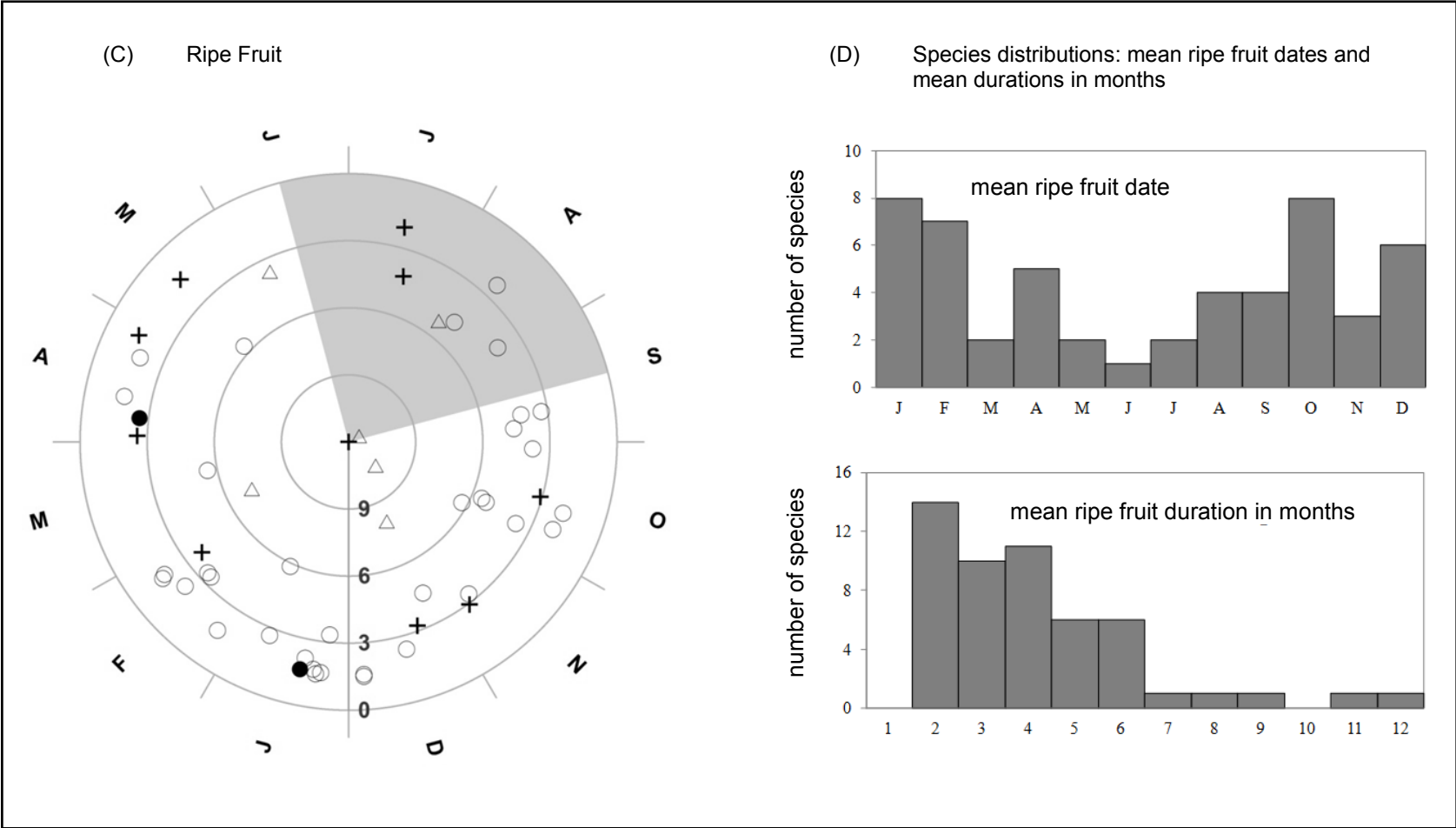


Figure 3.6, continued (C-D).



Covariates to species-level phenology traits

Fruit development times, measured as the average difference (in days) between mean flowering and fruiting dates, are positively correlated with seed (Spearman's $\rho = 0.4569$, $p = 0.0018$, $N = 44$) and fruit sizes (Spearman's $\rho = 0.4687$, $p = 0.0026$, $N = 39$). Unsurprisingly, larger fruits require, on average, longer development times. Under the assumption that species having longer development times should begin their reproductive cycles earlier in the second wet season in order to take advantage of a longer period of favorably wet conditions, I predict that larger fruits and seeds should be negatively correlated to mean flowering dates. Considering only drupaceous and berry-like fruits, mean flowering dates in the second wet season (September-December) are correlated with fruit length (Spearman's $\rho = -0.5310$, $p = 0.0193$, $N = 19$), and seed length (Spearman's $\rho = -0.5301$, $p = 0.0162$, $N = 20$). In the case of first wet season species, flowering dates are not correlated with fruit length (Spearman's $\rho = -0.0389$, $p = 0.9044$, $N = 12$), but are correlated with seed length (Spearman's $\rho = -0.7143$, $p = 0.0056$, $N = 14$). Fruit sizes in species that flower in the 1st wet season are, on average, smaller than those of the 2nd wet season, suggesting that dryer conditions after March constrain the development of large fruits. In summary, larger fruits (and seeds) are associated with species that begin their reproductive cycles earlier in the wet season. These results suggest that available water may be a constraint on species that produce large fruits and seeds.

Under the assumption that seedling shade tolerance (regeneration strategy) influences the timing of reproductive phenologies, I tested whether mean dates in flowering, fruiting, and ripe fruit availability differ between high and low wood densities. Using 0.6 as the density threshold between groups, mean dates in flowering, fruiting, or ripe fruit, are not significantly different between high and low wood-density categories (Watson's two sample U^2 test for homogeneity, Flowering: $U^2 = 0.0654$, $p > 0.10$, $N = 44$; Fruiting: $U^2 = 0.0503$, $p > 0.10$, $N = 44$; Ripe Fruit: $U^2 = 0.0455$, $p > 0.10$, $N = 44$). Regularities in the mean dates of phenophases are also not significantly different between density groups (Flowering: $\chi^2 = 0.3181$, $df = 1$, $p = 0.5727$; Fruiting: $\chi^2 = 0.2075$, $df = 1$, $p = 0.6487$; Ripe fruit: $\chi^2 = 0.297$, $df = 1$, $p = 0.5858$). Together,

these results suggest that shade-tolerance in seedlings (wood density, by proxy) does not influence the timing or regularity in a species' reproductive schedule.

Life form is expected to affect the timing of phenophases. For example, Chapman et al. (1999) found that fruiting peaks in mid-story and emergent trees were temporally offset in Uganda, concluding that both groups were therefore of critical importance to the frugivore community since together they provided a sustained period of fruit availability. To test this, I group life forms into two strata (shrub + lower canopy, and middle + upper canopy, species) and test for differences in mean phenophase dates. Lianas, climbing shrubs, and epiphytic types are excluded. Mean flowering and fruit development dates are not significantly different across forest strata (Watson's two sample U^2 test for homogeneity: Flowering: $U^2 = 0.0746$, $p > 0.10$; Fruiting: $U^2 = 0.0908$, $p > 0.10$). However, mean dates in ripe fruit availability are significantly different (though only slightly) across strata ($U^2 = 0.1864$, $p < 0.10$) with upper canopy species (> 15 m in height) bearing ripe fruit more often in the 2nd wet season (September-December), and lower canopy species more evenly distributed throughout the year.

To determine whether the two rainy seasons differ in terms of within-year regularity in phenophases, I test whether the circular deviations around the mean dates vary between the two wet seasons (January-May, and September-December). Within-year flowering regularities are nearly significant between seasons, with first season species having greater variation in mean dates (Flowering: Kruskal-Wallis $\chi^2 = 3.3654$, $df = 1$, $p = 0.0666$). Deviations in fruiting and ripe fruit dates are not significant between the seasons (Fruiting: $\chi^2 = 0.0255$, $df = 1$, $p = 0.8732$; Ripe fruit: $\chi^2 = 2.0158$, $df = 1$, $p = 0.1557$). Since the rains of the 1st season appear to be more variable than in the 2nd season, these results suggest that available water might be a constraint on flowering, however, the effect of variation in cloud cover and insolation can not be ruled out.

Between-year regularities (CV of flower-to-flower intervals) of species are not significantly different between the wet seasons (mean flowering dates: $\chi^2 = 1.445$, $df = 1$, $p = 0.2293$; mean fruiting dates: $\chi^2 = 0.4704$, $df = 1$, $p = 0.4928$; mean ripe-fruit dates: $\chi^2 = 0.082$, $df = 1$, $p = 0.7746$). Since ripe-to-ripe fruit intervals are expected to vary more than flower-to-flower intervals due to variation in fruit development times, fruit abortion, and the effects of fruit or seed predation, I also test for differences in

ripe-to-ripe fruit intervals between seasons. Again, no differences in ripe-ripe fruit intervals between wet seasons are observed (flowering: $\chi^2 = 0.7609$, $df = 1$, $p = 0.3831$; fruiting: $\chi^2 = 0.2445$, $df = 1$, $p = 0.621$; ripe fruit: $\chi^2 = 0.7321$, $df = 1$, $p = 0.3922$).

These results suggest that within- and between-year regularities in species are evenly distributed between the two wet seasons, with neither season emerging as the more variable one (in terms of a species' fidelity to their "entrained" reproductive schedule). Although regularity among species does not appear to be seasonal, a great amount of variation in ripe-fruit abundance does exist, at both the intra- and inter-year scales, as we shall see in the next section.

Community-level patterns

Forty species are used in regression analyses to test for significance among climatic covariates in predicting community-level phenology patterns. In all response variables, the periodicity that most closely fit the data is a 12-month cycle. A Fourier wave frequency of $\lambda = 12$ is therefore entered into all models below.

Flowering

The model that best fit the number of species in flower includes the cumulative monthly mean low temperature in the preceding 2-4 months and rainfall in the preceding 3rd month:

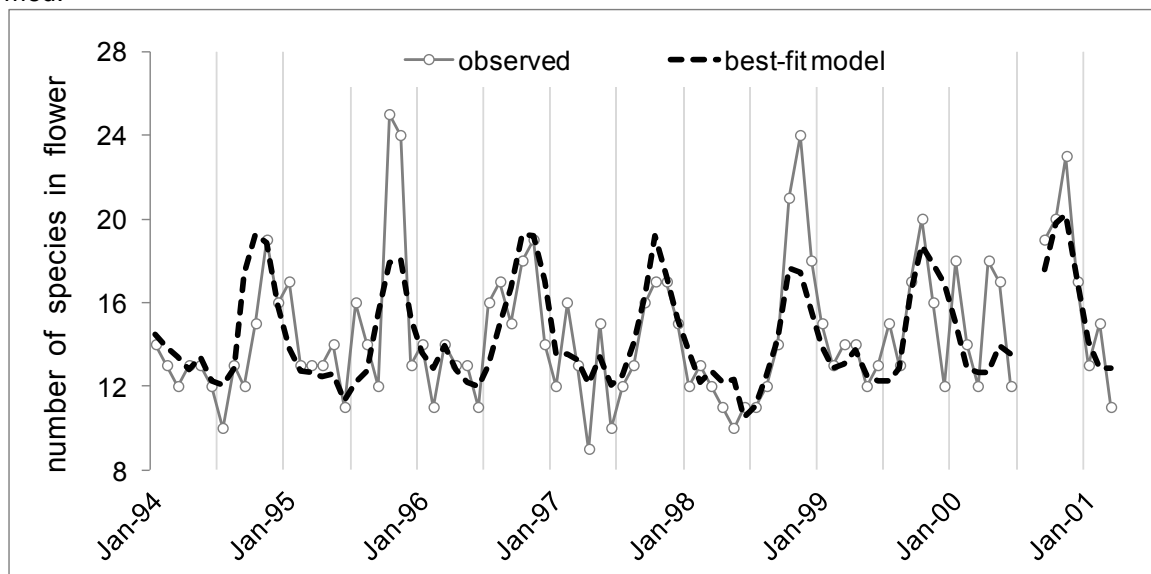
$$\log Sp_{fl} \sim 14.173 - 0.065(X_{sin}) + 0.061(X_{cos}) - 2.736(\log T_{t-2,t-3,t-4}^m) - 0.010(\sqrt{R_{t-3}})$$

Table 3.2 shows significance levels for model coefficients. The autoregressive order-1 covariance structure is not significant (Likelihood ratio test = 1.086, $df = (6, 7)$, $p = 0.2974$) and is therefore removed. The Fourier frequency is deemed necessary. A consistent maximum in annual flowering occurs between October and November (Fig. 3.7), with a less intense and highly variable peak occurring sometime between January and June. The best-fit model predicts reasonably well the minor shifts in the location of peak flowering, as well as the modest changes that occur in flowering durations (i.e., widths of peaks).

Table 3.2. Predictor variables of the best-fit model to the number of species in flower (Ln-transformed). The autoregressive order-1 term is not significant. Estimates are from a Type III test of fixed effects. P-values are from a model fitted using Maximum Likelihood.

Source	Estimate	Std. error	DF-error	F-value	P-value
Mean low temp. $\log T_{t-2,t-3,t-4}^m$	-2.736	0.9060	80	8.580	0.004
Rainfall $\sqrt{R_{t-3}}$	-0.010	0.0039	80	6.597	0.012
$X_{\sin,\lambda=12}$	-0.065	0.0254	80	6.106	0.016
$X_{\cos,\lambda=12}$	0.061	0.0320	80	3.398	0.069

Figure 3.7. The number of species in flower and the best-fit model. Predicted values are reverse-transformed.



Substantial noise is evident in the empirical flowering values, with radical amplitude differences occurring between sequential months. Some of this noise may be explained by the temporal resolution of data collection, since flower lifespans may be extremely brief, and intensities may vary on a scale that is shorter than the frequency of phenology monitoring. Additionally, flowers that are difficult to see (i.e., tiny flowers, or those positioned on the distal end of branches) may be underestimated. The best-fit model is notably unable to predict some of the extraordinary spikes in flowering, particularly those of 1995 and 1998 (see Fig. 3.7).

Vagaries notwithstanding, over the range of observed temperatures, a 1% increase in the cumulative monthly mean low temperatures in the preceding two-four months yields a 2.73% reduction in number of species flowering.

Fruiting

The best predictors of the number of fruiting species are cumulative monthly mean low temperatures in the preceding 4-6 and 10-12 months, and rainfall in the 11th month prior:

$$\log \text{Sp}_{\text{fr}} \sim 24.76 - 0.003(X_{\text{sin}}) - 0.162(X_{\text{cos}}) - 4.436(\log T_{t-4,t-5,t-6,t-10,t-11,t-12}^{\text{m}}) \\ - 0.005(\sqrt{R_{t-11}})$$

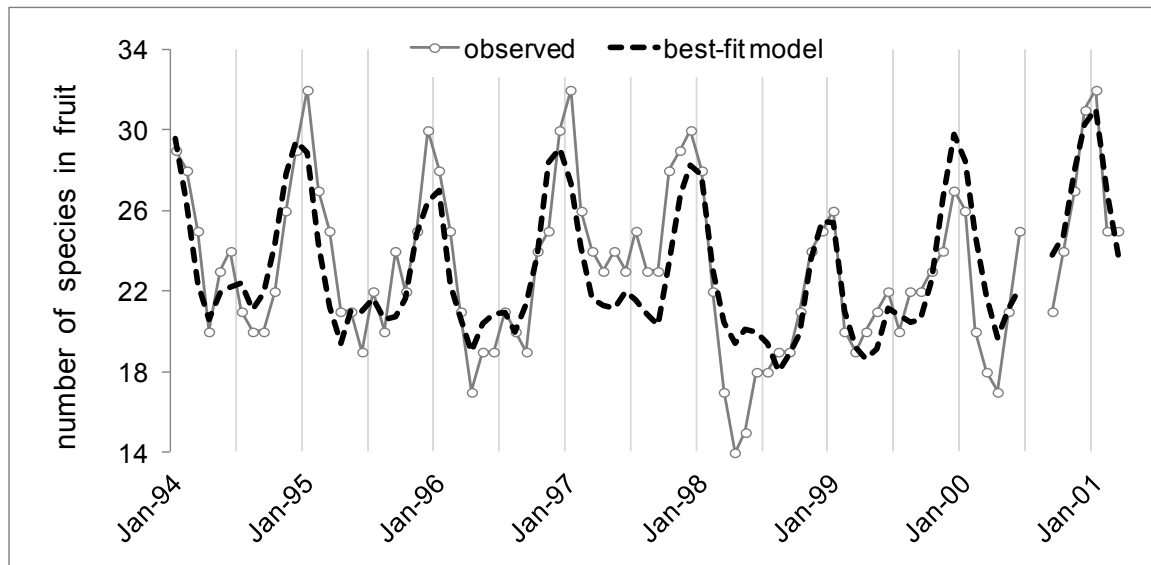
The autoregressive order-1 covariance structure is significant in the best-fit model (Likelihood ratio test= 38.709, df= (6, 7), $p < .0001$), as were the trigonometric terms. Model coefficients are shown in Table 3.3.

Table 3.3. Predictor variables of the best-fit model of the number of species in fruit (Ln-transformed). The autoregressive order-1 term is significant. Estimates are from a Type III test of fixed effects. P-values are from a model fitted using Maximum Likelihood.

Source	Estimate	Std. error	DF-error	F-value	P-value
Mean low temp. $\log T_{t-4,t-5,t-6,t-10,t-11,t-12}^{\text{m}}$	-4.436	0.990	80	18.904	<.0001
Rainfall $\sqrt{R_{t-11}}$	-0.005	0.002	80	4.935	0.029
$X_{\text{sin},\lambda=12}$	-0.003	0.022	80	0.019	0.892
$X_{\text{cos},\lambda=12}$	-0.162	0.023	80	44.857	<.0001

The observed number of species in fruit and fitted values are displayed in Figure 3.8. A consistent annual maximum in fruiting occurs each December – January, with a second, lesser, and more variable peak occurring in the middle of the year. The best-fit model predicts peak fruit timing and intensity remarkably well. However, a notable overestimation of fruiting nadirs occurs between March and May in some years, including the extraordinary drop in fruiting between January and July of 1998.

Figure 3.8. The number of species in fruit and the best-fit model. Predicted values were reverse-transformed.



Developing fruit increases dramatically after the start of the September/October rains, peaking in the middle of the brief, mild dry season (January – February). By the end of this dry season (March), fruiting decreases substantially, and decreases in some years (i.e., 1996, 1998, 2000) to global minima of 14-17 out of 40 species in April. Over the range of observed temperatures, a 1% increase in the cumulative monthly mean low temperatures in the preceding 4-6 and 10-12 months yields a 4.44% reduction in the number of species fruiting.

Ripe fruit abundance in Marantaceae forest

Stem densities and basal areas in Marantaceae forest were available for twenty-four species analyzed here (White, 1992; Ham, 1994; Tutin et al., 1994). In order to ensure that values correspond to the taxonomic levels collected during phenology data collection, certain species-level densities and basal areas are summed, giving a Genus-level estimate, e.g., the phenologies of two closely related *Klainedoxa* spp. are simultaneously sampled as one species during data collection. Species found commonly in rare habitats in the study area (i.e., rocky, savanna-forest edge, gallery forest) are not included in this analysis. These include important, albeit localized, gorilla food species such as *Uapaca* spp. and *Diospyros zenkeri*. Given the high abundance of *Cola lizae* in the study site (4720 stems > 15 cm DBH

per km²), this species can bias heavily any abundance index, warranting a special consideration during analyses. From transect data, Voysey (1995) found that only trees ≥ 15 cm DBH produced fruit in this species. Additionally, of those *Cola* trees that were large enough to reproduce, only $24.3 \pm 13.5\%$ of individuals bore fruit (in any one year) among 6 linear transects (Voysey, 1995). For this species, therefore, I adjusted ripe fruit abundances accordingly.

Ripe fruit abundance varies radically throughout the year (Fig. 3.9). The timing of the greatest ripe fruit abundance occurs between January and April (during the 1st rainy season), though notable crop failures were seen in some years (i.e., 1998, 2000). Most of the ripe fruit availability is due to a few common tree species, e.g., large-sized species that have high average basal areas, and species that have a high proportion of simultaneously reproducing individuals, such as *Cola lizae*, *Diospyros polystemon*, *Diospyros dendo*, and *Dialium Lopense*. A period of low ripe fruit abundance consistently occurs during the long dry season, from mid-June to mid-September.

The best predictors of fruit abundance (A_t) are a Fourier wave frequency of 12 months, the monthly mean low temperature in the preceding 6th month, the monthly mean high temperature in the preceding 2nd month, and rainfall in the preceding 3rd month (see Table 3.4):

$$\log A_{rf} \sim 24.76 + 0.515(X_{\sin}) + 0.716(X_{\cos}) - 10.809(\log T_{t-6}^m) - 5.021(\log T_{t-2}^x) - 0.063(\sqrt{R_{t-3}})$$

The autocorrelation term is significant (Likelihood ratio test= 42.11, df= (7, 8), $p < .0001$) and is therefore retained. The model with climatic variables only, i.e., without sine and cosine terms, is slightly less well-fit, having a greater residual standard error. The Fourier frequency terms are therefore retained.

Figure 3.9. Ripe fruit abundance index ($A_{rf,t}$) among twenty-four species, with and without *Cola lizae*. The temporally ephemeral nature of ripe fruit in the gorilla diet can be seen in the graphs. Peaks are indicated with numeric A_{rf} labels. In the upper graph, Ln-transformed data demonstrate the complex periodicity of ripe fruit abundance.

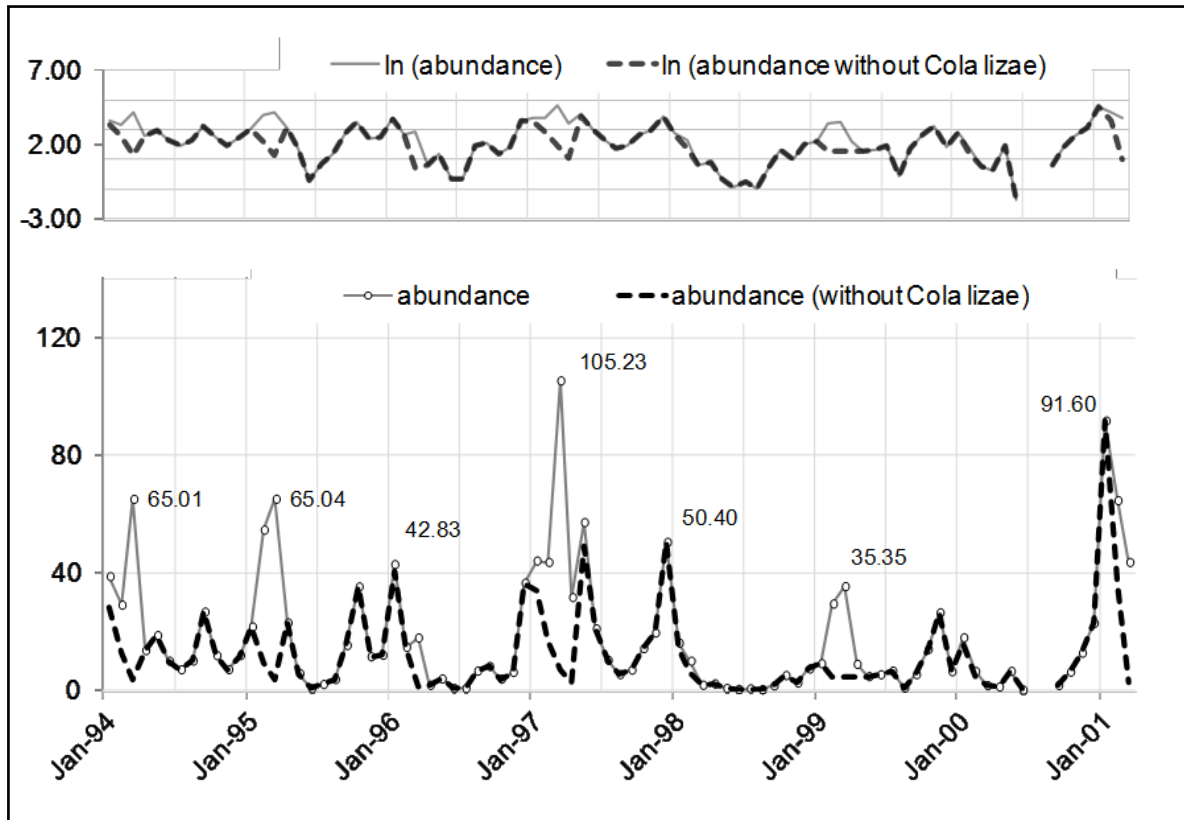
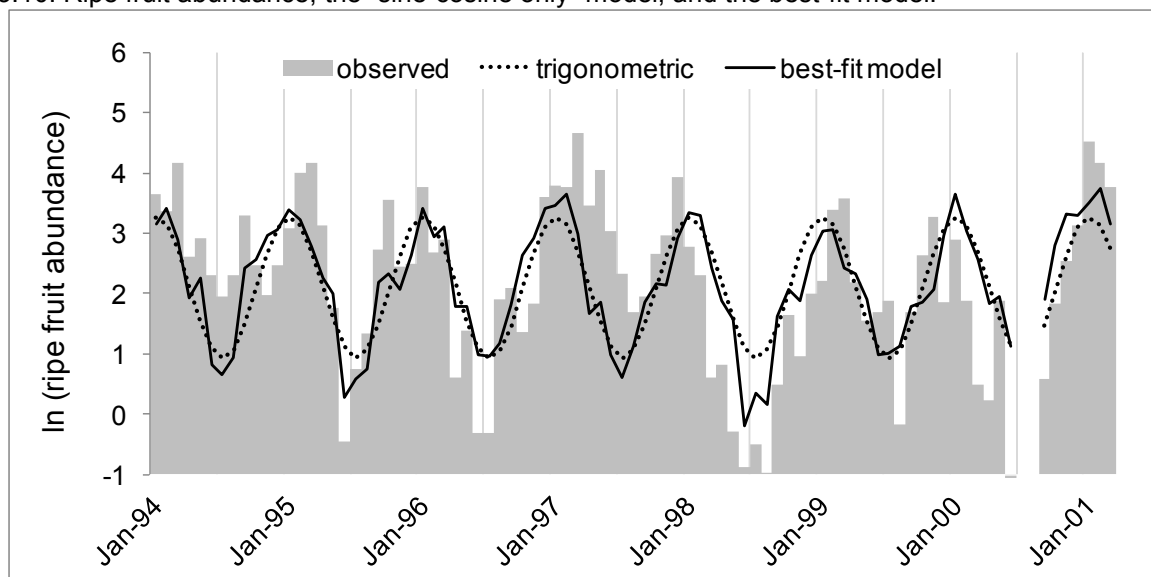


Table 3.4. Predictor variables of ripe fruit abundance (Ln-transformed) in twenty-four gorilla fruit species. Autoregressive order-1 term is significant. Estimates are from a Type III test of fixed effects. P-values are from a model fitted using Maximum Likelihood.

Source		Estimate	Std. error	DF-error	F-value	P-value
Mean low temp	$\log T_{t-6}^m$	-10.809	3.467	79	8.995	0.0036
Mean high temp	$\log T_{t-2}^x$	-5.021	2.168	79	5.019	0.0279
Rainfall	$\sqrt{R_{t-3}}$	-0.063	0.0209	79	8.334	0.0050
	$X_{\sin, \lambda=12}$	0.515	0.249	79	4.066	0.0471
	$X_{\cos, \lambda=12}$	0.716	0.243	79	8.112	0.0056

The availability of ripe fruit in gorilla fruit species is very erratic with highly variable peaks between January and April in most years. Despite being a better fit to the data than the “sine-cosine only” model (Fig. 3.10), the best-fit model still fails to capture the near complete failures of the fruit crops during the first halves of 1998 and 2000, and the unusually large crop in the first half of 1997. As seen with flowering and fruiting frequencies, mean low temperatures influences ripe fruit abundances. In this case, a 1% percent increase in monthly low temperatures in the preceding sixth months yields a ~10.8% decrease in ripe fruit abundance. It is unclear whether higher, low temperatures are the cause of low abundances in ripe fruit, or whether the observed effect is simply a “residual” effect, leftover from its effect on flowering. Mean high temperatures emerge in the best-fit model. If fruit development depends on higher temperatures, that dependency is not observed here. As with low temperatures, a 1% *increase* in mean monthly high temperatures in the preceding 2nd month yields a drop of 5% in ripe fruit abundance.

Figure 3.10. Ripe fruit abundance, the “sine-cosine only” model, and the best-fit model.

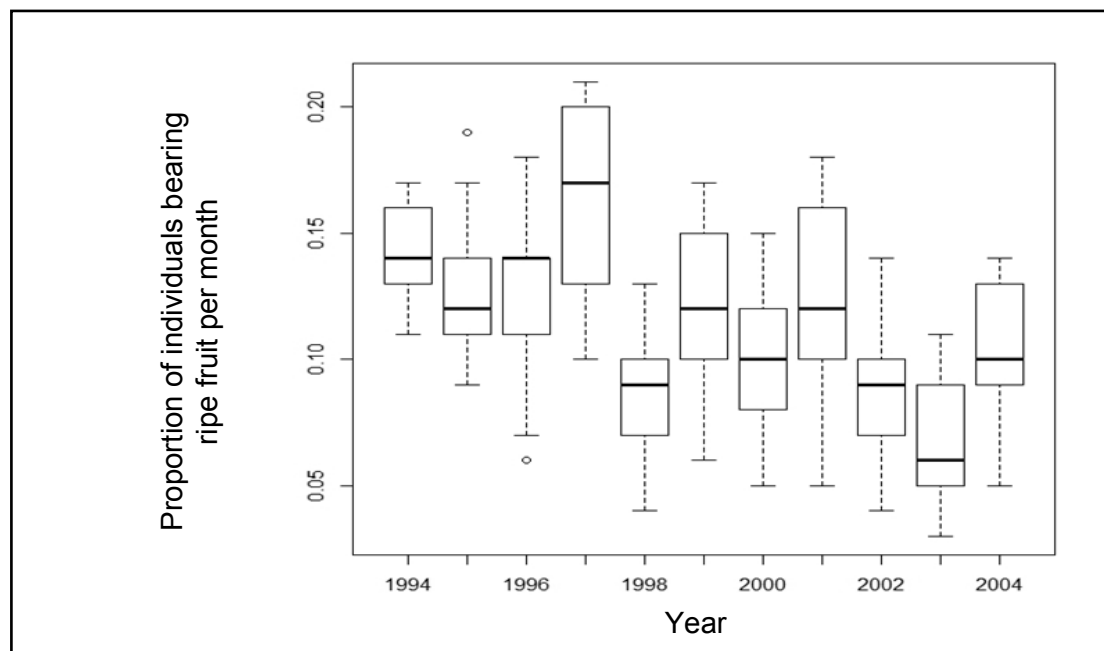


Clearly, temperature is an important variable in the in the timing and intensity of community-level fruiting phenologies at Lopé. Although none of the response variables in this analysis (SP_{fl} , SP_{fr} , or A_{rf}) demonstrate a clear long-term trend (Figs. 3.7, 3.8, and 3.10), species-level analyses show a high degree of variability in the proportion of years that individuals reproduce (see Fig. 3.5), suggesting that much of the plasticity in reproduction falls upon individuals. Over the entire dataset, the average proportion of

individuals bearing ripe fruit during wet months (i.e., September-May), differs significantly between years (Kruskal-Wallis $\chi^2 = 38.463$, $df = 10$, $p < 0.0001$). Across eleven years of data, and an average of 336 individuals sampled per month, the proportion of individuals bearing ripe fruit appears to have decreased from 1994 to 2004 (Fig. 3.11).

The negative relationship found between mean monthly low temperatures (2-4 months prior) and flowering corroborates with findings that plants at Lopé use temperature as a cue to synchronize flowering (Tutin and Fernandez, 1993b). The implications of this relationship are potentially severe in the context of a warming environment in the tropics. Without knowing anything about the effect of plant-level, environmental factors on phenology (not tested here), an increase in average temperatures should lead to a decrease in fruit production given the inverse effects of temperature in community-level flowering and fruiting. If average temperatures at Lopé increase, as they are expected to under models of climate change, warmer climates may inhibit flowering in species important to the gorilla, and the greater frugivore community.

Figure 3.11. Average proportion of individuals bearing ripe fruit during a wet month (N= 9 months per year). Boxes are ± 1 standard deviation, and whiskers indicate range.



DISCUSSION

Although gorillas eat from fruit species that vary greatly in their reproductive schedules (timing and intensity), the timing of flowering and fruiting, within species, has a surprisingly high degree of regularity. The majority of dietary species have predictably regular schedules, with deviations of greater than thirty days from their 10-year mean dates more the exception than the rule. It is unclear, however, whether the regularities (and frequencies) with which species reproduce in the gorilla diet are representative of those that exist in the greater plant community, or whether gorillas are selecting these qualities from those available in the community at large. Either way, the gorilla fruit diet at the community level appears to be more predictable, year-to-year, than it might be given the range of phenological patterns that are observed in tropical plant species (Newstrom et al., 1994).

In general, gorillas at Lopé choose succulent fruits (drupes and berries), and the majority of these ripen during the wet seasons. Ripe fruit is available during any month of the year, including the severe dry-season months, a period that is reportedly fruit scarce. In some years, for example, ripe fruit in the dry-season is found on a maximum of 26% of species (i.e., August 1997), though the average is 17%. This general pattern does not support, at least on the surface, the hypothesis that fruiting should occur only in the wet season in order to avoid the effects of water stress on fruit maturation.

Gorillas choose to eat large fruits whenever available. The high physiological demand of producing large fruits and seeds appears to place constraints on reproduction schedules. Although producing a large fruit and seed may have advantages in attracting large, wide-ranging mammals for dispersal, as well as in equipping a seed with adequate nutrients to see it through stresses (understory shade and herbivory), it does not come without its share of scheduling problems. In this study, I demonstrate that large-fruit species should begin their reproductive cycles as early as possible, and in favorably wet conditions, to ensure that favorably wet conditions prevail throughout fruit maturation. Whether insolation or available moisture is the most important determinant in fruiting schedules is unclear.

Regeneration strategies in plant species (and their associated tolerances for shade) are not correlated to the timing of phenology schedules, suggested that either (1) germination is not negatively

affected by the drier conditions that occur during the short dry-season (January-February), or (2) humidity levels are not important for successful germination. Lopé, however, does not experience significant variation in relative humidity throughout the year, and this may mitigate any effect that periods of low rainfall might have on germination.

Species' canopy-levels are correlated (though weakly) to the timing of reproductive events, with upper-canopy species reproducing (ripe-fruit) more often during the 2nd wet season. Since lower-canopy species are more evenly distributed across seasons, the importance of both strata in the diets of gorillas, as well as the greater frugivore community, cannot be understated.

There is no clear distinction between the wet seasons in terms of regularity in gorilla fruit species. Species range from predictable to unpredictable in flowering and fruiting. Variation in regularities is distributed evenly among species and seasons, suggesting that, at least from the gorilla's perspective, there are at least some reliably reproducing species regardless of the month (excluding the dry season).

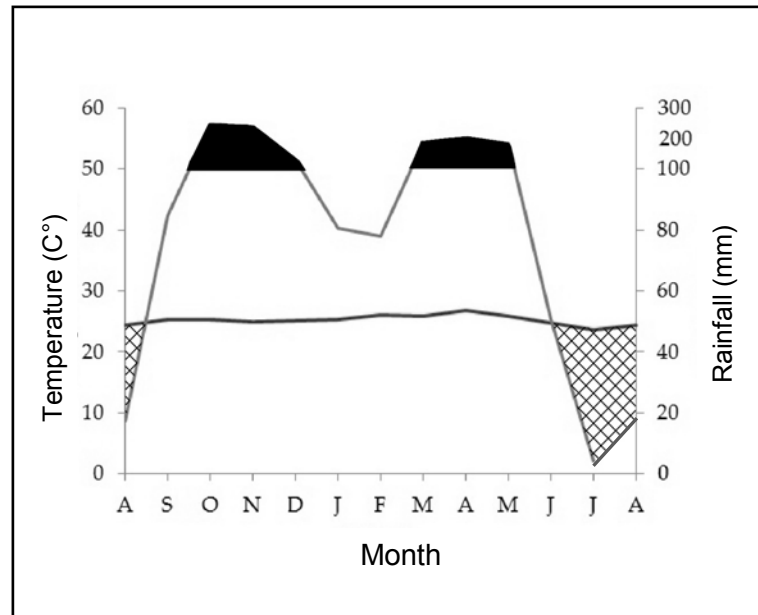
Some explanation for the absence of significant differences between the two wet seasons may be found by looking at a climate diagram for Lopé (Fig. 3.12; Walter, 1985). Although rainfall decreases to well below 100 mm/month during the mild dry-season months of January and February, it does not decrease by enough to create dry conditions (i.e., falling below the evapotranspiration line).

Flowering phenology

At the community-level, gorillas experience a great amount of variability in fruit resources over the year with reproductive cycles typically wax and wane on a 12-month cycle. Climatic fluctuations in rainfall and minimum temperature explain some of this variation, highlighting their role as potential triggers to the onset of reproduction in some species.

Flowering peaks from September to mid-November, are predicted from mean monthly low temperatures during the preceding severe dry season. This corroborates statistically with the previously reported relationship between temperature and flowering in some species at Lopé (Tutin and Fernandez, 1993b). Since these peaks coincide with the southward zenithal passing of the sun, insolation may place a physiological constraint on flowering.

Figure 3.12. Climate diagram (Walter, 1985) based on 10 years of meteorological data collected in Lopé National Park from 1990 – 2000. Data are monthly means. Temperature is plotted in the dark solid line and precipitation in the light solid line. The area in black corresponds to months when rain exceeded 100 mm, on average. Temperature and rainfall axes are calibrated to each other ($10^{\circ}\text{C} = 20 \text{ mm}$ rainfall) such that they indicate the potential evaporation rate. Dry months are represented with crosshatching, and indicate “water stress”.



The near-complete absence of species with mean flowering dates during the severe-dry season (i.e., only four out of forty species flower between mid-June and September) suggests that flowering might also be inhibited by water stress, a phenomenon seen in some tropical dry forests (Borchert 1983). However, cloud cover over Lopé during this period might help to mitigate this effect. The number of species flowering in the short dry season (January-February) however, remains high, with an 11-year average of 13.8 out of 40 species ($SD = 1.69$). If water stress is typically a constraint on flowering, here again humidity at Lopé may not be low enough for it to have an effect (see Fig. 3.12).

Some species in the fruiting community use temperature as a trigger to synchronize flowering. Producing large fruit and large seeds, for dispersal by larger vertebrate dispersers, may place constraints on phenological schedules in plants. It appears that very large fruit must begin their reproductive cycles at the onset of the September rains, in order to have wet conditions throughout fruit development.

Additionally, community-wide flowering and fruit production at Lopé might be limited by insolation, and to a lesser extent, available moisture. Irradiance is a function of latitude and cloud cover, with cloud

cover becoming more important as one approaches the equator. It is during this period that Lopé begins to experience more cloudless days as storm systems come and go, in stark contrast to the persistent cloud cover that occurs in the severe dry season. With the onset of rains in September, clouds begin to lift, giving the forest a boost in solar energy for photosynthesis and floral production. A second and less obvious peak in flowering (March) corresponds with the northward zenithal passing, circumstantially supporting the insolation theory. Thus, my results here lend some support to the insolation-limitation hypothesis of floral induction in tropical forests (*sensu* van Schaik et al., 1993).

Fruiting phenology

Community-wide fruiting is, for obvious reasons, in part contingent on flowering phenology. Flower loss through predation by insects and other animals, fluctuations in pollinator populations, and a host of other factors that affect fruit maturation, all play a role in determining whether flowering will produce a fruit. Despite the variation that exists in development times among species, a consistent peak in fruiting is observed between December and March, straddling the short dry season (January-February). In some years, a noticeable (though smaller) peak occurs in the middle of the major wet season (October-November). This general pattern does not appear to support directly the hypothesis that fruiting should peak during the wet season if fruit maturation is dependent upon water availability (Lieberman, 1982; Rathcke and Lacey, 1985).

Monthly mean low temperatures in the preceding 10 to 12 months, and rainfall in the preceding 11th month, have a negative effect on fruiting, suggesting that the severity of the previous short dry-season influences the number of species bearing fruit. Unlike the positive relationship found in Tai NP (Anderson, 2001), these results might that rainfall and temperature oscillate on a scale that is greater than one year (i.e., low rainfall in one year begets high rainfall the next).

The effects of temperature and rainfall on fruiting appear to be site-specific, and perhaps secondary, to their effects on flowering, since neither variable remained significant once the trigonometric variables were removed. Rain and temperature are, therefore, not the primary factors that influence fruiting, though they may help to drive some of the more subtle deviations from entrained reproductive patterns.

Community-wide ripe fruit abundance shows a 12-month cyclical pattern with very low fruit abundances during the long dry season. Low temperatures in the preceding 6th month, high temperatures in the preceding 2nd month, and rainfall in the preceding 3rd month, are all negatively associated with ripe fruit abundance. Predictors are each individually significant when entered singly (in models with sine and cosine terms), and remain significant after removal of the trigonometric terms. Unlike in the number of species fruiting, these variables have a primary role in shaping the pattern of ripe fruit availability at Lopé. Both the number of fruiting species and the abundance of ripe fruit are negatively related to the mean minimum temperature in the preceding months, similar to the relationship found in Uganda (Chapman et al., 1999), but contrary to the positive relationship found in Taï NP (Anderson et al., 2005).

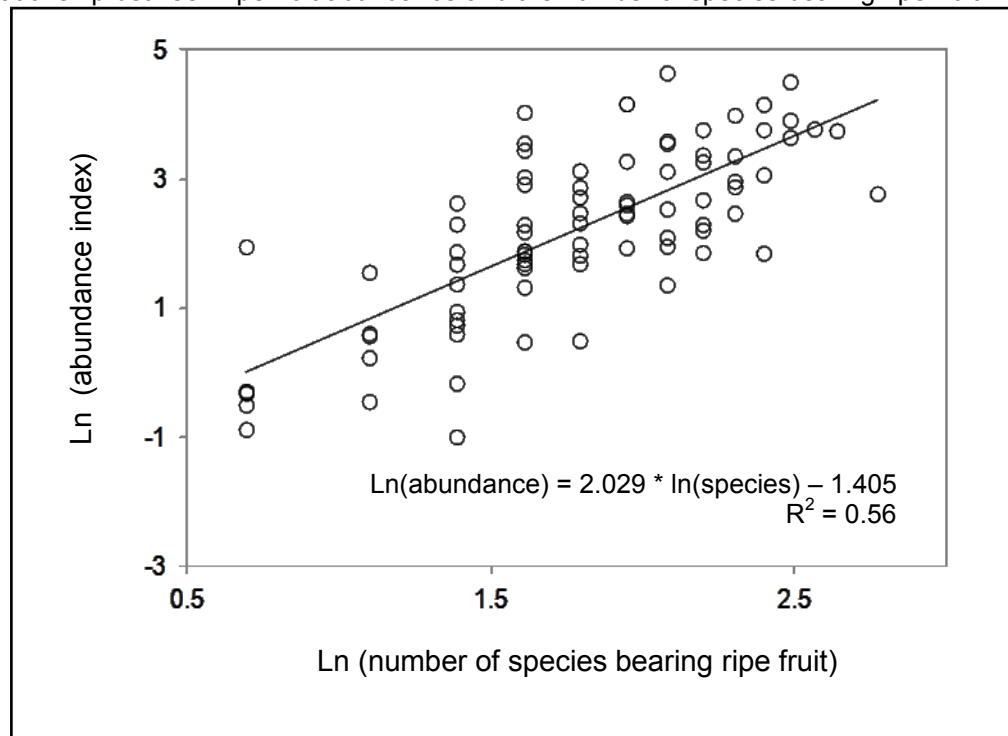
Comparing the fixed effects that predict fruiting species with those that predict ripe fruit abundance is problematic, since abundance factors in population densities and mean basal areas. Large and abundant trees, relative to small and rare ones, have a disproportionately high influence in abundance indices. Therefore, measuring resource abundances (with these factors included) is vital to evaluating animal responses to variations in the plant phenologies,

The natural log of the number of species bearing ripe fruit (Fig. 3.13) explains 56% of the variation in ripe fruit abundance (ln-transformed). Despite differences between species in their contribution to ripe fruit abundance, a 1% increase in the number of species bearing ripe fruit yields a 2% increase in the abundance of ripe fruit.

Gorilla responses to fruiting phenology schedules

The availability of fruit strongly influences the composition of the gorilla diet, and a flexible foraging strategy enables gorillas to cope with periods of fruit scarcity, particularly during the major dry season (Williamson, 1988). The vegetative parts of terrestrial herbs belonging to Zingerberaceae and Marantaceae are abundant, accessible, and available year-round. These staple foods, along with the bast of *Chlorophora excelsa*, form the bulk of the gorilla diet at Lopé during the long dry season when ripe fruit is scarce (Rogers et al., 2004).

Figure 3.13. The relationship between ripe fruit abundance and the number of species bearing ripe fruit.



The benefits of seed dispersal place particular emphasis on the individual plant (e.g., the quantity component of dispersal; *sensu* Schupp, 1993). The degree of synchronicity in fruiting plants (at both species and community levels) influences the probability that an individual will receive a would-be disperser, since it affects the fruiting neighborhood. Holding preferences for any particular food item constant, individuals of abundant species, or of those with a high degree of synchronicity, are less likely to “acquire” a gorilla than those of rare species or species with a low degree of synchronicity.

In the next chapter, I correlate some of the phenological variables (from this chapter) with the quantity and identity of seeds dispersed in gorilla dung in order to assess the effect of plant reproductive schedules on gorilla-mediated seed dispersal at Lopé.

CHAPTER IV

COMPOSITION AND CLUMPING OF SEEDS DISPERSED BY GORILLAS

INTRODUCTION

Seed rain is the combined result of the contribution of all plants whose seeds are dispersed; though the term is not necessarily spatially explicit, e.g., some researchers use “total dispersal kernel” to incorporate explicitly a spatial dimension. Spatio-temporal patterns of seed rain are the template for all subsequent recruitment of individuals into plant communities. Further, distributions of dispersed seeds often reflect habitat structure, the phenologies of food plants, and the habitats and dietary preferences of dispersers (Kollmann, 2000; Calviño-Cancela, 2002, Santamaría et al., 2007).

Aggregations of dispersed seeds occur on spatial scales ranging from small-scale clumping in dung to large-scale changes in seed rain densities between habitats driven by differences in the post-feeding, habitat use of dispersers. When the arrival of high densities of seeds to a location (favorable or not) is coupled with the denial of seeds to some potentially favorable sites it is termed “dispersal limitation” (Schupp et al., 2002).

Depending on their behavioral ecologies, vertebrate seed dispersers variably affect the composition and abundance of the seed rain. The more frequent deposition of seeds to particular sites beneficial to germination and growth (e.g., sleeping sites) could be a key mechanism to imposing spatial limitations to the distribution of plants dispersed by animal vectors. “Dispersion of vertebrate-dispersed tree species, then, can be viewed in terms of the balance between dispersal processes that aggregate seeds and post-dispersal processes that alter the initial offspring dispersion pattern through non-random survival” (Russo and Augspurger, 2004:1059). This directed dispersal of seed could ultimately contribute to the coexistence of species.

Gorilla-mediated seed aggregations

Spatial contagion

Gorillas disperse conspecific and heterospecific seeds away from parent trees in the same individual fecal clump (Rogers et al., 1998). These clumps are aggregated sources of seeds that may be preferentially (i.e., directed dispersal) deposited to some sites over others, creating spatially contagious patterns of deposition. Some sites may receive very high densities and it is possible that certain sites, and even some habitats, receive none at all.

The effects of density-dependent mortality on seed germination and seedling survival in clumps may be enhanced due to a decoupling of distance-density relationships with mortalities. Higher seed densities within contagion, for example, despite being far from parents, could suffer the same density-dependent mortality as seeds that are dropped under parent canopies. Barring secondary dispersal, a process that would scatter seeds more widely, aggregation sites are likely to experience increased competition between seeds and seedlings above and below ground (e.g., competitive superiority, *sensu* Loiselle, 1990) in co-dispersed seeds and seedlings. Additionally, seeds or seedlings may allelochemically alter the environment immediately surrounding clumps, suppressing growth (Traveset et al., 2007). Seed and seedling herbivory may be a common source of mortality if clumps are more easily found by herbivores. Wherever density-dependent mortalities are not enhanced, contagious dispersal can directly affect patterns of recruitment and ultimately adult tree distributions, making them more clumped in nature (Howe, 1989; Schupp et al., 2002).

Taxonomic contagion

Gorillas also tend to concurrently disperse more than one species of seed at a time (Voysey, 1995), resulting in suites of species being dispersed to specific sites together (Loiselle, 1990; Clark et al., 2004). In the absence of complete density-dependent mortality, gorilla-mediated dispersal of these 'taxonomic contagion' (*sensu* Clark et al., 2004) could result in the presence of recurrent associations of tree species in relatively close spatial proximity (Tewksbury et al., 1999; Blendinger et al., 2011).

If high-density seed associations do in fact contribute to both species- and community-level distributions, they might appear to contradict one of the advantages of seed dispersal, namely, the avoidance of high density-dependent mortality of seeds and seedlings beneath the mother plant (Kwit et al., 2004). Similarly, it could limit the arrival of seeds to additional sites that are adequate for establishment, with consequences that scale from altering population dynamics of one species (Herrera et al., 1994; Russo and Augspurger, 2004) to the maintenance of plant diversity in the entire community (Nathan and Muller-Landau, 2000; but see Howe, 1989).

Spatial scales of contagion in gorilla-mediated seed dispersal

Microsites are characterized by particular environmental conditions and are often grouped by their suitability for a given seed species at a given stage. For example, gorillas prefer to make a new nest each night, placing them on the ground (~64% at Lopé), and in canopy gaps, while 'in-transit' dung are often left on elephant paths where trampling by animals may be high. Voysey (1995) observed that trail dung was often left behind a log or root system, perhaps affording growing seedlings some protection from trampling. The different sets of distinct environmental characteristics associated with trails and nest-sites, make them separate microsites (Nathan and Muller-Landau, 2000). Among dispersed seed species, the suitability of any one microsite for a species may not be equal to that of another. For example, nest-sites may receive more sunlight than trail sites, and while light may be beneficial to growth for some plant species, it may decrease survival in others. Alternatively, greater exposure to sunlight may cause death by desiccation in species that have a low tolerance for dry conditions.

Gorilla ranging behavior primarily aggregates seeds on two scales. The dung pile itself occupies a small space approximately 0.25 m². In some cases, this may be the only scale that seeds are aggregated, as in the case of dung left while the animals are in transit. A second scale occurs around the distribution of dung left at a nest-site. Since group sizes and nest-site cohesiveness varies substantially (Williamson, 1988), clumping at the scale of the nest-site also varies.

Seed deposition sites (microsites), gorilla preferences for different habitats, and the composition and abundance of co-dispersed seeds, are the primary factors influencing the community-level, seed rain mediated by gorilla dispersing behaviors.

Gorilla behaviors that influence seed rain

Spatio-temporal characteristics in disperser feeding and ranging behaviors affect seed rain (Santamaría et al., 2007). Changes in frugivory in the gorilla diet are a direct response to changes in fruit availability (Doran-Sheehy et al., 2009). Gorillas have a typical “ape pattern” diet, with ripe, succulent fruit constituting the greatest part of the diet during periods of fruit abundance, and fibrous fruits, herbs, leaves, and bark, are incorporated to a greater degree during times of ripe fruit scarcity (Calvert, 1985; Rogers et al., 1990; Williamson et al., 1990; Nishihara, 1995; Kuroda et al., 1996; Remis, 1997; Doran and McNeilage, 1998; Goldsmith, 1999; Doran et al., 2002). Gorillas spend less time feeding and more time traveling during high frugivory periods than during low-frugivory periods, reflecting the greater dispersion of fruit resources over non-reproductive, terrestrial plant resources, (Tutin et al., 1991b; Tutin and Fernandez, 1993a; Doran-Sheehy et al., 2009; Masi et al., 2009).

Gorillas routinely begin their day by eating fibrous, non-reproductive plant parts near (and often while still in) their night nests (pers. obs.; Voysey, 1995). In the evening, they often construct nest-sites in open areas, such as natural treefall gaps that have a high degree of terrestrial vegetation (Williamson, 1988; Tutin et al., 1991a; Tutin et al., 1995; Rogers et al., 1998). Nests are often made on the ground (64% of 2435 nests, Tutin et al., 1995), with the type of nest (ground or tree) being influenced by habitat type. These behaviors result in defecated seeds being disproportionately deposited to areas of less shade, which may benefit shade-intolerant plant species.

Lowland gorillas have large home ranges (4-14 km²), and mean daily-path lengths of 1172 m (Tutin et al., 1992), often visiting only half of their home range in a given month (Cipolletta, 2003; Doran-Sheehy et al., 2004). Thus, cumulative gorilla displacements, over a period that is associated with maximum gut retention times (i.e., 35.4 ± 12.1 hours for solutes, 62.3 ± 20.4 hours for particles; Caton, 1999), are unlikely to saturate the entire home range before a swallowed seed is dispersed. For this reason, home-range size is unlikely to determine the shape of seed rain. However, small-scale ranging behaviors, including daily path lengths and habitat preferences, are more likely to determine how far and where a seed is dispersed. A typical gorilla group travels 320-2600 meters or more during a day (Tutin et al., 1992), and visits a varied “habitat template” (Jordano, 2000) over which they disperse seeds. While

not straight-line vectors, daily displacements are not random, as gorillas track fruiting resources often travelling from tree to tree during high fruiting periods.

According to Warner (1981), the amount and timing of fecal output is expected to be a function of feeding behavior and gut passage time. Defecation patterns of hominids and most primates have a 24-h cycle, and most of the feces is eliminated in the early morning, with a marked reduction in output during the afternoon, and almost none during the night (Heaton et al., 1992; Julliot, 1996; Caton, 1999; Lambert, 2002; Todd et al., 2008). Gorilla defecation rates are expected to vary with season (i.e., rainfall), diet (i.e., the proportion of fruit versus non-reproductive parts), age, and the health of the animal (White and Edwards, 2000). Since very few lowland gorillas groups are habituated to date, direct information on defecation behavior is scant. However, researchers from Bai Hokou in The Central African Republic, have shown that defecation rates can vary seasonally and diurnally (Todd et al., 2008).

It is important to distinguish between the dung pile itself and defecation events (which can be comprised of multiple dung piles) since the distinction can drastically alter the spatial scale of seed clumping, as well as any inferences from censusing methodologies that may be based on dung (Kuehl et al., 2007; Todd et al., 2008). Gorillas in Lopé defecate a minimum of 3-5 times per day (Tutin et al., 1991a), and a high proportion of this output is to nest-sites (Rogers et al., 1998). In southwestern Central African Republic, Todd et al. (2008) reported a mean dung production rate of five dung piles per day, and much the fecal output is at the nest-site, since they frequently defecate in the evening and again in the morning before moving (Voysey, 1995).

In CAR, gorillas typically remained in or nearby their nests between 1800 and 0600 hours (Todd et al., 2008). Feeding peaks occurred between 0700 and 1000 hours and again between 1300 and 1700 hours. These data, together with information on mean gut retention times (MRT) of captive individuals (23.4-62.3 hours, Caton, 1999; 50 hours, Remis, 2000; Remis and Dierenfeld, 2004) suggest that peak fecal output occurs during the night or immediately after waking in the early morning. Todd et al. (2008) found peak defecation occurred at the time that gorillas left their sleeping sites in the morning, and again at the end of the mid-afternoon rest period (between 1000 and 1300 hours). Peak output was not the same across age classes, however, with defecations at silverback (SB) nests found on 96% of days,

while only 35.5% of days at subadult (SA) nests. Evening-time defecations (defined as after 1800 hours) were low, occurring only on 27.6% and 14.5% of days at SB and SA nests, respectively. Daily defecation events were between 4.51 and 3.39 per day, and between 6.28 and 4.12 dung piles, for silverbacks and subadults, respectively (Todd et al., 2008), comparable to the numbers found at Lopé (Tutin et al., 1991a).

The effect of season on dung production was significant, with dung production increasing as daily rainfall increased. It was unclear whether this relationship was due to an actual increase in defecation rates on rainy days or to an increase in probability of dung detection, since gorillas moved less on rainy days. Over a longer period of time, defecation rates *decreased* with increasing 10-day rainfall totals (Todd et al., 2008). Production rates ranged greatly, and predicted outputs ranged 2-fold over the range of covariates tested in their predictive model (Todd et al., 2008). The observed decline in dung production during drier periods might reflect an increase in the dietary intake of fiber during the dry season, though this appears to contradict Milton (1999a,b), who showed an increase in gut passage rates in chimpanzees and humans as dietary fiber increased. Defecation rates in gorillas at Bai Hokou may be more analogous to those found in forest elephants. Elephants, whose diet closely resembles that of gorillas, have higher rates of defecation in the wet season (Ruggiero, 1992). At this point, it is impossible to say whether defecation rates change due to dietary quality or to the amount of food ingested.

The environmental conditions surrounding dung at nest-sites differs from those surrounding dung deposited along gorilla feeding trails, and from those that exist under fruiting trees (Voysey, 1999b). The effect of deposition site on seedling growth and survival have been studied at Lopé (Voysey, 1995, 1999b). Across four tree species, nest-sites were not always favorable to germination, but they were the best sites in terms of long-term survival and growth (Rogers et al., 1998; Voysey, 1999a,b). Germination success, growth rates, and seedling survival, were greater at *favorable* nest-sites than along gorilla trails and under parent trees (Rogers et al., 1998). The main factors associated with seed fate at nest-sites were increased light conditions and protection from desiccation. In addition, the high seed densities found in gorilla dung did not appear to influence negatively the survival of seedlings, in apparent contradiction to theories on competitive exclusion among co-dispersed seeds (Voysey, 1995; Voysey et al., 1999a,b).

Seed/seedling growth and survival are expected to vary, however, depending on the seed species considered.

Specific research questions

Despite the body of research in support of beneficial consequences of gorilla-mediated seed dispersal to seed removal and survival in some plant species (Tutin et al., 1991a; Rogers et al., 1998; Voysey et al., 1999a,b), I am unaware of any study that has quantified the effect of gorilla behavior on seed rain at the level of the plant community. Of particular interest is (1) how does contagious dispersal, as mediated by gorillas, vary in terms of the abundance and composition of dispersed seeds, (2) how are dispersed seed combinations related to fruit production, and (3) how do gorilla responses to fruit availability in a simultaneously fruiting environment, influence the structure of gorilla-mediated seed rain.

Here, I investigate the composition of co-dispersed seed by gorillas, taking into account both the microsite where seeds are deposited and the production of fruit in the simultaneously fruiting environment. My first objective is to quantify the temporal component of seed contagion in terms of abundance and composition of seeds dispersed. My second objective is to determine how the fruiting environment influences the combinations of seeds deposited by gorillas. Lastly, I determine whether the combinations of dispersed seeds vary between the different microsites into which gorillas disperse them. To examine the patterns of seed deposition, I evaluate the following specific questions:

- What are the temporal patterns of seed deposition in gorilla-mediated seed dispersal at Lopé and how are they related to the synchronously fruiting phenologies in the fruiting environment?
- How is the deposition of seeds affected by the temporal variation in fruit production?
- How do the combinations of co-dispersed seeds arriving to different microsites vary in terms of composition and abundance?

To answer these questions, I evaluate the gorilla-mediated component of the seed rain over the 12-month fruiting cycle at Lopé, by separating gorilla dung into temporal categories of co-dispersed species and analyzing the combinations of seeds deposited to two separate microsites: trails and nest-sites.

METHODS

Dung sampling

Between June 1993 and December 2000, gorilla dung was collected by SEGC researchers and staff for routine analysis and samples were weighed and washed through a 1 mm mesh sieve. Large seeds (> 0.5 cm) were counted, and identified to the level of species or genus. Relative quantities of seeds smaller than 0.5 cm were assessed using a four-point ranked abundance scale of rare, few, common, or abundant (Tutin & Fernandez 1993b). The relative proportions of leaf fragments, fiber, fruit remains, as well as of any insect remains, were ranked in the same way. In addition, the location and microsite (e.g. trail, nest, other) were recorded. As in phenology sampling, certain taxa are recorded as morphospecies, and assigned to the most specific classification possible. I refer to all seed taxa as “species” in this analysis.

From the full dataset, I removed all dung samples weighing less than 100 grams, and those that did not contain at least one intact, large seed (defined as > 0.5 cm). This resulted in a filtered dataset of 990 fecal samples, containing seeds from 33 species of large-seeded plants.

DATA ANALYSES

Composition of gorilla-dispersed clumps

The composition of gorilla-mediated seed rain depends on (1) the availability of foods in the environment, (2) the electivity of those foods in the diet, and (3) the treatment or handling of fruits and seeds both during and following consumption. Disperser effectiveness is a function of the number of plant species consumed and the relative proportions in which they are dispersed. I standardized within-dung seed abundances by dividing abundances by the dung mass then multiplying by 100, resulting in the number of seeds per 100 grams.

Spatio-temporal variation in combinations of dispersed seeds

To describe the temporal variation in seed combinations in dung, I analyze the data using a correspondence analysis (CA) of the table of whole seed abundances for each species, and in each dung

sample (Härdle and Samar, 2003). CA projects a multidimensional swarm of data points onto a two-dimensional space (Gauch, 1982; Pielou, 1984) by maximizing the correspondence (i.e., the χ^2 distance) between samples and seed species. Since the “dispersed-seed table” consists of the number of seeds per species for each sample, it accounts for both the presence/absence as well as the abundance of each seed species. A plot of the first two CA axes positions plant species having similar spatio-temporal dispersal profiles closer to each other.

Prior to analysis, sample seed abundances were standardized by their sample masses (grams), then Ln-transformed, a process that gives less weight to hyper-abundant species relative to rare species. Abundances were then Wisconsin double standardized, where species are first divided by their margin maximums, then samples by their margin totals, resulting in a dataset that weighed seed species and samples equally. Since the composition of seeds in dung changes dramatically over the course of the year, the dataset contains many zeros, making it necessary to group the data into months by performing a between-group CA, or BCA.

I complemented the BCA with a hierarchical cluster analysis in order to separate dung samples into groups. For this I used Euclidean distances between dung samples in the plane formed by the first two BCA axes and Ward’s method to cluster groups, following Palla et al. (2011). Since the clusters are based on similarities in within-dung seed abundances among co-dispersed species, I hereafter called them “co-dispersed seed groups”. The relationships between co-dispersed groups and dung-level, environmental variables, including dung mass and deposition site, are tested using χ^2 tests.

Taxonomic composition of seeds in gorilla dung

To test for differences in the composition of co-dispersed seed groups, I use the Shannon-Wiener formula of species diversity. This formula measures the uncertainty of predicting correctly the identity of the next randomly sampled seed in a dung sample, and is given by:

$$H' = - \sum p_j \log_e p_j$$

where p_j is the proportion of individual seeds of species j . The larger the value of H' , the greater the uncertainty, and a sample with only one species has zero uncertainty (i.e., $H' = 0$). I calculate H' for each sample, and analyze its variance across co-dispersed groups. Since the units of information for base e logs are difficult to comprehend, I express H' in units of numbers of species using:

$$N_1 = e^{H'}$$

where N_1 is the number of equally common species that would produce the same diversity as H' (MacArthur, 1965).

To assess the evenness (or equitability) of species distributions within dung, I standardize H' on a scale of 0-1 using the Pielou's evenness measure:

$$J' = \frac{H'}{\log S}$$

where S is species richness (i.e., the total number of seed species represented in a sample). The lesser the variation in seed abundances between species, the higher J' is.

Gorilla-mediated seed dispersal in a simultaneously fruiting neighborhood

To understand how variation in available fruit is related to seed dispersal, I analyze the data in two ways. First, I calculate a “seed source availability” index (similar to the ripe fruit abundance index, A_t , from Chapter Three) for each species, which represents the amount of seeds in the environment. The calculation follows the formula:

$$SA_{sp,t} = \sum_{k=1}^n D_k P_{k,t} I_{k,t} M_k$$

where D_k is the density of species k (individuals / km²) in the study area, $P_{k,t}$ is the proportion of individuals having fruit in species k at time t , $I_{k,t}$ is the average intensity score of those individuals that are in fruit phase for species k at time t , and M_k is a dioecy index equal to 0.5 if male and female organs are on distinct individuals and 1 if all individuals have female organs. In this index, I use fruit instead of ripe

fruit scores, since ripe fruit scores may underestimate availability in species with short ripe fruit durations. Additionally, Lopé gorillas sometimes eat unripe fruit, especially during periods of resource scarcity, i.e., in the dry-season and “bad” fruiting years (Tutin et al., 1991a,b). Basal area is not included in the formula, since I lacked data for some important gorilla food species. Lastly, I do not consider the number of seeds that a given fruit contains, although this variable may be important for a finer-scale estimation of the number of available seeds in the environment.

Using this source availability index, I calculate a “seed dispersal index” which measures the tendency for gorillas to disperse a particular seed species against randomness. Random dispersal here is defined as dispersal a seed in direct accordance to its availability.

The seed dispersal index, as used here, is adapted from a classic measure of food preference (Boesch et al., 2006), and is calculated as follows: First, from each month, I randomly sample ten dung samples, resulting in 330 dung samples across 33 months for which 10 or more samples are available. I then rank seed species according to their abundance in the dung for each month. Similarly, I rank species according to their seed source availabilities (SA_i) for all species that bore fruit in a given month. Lastly, for each species, I calculate the difference between its dispersed-seed rank (from dung) and its source availability rank. The species Seed Dispersal Index (SDI_{sp}) is calculated as:

$$SDI_{sp} = \frac{\sum(\text{Rank}_{\text{dispersed}} - \text{Rank}_{\text{seed abundance}})}{N_{\text{months}}}$$

The SDI_{sp} is a mean rank score of dispersal across all months that a seed is available. Index values are lowest in species that are dispersed to a greater degree than expected by availability, and highest in species dispersed to a lesser degree than expected.

Dynamic seed dispersal

The dispersal index (based on ranked availabilities) does not adequately measure the absolute level of seed dispersal however, since gorillas may disproportionately increase their feeding time on a given species the more it becomes available (see Lechowicz, 1982). In order to address specifically this critical aspect, I calculate a second dispersal measure called the “dynamic seed dispersal index”. This

measure takes into account the *relative* abundance of a seed species, and describes the rate of increase in dispersal relative to a seed's availability after the formula:

$$y = \exp (c + \beta x)$$

where y stands for the relative number of dispersed seeds and x for relative fruit (seed) availability. In this formula, c describes the dispersal of seeds when the availability is (close to) zero, whereas β describes the increment in dispersal as seed abundance increases. The relationship between seed availability and dispersal is therefore modeled exponentially, not linearly.

The value of c in this formula is related to SDI_{sp} , since both measure dispersal compared to a fixed measure of availability (c correlates strongly with SDI; Spearman's $\rho = -0.72$, $p < 0.0001$, $N = 25$). Beta greater than zero indicate a greater degree of seed dispersal the more a species becomes available, while negative β indicate seed dispersal becomes limited as source availability increases.

By using the natural logarithm of the relative abundances of dispersed seeds, I modeled an exponential (rather than a linear) relationship between relative seed availabilities and their relative dispersal in gorilla dung:

$$\ln(y + 1) = c + \beta x$$

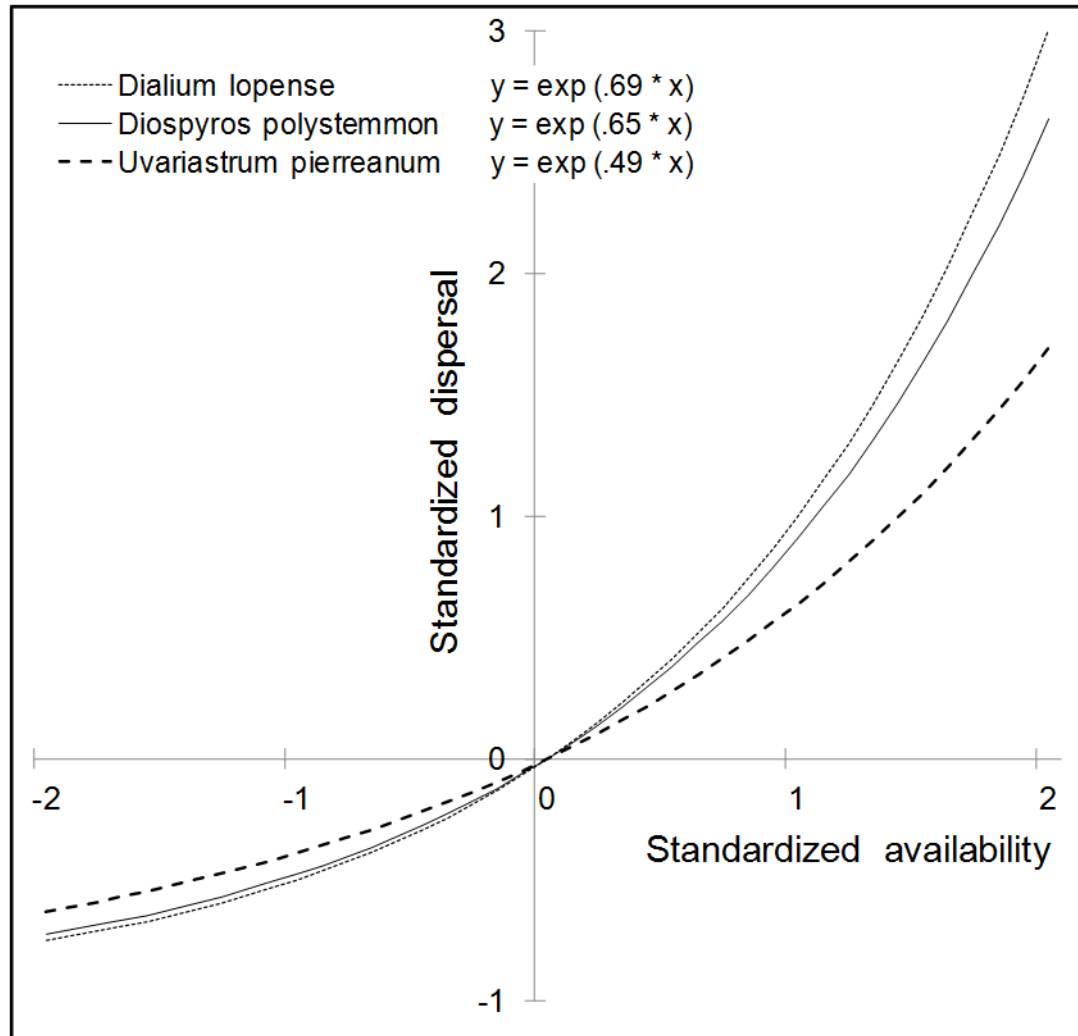
which is equivalent to:

$$y = e^{c+\beta x} - 1$$

I define the estimated regression coefficient β for each species as the “dynamic seed dispersal” index. In order to compare β of different species, I calculate a standardized β (Quinn and Keough, 2002). Standardized β 's enable comparisons to be made of models with variables of differing magnitudes and distributions. Here, it allows the comparison of β 's among species with different seed (source) availabilities. Standardized Beta are calculated by using z-transformed data for calculating the usual regression slope. Regressions in a species, are only conducted if fruit was available for at least six months.

As described above, the Dynamic Seed Dispersal, measured by β , quantifies how gorilla-mediated seed dispersal varies as seed availabilities vary (see Fig. 4.1). In my analysis, I use both indices of seed dispersal (SDI_{sp} and β) to analyze the dispersal consequences of gorilla foraging and handling behaviors, relative to fruit/seed availability.

Figure 4.1. Three examples of dynamic dispersal curves.



Variation in seed combinations between microsites

To test for differences in the combinations of seeds to different deposition sites, I use a nonparametric analysis of similarity (ANOSIM) to determine (1) whether trail and nest microsites receive different combinations (i.e., composition and abundance) of dispersed seeds, and (2) whether seeds that are co-dispersed with the five most frequently dispersed seeds, differ across microsites. In the first case, I

include all dung samples containing large seeds. In the second case, I consider only fecal samples containing the seeds of targeted species. Prior to analysis, I grouped dung samples according to their “co-dispersed seed groups”, since doing so allowed me to focus on only the within-group variation in seed combinations. The analysis of similarity determines whether combinations of seeds dispersed to a particular microsite are more similar than if dung are selected at random with respect to microsite. For this analysis, I considered only those dung samples collected in 1993 and 1994 to control for inter-year variation (in sample size) that might influence my results.

The non-parametric permutation procedure applied to a rank-ordered similarity matrix (ANOSIM) provides a more valid testing framework compared to ANOVA or MANOVA because it removes the assumption of normality (Clarke and Warwick, 1994), and enabled me to evaluate taxonomic variation among microsites in a simple and easily interpreted way (see Bonuso et al., 2002). ANOSIM calculates the level of global difference among all samples as well as the level of difference among microsites. Significance of ANOSIM test statistics are determined by comparisons with values obtained by Monte Carlo randomization procedures (9999 permutations).

Prior to analysis, the sampled dataset is standardized by dividing each species' abundance by the species total and multiplying by 100. In implementing the ANOSIM, I used the Bray-Curtis similarity index without data transformation, following Blendinger et al. (2011). In order to investigate differences in both species composition and abundances across microsites, I conduct separate analyses on matrices of presence/absence and seed abundances.

All statistics are performed in the R programming language (R Core Team, 2012). All ordinations and cluster analyses are performed using the “ade4” package (Chessel et al., 2004; Dray and Dufour, 2007; Dray et al., 2007). Significance of clusters is tested using the package “pscl” (Jackman, 2012). Species diversity indices and similarity of distance matrices (ANOSIM) are calculated using the “vegan” package (Oksanen et al., 2012).

The relationships between sample sizes and month (in “co-dispersed seed groups” and microsites), and between single- versus multiple-species samples, are tested using the χ^2 test. I use non-parametric Spearman coefficients to test for correlations between continuous variables. Finally, I use an

ANOVA with Tukey's HSD Post Hoc Test to compare mean values in species diversity indices among pair-wise, co-dispersed seed groups. In all hypothesis testing, I set significance levels at $p = 0.05$.

RESULTS

Of the 1528 gorilla dung samples collected between June 1993 and December 2000, 65% ($N = 990$) contained 57,826 large seeds, across 33 species. Seeds were distributed between nest-site (34,746) and trail dung (23,080). The greatest number of large seeds in a single dung sample was 384 for trail, and 699 for nest-site. The number of samples collected varied each month, ranging from 0-31 for trail, and 0-34 for nest-sites.

Seventy-eight percent of large-seeded dung samples contained seeds from at least one of five plant species (Table 4.1): *Cola lizae*, *Dialium lopense*, *Ganophyllum giganteum*, *Uapaca* spp., and *Monanthotaxis congolensis*. Large-seeded species were often co-dispersed, with 54.4% of samples containing two or more species, and 18.7% containing three or more.

Sample sizes across microsites (Table 4.2) are not distributed evenly ($\chi^2 = 26.30$, $df = 11$, $p = 0.0059$); however, chi-squared residuals do not indicate a deviation in any month relative to the overall average (i.e., absolute residual values are never greater than 2). Expected values do indicate that nest-sites may be over-represented for the months of January (12.7), February (9.3), June (8.0), and September (5.0); and trails in March (12.8), May (5.7), July (4.9), October (4.0), November (4.9), and December (4.6).

The number of species (Spearman's $\rho = 0.08$, $p = 0.0148$) and seeds (Spearman's $\rho = 0.15$, $p < 0.0001$) in dung are positively correlated with dung mass; as well as being correlated to each other (Spearman's $\rho = 0.41$, $p < 0.0001$). There is no relationship between the microsite and the number of seed species across *all* dung samples (Kruskal-Wallis $\chi^2 = 2.87$, $df = 1$, $p = 0.0903$). Number of seeds, however, is correlated with microsite (Kruskal-Wallis $\chi^2 = 10.34$, $df = 1$, $p = 0.0013$), with nest-associated dung (median = 30 seeds/100 grams) containing greater seed densities than trail dung (median = 20 seeds/100 grams).

Table 4.1. Thirty-three large-seeded plant species observed in gorilla dung (N=990). Bold entries indicate the five species that are present in 78% of samples.

Species	% samples (N)		seed size (cm)		no. seeds / sample		
			l	w	μ	se	(max)
<i>Annickia chlorantha</i>	1.8%	(18)	2.1	× 1.1	6.8	± 3.1	(53)
<i>Apocynaceae</i> spp.	1.2%	(12)	n.a.		3.5	± 1.2	(13)
<i>Celtis tesmanni</i>	4.5%	(45)	1.5	× 1.5	36.8	± 5.7	(155)
<i>Cissus dinklagii</i>	1.7%	(17)	1.4	× 0.8	6.4	± 1.7	(24)
<i>Cola lizae</i>	13.0%	(129)	2.8	× 1.9	26.3	± 2.3	(124)
<i>Dacryodes normandii</i>	5.1%	(50)	2.9	× 1.8	27.6	± 6.5	(214)
<i>Dialium lopesense</i>	13.6%	(135)	1	× 0.8	66.9	± 8.0	(479)
<i>Diospyros dendo</i>	0.8%	(8)	0.7	× 0.4	53.5	± 23.2	(174)
<i>Diospyros mannii</i>	0.2%	(2)	5.2	× 3.3	1.0	± 0.0	(1)
<i>Diospyros polystemon</i>	3.3%	(33)	1.5	× 0.8	52.5	± 11.0	(200)
<i>Diospyros</i> spp.	3.2%	(32)	n.a.		16.9	± 4.0	(90)
<i>Diospyros zenkeri</i>	4.9%	(49)	2	× 0.9	11.9	± 2.4	(89)
<i>Gambeya africana</i>	5.8%	(57)	3.5	× 1.9	11.8	± 1.8	(55)
<i>Gambeya subnuda</i>	0.5%	(5)	2.1	× 1.1	12.0	± 5.6	(34)
<i>Ganophyllum giganteum</i>	15.6%	(154)	1.9	× 1	98.1	± 7.4	(436)
<i>Haumania liebrechtsiana</i>	0.7%	(7)			3.7	± 1.3	(10)
<i>Heisteria parvifolia</i>	3.6%	(36)	1.4	× 1	48.4	± 11.1	(323)
<i>Klainedoxa gabonensis</i>	3.2%	(32)	4.3	× 3.2	1.6	± 0.2	(6)
<i>Landolphia mannii</i>	0.7%	(7)			3.1	± 1.0	(9)
<i>Megaphrynium macrostachyum</i>	4.7%	(47)			3.4	± 0.8	(31)
<i>Monanthotaxis congolensis</i>	14.6%	(145)	1.5	× 0.6	5.8	± 0.8	(52)
<i>Myrianthus arboreus</i>	1.6%	(16)	1.7	× 0.8	3.6	± 1.1	(16)
<i>Parkia</i> spp.	2.2%	(22)	1.5	× 1	19.4	± 10.3	(224)
<i>Pseudospondias longifolia</i>	6.1%	(60)	1.8	× 1	10.0	± 1.7	(66)
<i>Pseudospondias microcarpa</i>	2.6%	(26)	1.8	× 1	14.3	± 3.3	(56)
<i>Sacoglottis gabonensis</i>	0.1%	(1)	3.6	× 2.4	1.0	± na	(1)
<i>Santiria trimera</i>	4.2%	(42)	2.4	× 1.6	18.3	± 4.0	(115)
<i>Scytometalum</i> sp.	6.0%	(59)	2.5	× 1.5	32.3	± 7.1	(248)
<i>Treculia africana</i>	1.2%	(12)			12.2	± 7.2	(90)
<i>Trichoscypha acuminata</i>	7.1%	(70)	3	× 1.6	6.8	± 1.1	(42)
<i>Uapaca</i> spp.	33.8%	(335)	2	× 1.2	42.1	± 4.5	(655)
<i>Uvariastrium pierreanum</i>	9.2%	(91)	2	× 1	13.5	± 2.1	(107)
<i>Vitex doniana</i>	0.9%	(9)	2	× 2	4.2	± 2.1	(20)

Table 4.2. Monthly distribution of sample sizes across two microsites: trails and nests (N= 990).

Site	Month												Sum
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
Trail	61	45	65	25	38	36	32	28	17	45	73	42	507
Nest	83	61	37	27	25	50	21	27	26	35	60	31	483
Sum	144	106	102	52	63	86	53	55	43	80	133	73	990

Composition of gorilla-dispersed clumps

Dispersal Group Characteristics

The BCA of seed abundances in gorilla dung (Fig. 4.2) presents a “horse-shoe” effect because of the temporal turnover in dung composition over the year, and the dendrogram of the hierarchical clusters (Fig. 4.3) suggests dividing the 990 samples into five “co-dispersed seed groups”.

These groups tentatively reflect the interaction between the relative ripe-fruit availability, electivity of food items by gorillas, and the gorilla’s effectiveness as a disperser. Additionally, they represent statistical similarities (i.e., χ^2 distances and Ward’s method), with species-to-species distances representing inversely the degree of spatial and taxonomic association among co-dispersed seeds. Table 4.3 shows the distribution of dung samples across co-dispersed seed groups and months.

Distinct species associations characterize each co-dispersed seed group. Group 1 contains 154 dung samples, twenty-two species, and is the only group to be largely comprised of one month, January (e.g., 115 out of 154 samples). Characteristic species include *Ganophyllum giganteum*, *Dacryodes normandii*, *Santiria trimera*, *Heisteria parvifolia*, and the occasional early-season *Cola lizae*. Whole seeds of *Treculia africana* and *Landolphia manni* are not often found in dung, but are also represented here. *Annickia chlorantha* seeds are rare and equally shared with group five.

Figure 4.2. Seed-species associations in gorilla dung samples at Lopé. Projections are of species and months (red numbers) in the plane formed by the first two axes from the between-month correspondence analysis of seed species abundances. The size of each circle is proportional to the square root of total seed species abundances in dung.

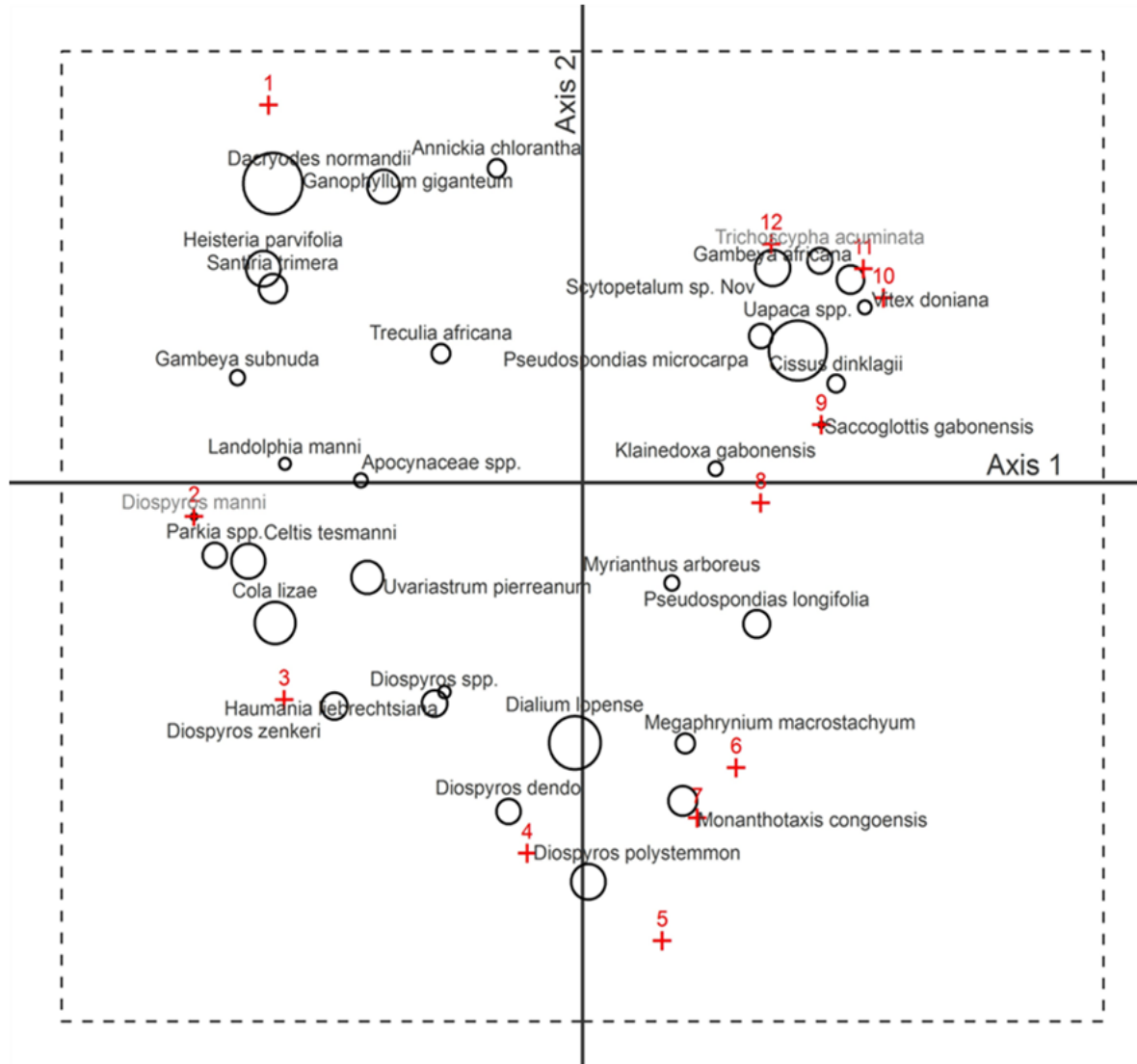


Figure 4.3. Dendrogram of the hierarchical cluster analysis of 990 gorilla dung samples containing large-seeds at Lopé, Gabon. Analysis uses Euclidean distances in the plane formed by the first two axes from a BCA of seed abundances. Boxes indicate where the dendrogram was cut to define the “co-dispersed seed groups”. Clusters are determined using Ward’s method.

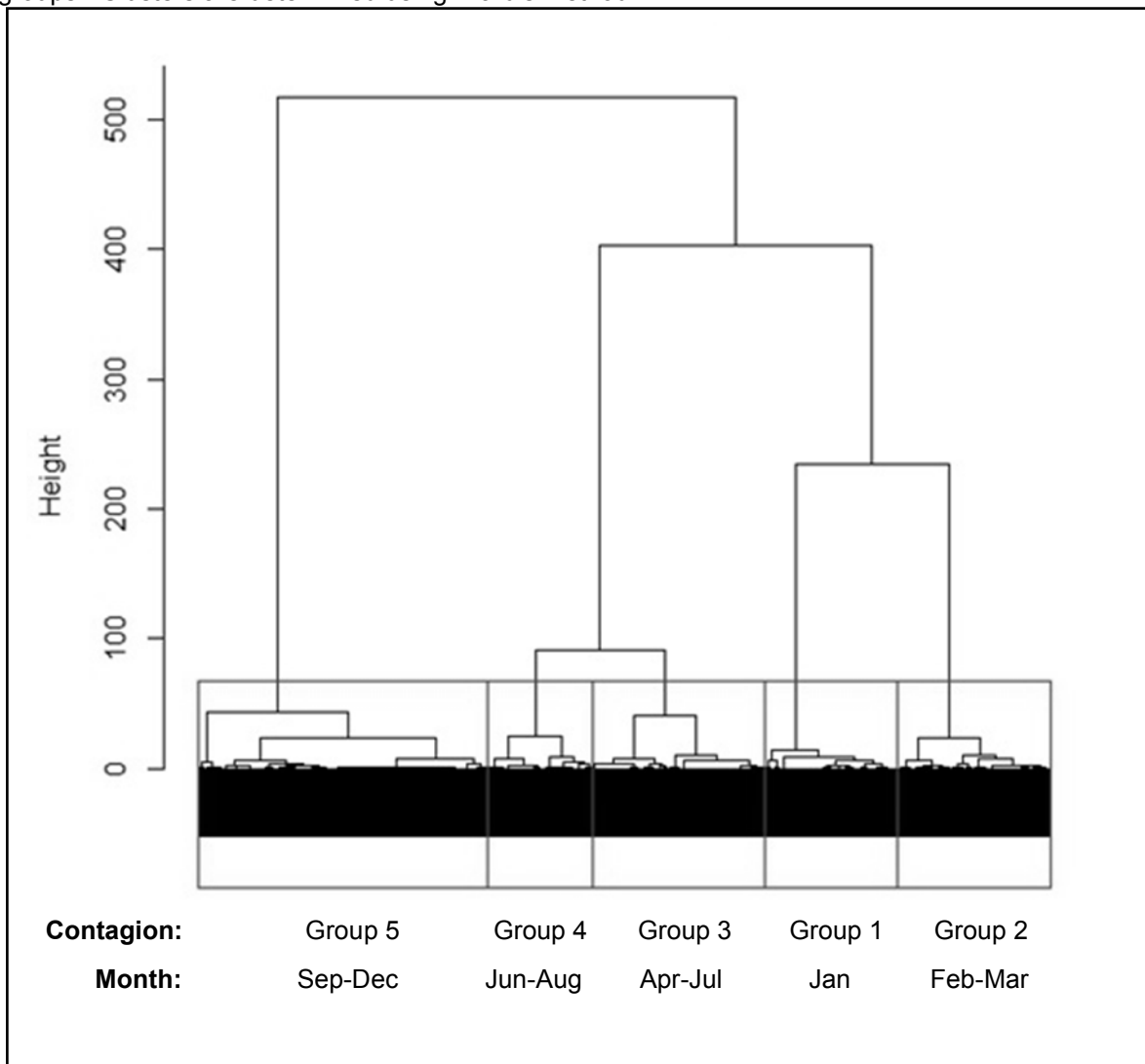


Table 4.3. Monthly distribution of dung samples across the five, co-dispersed seed groups. Dark-shaded cells are column maximums, and represent greater than 70% of column totals. Light-shaded cells are in months that less clearly fall into a unique group. These occur during the dry season, and samples from these months belong to two distinct groups.

Group	Month												Sum
	1	2	3	4	5	6	7	8	9	10	11	12	
1	115	30	5	1								3	154
2	5	69	84	10	2	2		3			2		177
3	1	7	10	38	52	34	39	6	5	3	2	3	200
4	4		2	2	9	45	11	22	10	4	13	1	123
5	19		1	1		5	3	24	28	73	116	66	336
Sum	144	106	102	52	63	86	53	55	43	80	133	73	990

Group 2 contains 177 dung samples and twenty-three species (70% of all large-seeded species dispersed by gorillas) and is highly focused on the months of February and March. Characteristic species include (in order of importance): *Cola lizae*, *Uvariastrum pierreanum*, *Celtis tesmanni*, *Diospyros zenkeri*, *Diospyros* spp. (a species group that is also shared with cluster 3), *Parkia* spp., and Apocynaceae spp. A favored gorilla fruit, *Dialium lopense*, is also found here, though it is most common in group three. *Apocynaceae* spp., and *Diospyros mannii* are rarely dispersed when their fruits are eaten by gorillas due to their very large seed sizes (> 3-5 cm).

Monanthotaxis congolensis, *Dialium lopense*, *Megaphrynium macrostachyum*, *Diospyros polystemon*, *Diospyros dendo*, and *Diospyros* spp. (equally shared with group two) are characteristic of group 3. Dung in this cluster (200 dung samples, and 16 species) are late rainy-season / early dry-season species, bearing ripe fruit between April and July. *Haumania liebrechtsiana*, the terrestrial herb, is dispersed in this cluster, but it is rarely swallowed due to its large seed size.

Group 4 consists of 123 dung samples and 14 species, and focuses on the major dry-season months of June, July, and August. Characteristic species include *Pseudospondias longifolia*, *Klainedoxa gabonensis*, and *Myrianthus arboreus*. Some seeds of *Dialium lopense* also appear here. Other long-season species are represented here, outside of their primary groups, including *Uapaca* spp., *Monanthotaxis congolensis*, and *Uvariastrum pierreanum*.

Group 5 is a large category containing 336 samples and 21 species. It is comprised of fruit species that ripen between September and December. *Uapaca* spp., *Trichoscypha acuminata*, *Gambeya africana*, *Scytopetalum* sp., *Pseudospondias microcarpa*, and *Cissus dinklagii*, characterize this cluster in order of importance. *Vitex doniana* and *Sacoglottis gabonensis* seeds are not commonly swallowed but are found in this group, and *Annickia chlorantha* seeds are shared between group five and group one (though they are infrequently dispersed in dung).

Table 4.4 is a list of seed abundances in the thirty-three, large-seeded plant species dispersed in gorilla dung. Species are ranked in decreasing order of seed abundances across the co-dispersed seed groups.

Dung-level covariates to co-dispersed seed groups

Dung samples (in co-dispersed seed groups) are not evenly distributed across deposition sites ($\chi^2 = 19.74$, $df = 4$, $p = 0.0006$) with trail samples under-represented (χ^2 residual = -2.46) and nest samples over-represented (χ^2 residual = 2.52) in group one (Table 4.5). This is not surprising since group one is comprised largely of January samples (see Table 4.3 above), and nests in January had 12.7 more samples than expected (see Table 4.2 above). Thus, excluding group one, there is not strong support for a significant relationship between sample sizes and deposition site or seed.

Dung containing a single large-seeded species, and those containing multiple species are not evenly distributed across seed groups ($\chi^2 = 41.04$, $df = 4$, $p < 0.0001$). Single-species dung are more prevalent in group three (χ^2 residuals = 3.11), and multiple-species dung more prevalent in group two (χ^2 residuals = 2.22), suggesting that known differences in levels of availability and frugivory, throughout the year, affect the degree of taxonomic associations among dispersed seeds.

Table 4.4. Seed abundances of thirty-three large-seeded species dispersed in gorilla dung, organized by co-dispersed seed group number. N= 990 dung samples.

Species	Co-dispersed seed group					Total
	1	2	3	4	5	
<i>Ganophyllum giganteum</i>	14,602	46			460	15,108
<i>Uapaca</i> spp.	47	1	3	620	13,430	14,101
<i>Dialium lopense</i>		1,038	7,812	177		9,027
<i>Cola lizae</i>	181	3,125		84	3	3,393
<i>Scytopetalum</i> sp.		3	1	17	1,883	1,904
<i>Heisteria parvifolia</i>	1,731	9			1	1,741
<i>Diospyros polystemon</i>		3	1,713	15		1,731
<i>Celtis tesmanni</i>	5	1,653				1,658
<i>Dacryodes normandii</i>	1,005				376	1,381
<i>Uvariastrium pierreanum</i>	2	1,095	33	99		1,229
<i>Monanthotaxis congoensis</i>		4	546	291	7	848
<i>Santiria trimera</i>	763			4	1	768
<i>Gambeya africana</i>	7				666	673
<i>Pseudospondias longifolia</i>	5		3	571	23	602
<i>Diospyros zenkeri</i>		567	18			585
<i>Diospyros</i> spp.	5	335	200			540
<i>Trichoscypha acuminata</i>	2				472	474
<i>Diospyros dendo</i>		3	424		1	428
<i>Parkia</i> spp.	5	421	1			427
<i>Pseudospondias microcarpa</i>	22				350	372
<i>Megaphrynium macrostachyum</i> *	1	5	109	46		161
<i>Treculia africana</i>	47	4			95	146
<i>Annickia chlorantha</i>	43	1			79	123
<i>Cissus dinklagii</i>				2	106	108
<i>Gambeya subnuda</i>	11	4		11	34	60
<i>Myrianthus arboreus</i>	1		3	52	1	57
<i>Klainedoxa gabonensis</i>	1	1	3	30	15	50
<i>Apocynaceae</i> spp.	1	41				42
<i>Vitex doniana</i>					38	38
<i>Haumania liebrechtsiana</i> *		18	8			26
<i>Landolphia manni</i>	10	11	1			22
<i>Diospyros mannii</i>		2				2
<i>Sacoglottis gabonensis</i>					1	1
Total	18,497	8,390	10,878	2,019	18,042	57,826
No. of species (> 10 seeds)	11	11	8	12	14	
No. of species (> 100 seeds)	5	7	6	4	8	

*Terrestrial herbaceous herb

Table 4.5. Distribution of dung samples across co-dispersed seed groups and two deposition microsites: trails and nests.

Microsite	Co-dispersed seed group				
	1	2	3	4	5
Trail	57	104	102	73	171
Nest	97	73	98	50	165

Dung mass differs significantly across seed groups ($\chi^2 = 2.892$, $p < 0.05$; Table 4.6). Group 3 has, on average, the smallest dung mass, and group 4 the greatest, perhaps due to the amount of non-reproductive (vegetative), fibrous foods in the gorilla diet during the major dry season. Seed densities are greatest in group 1 (January), with an average of ~42/100 grams of dung, and lowest in group 4, with an average of only 5.68. In general, the density of seeds in dung is greatest during the period of greatest ripe-fruit availability (December-March; see Fig. 3.10).

Dung from groups 1 and 2 (January-March) contain more species (i.e., richness), on average, than any other group. Despite having greater seed densities, heterogeneity and evenness are lower in group 1 than in groups 2 and 4, suggesting that gorillas focus (their foraging) on fewer species at this time of typically fruit availability. Surprisingly, the driest part of the year (group 4) does not have the lowest species richness (mean $S = 1.82$ spp./100g) or heterogeneity (mean $H' = 0.39$). Evenness in this seed group ($J = 0.79$) is greater than at any other time of year, indicating that gorillas are more eclectic in their foraging for fruit at this time. The low number of seeds (mean = 5.68/100g), however, during this period reflects the low availability that exists in ripe fruit.

Table 4.6. Analysis of variance of dung-level covariates and within-dung species diversity indices with respect to large-seeded species dispersed by gorillas at Lopé, Gabon. Groups occurring primarily in the dry-season are shaded.

		mean values in co-dispersed seed groups ^a					all samples	F	p-value
Variable or Indices		1: Jan	2: Feb-Mar	3: Apr-Jul	4: Jun-Aug	5: Sep-Dec			
sample size		154	177	200	123	336	990		
mass		292.5	291.5 ⁴	287.2 ^{2,4}	369.3 ³	310.0	306.7	2.892	<0.05
<i>N</i> (seeds) ^b		42.26 ^{2,3,4,5}	17.93 ^{1,4}	25.01 ^{1,4,5}	5.68 ^{1,2,3,5}	18.54 ^{1,3,4}	21.83	37.35	<0.0001
richness	<i>S</i>	2.01 ^{3,5}	2.17 ^{3,4,5}	1.48 ^{1,2,4}	1.82 ^{2,3}	1.64 ^{1,2}	1.78	21.72	<0.0001
heterogeneity	<i>H'</i>	0.28 ^{2,3,4}	0.43 ^{1,3,5}	0.17 ^{1,2,4}	0.39 ^{1,3,5}	0.24 ^{2,4}	0.28	19.57	<0.0001
	<i>N₁</i>	1.40	1.66	1.24	1.58	1.33	1.41	19.7 ^c	<0.0001
evenness	<i>J</i> ^d	0.48 ^{2,4,5}	0.67 ^{1,4}	0.55 ⁴	0.79 ^{1,2,3,5}	0.59 ^{1,4}	0.61	14.65	<0.0001

^a super-scripted numbers indicate the different levels (cluster #) that are significant at p=0.05 in Tukey's multiple paired comparison tests (5% honest significant difference, HSD).

^b summed number of seeds per sample is standardized by dividing the original matrix by its mass and multiplying by 100. Units= seeds * 100 gram⁻¹.

^c significant differences in *N₁* paired comparison tests are the same as in *H'*.

^d evenness (*J*) is undefined in samples with only one species.

Dynamic dispersal: Fruit availability and dispersed seeds

Twelve out of twenty-five species have seed dispersal indexes less than zero (Fig. 4.4), indicating they are dispersed to a greater extent than their availability in the forest (Table 4.7). From these, I classify a species as “well dispersed” if it was a part of the 20% top-ranked species ($SDI_{sp} \leq -3.83$). These include *Trichoscypha* spp., *Santiria trimera*, *Ganophyllum giganteum*, *Monanthotaxis congoensis*, and *Dacryodes normandii*. I define “poorly dispersed” species as those in the bottom 20% of ranked species ($SDI_{sp} \geq 3.31$). These included *Diospyros polystemon*, *Diospyros dendo*, *Cola lizae*, *Klainedoxa* spp., and *Diospyros mannii*.

Within poorly dispersed species, the SDI identifies two potential deficiencies of gorillas in terms of dispersal quantity; namely (1) that individual plants in species with high stem densities are not likely to receive a gorilla visits (i.e., low disperser acquisition), and (2) that species having seeds above a threshold size will not have their seeds removed during a gorilla visit. In the latter case, seeds of *Klainedoxa* spp. and *Diospyros mannii* are rarely dispersed by gorillas since their very large sizes (3-5 cm) are greater than the gorilla’s swallowing threshold. In the former case, *Diospyros polystemon*, *Diospyros dendo*, and *Cola lizae* all have the highest stem densities of any gorilla fruit species at Lopé. The number of seeds dispersed by gorillas in these species (as measured by SDI) will always be low relative to their high availabilities in the environment.

Species are not necessarily dispersed more as the proportion of trees producing fruit decreases (correlation of SDI_{sp} and mean proportion of individuals fruiting in a species: Spearman’s $\rho = 0.186$, $p = 0.3728$), nor are they dispersed in proportion to the length of time they bear fruit (SDI_{sp} and r_c : Spearman’s $\rho = -0.3208$, $p = 0.1181$). Well dispersed species are, however, those species with the smallest relative seed abundances (SDI_{sp} and mean relative SA: Spearman’s $\rho = 0.7632$, $p < 0.0001$) and lowest stem densities (SDI_{sp} and Ln-density: Spearman’s $\rho = 0.59406$, $p = 0.0017$). SDI, therefore, suffers the same bias associated with dietary preference indices (see Boesch et al., 2006); namely, that an abundant plant must be dispersed in much greater quantities in order to produce the same index value as an uncommon one.

Table 4.7. Seed dispersal indices across large-seeded fruit species dispersed by gorillas. See text for definitions of SDI, c , β , and standardized β . Species are ranked according to their SDI values. Bold values indicate significant ($p \leq 0.05$) departures from zero in c and β . Shaded species are either “high acquisition” or “low acquisition” based on SDI values.

Species	SDI	c	β	standardized β	
<i>Trichoscypha</i> spp.	-9.29	0.032	6.833	0.316	“high acquisition”
<i>Santiria trimera</i>	-9.23	0.094	-41.517	-0.354	
<i>Ganophyllum giganteum</i>	-8.04	0.392	-15.418	-0.348	
<i>Monanthotaxis congoensis</i>	-4.07	0.051	5.402	0.115	
<i>Dacryodes normandii</i>	-3.83	0.011	-0.105	-0.331	
<i>Celtis tesmanni</i>	-2.95	0.281	-8.930	-0.499	“low acquisition”
<i>Irvingia gabonensis</i>	-2.83	0.001	-0.007	-0.349	
<i>Gambeya africana</i>	-2.29	0.029	-0.174	-0.137	
<i>Parkia</i> spp.	-1.94	0.016	-0.697	-0.042	
<i>Uapaca</i> spp.	-1.74	0.162	-0.240	-0.026	
<i>Scytopetalum</i> sp.	-1.68	0.080	-0.103	-0.128	
<i>Cissus dinklagii</i>	-1.67	0.002	0.062	0.038	
<i>Myrianthus arboreus</i>	0.14	0.004	0.797	0.114	
<i>Pseudospondias microcarpa</i>	0.53	-0.010	1.062	0.668	
<i>Heisteria parvifolia</i>	1.19	0.029	-0.294	-0.122	
<i>Sacoglottis gabonensis</i>	1.39	0.000	0.003	0.296	
<i>Diospyros zenkeri</i>	1.53	0.009	0.052	0.059	
<i>Dialium lopense</i>	1.78	0.048	2.817	0.694	
<i>Uvariastrum pierreanum</i>	2.73	-0.005	0.568	0.495	
<i>Annickia chlorantha</i>	3.23	0.002	-0.004	-0.154	
<i>Diospyros mannii</i>	3.31	0.000	-0.002	-0.072	
<i>Klainedoxa</i> spp.	4.52	0.004	0.027	0.203	
<i>Cola lizae</i>	5.43	-0.008	0.188	0.216	
<i>Diospyros dendo</i>	7.86	-0.005	0.174	0.165	
<i>Diospyros polystemon</i>	8.03	-0.123	1.035	0.646	

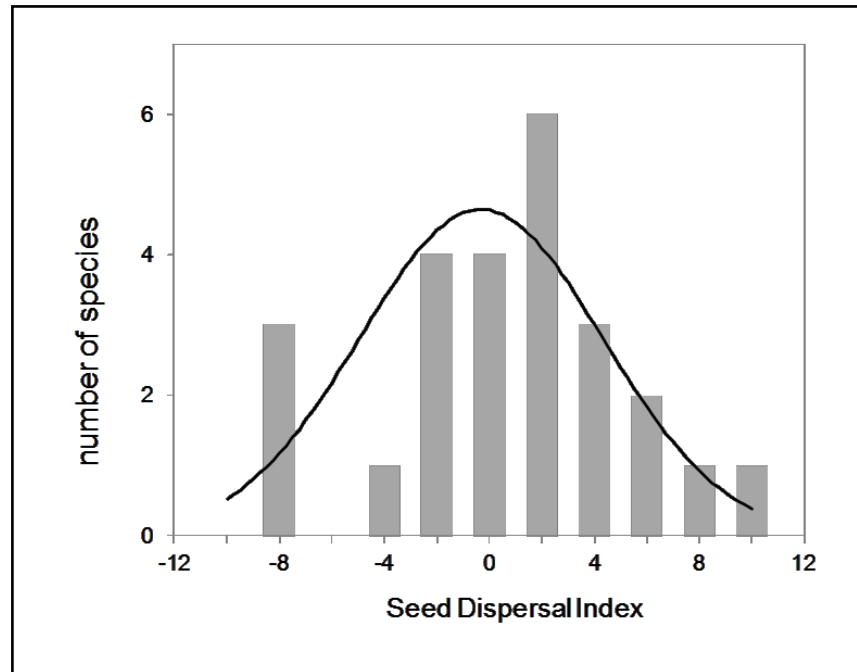
To better analyze the interaction between fruit availability and dispersal, I conducted simple linear regressions for each species separately. Of the 25 species present in the dung for at least six months, only four show a significantly positive relationship between relative fruit abundance and relative number of dispersed seeds, while in the other 21 species, no significant relationships are detected. The standardized regression coefficient, beta, for these regressions represent the dynamic dispersal index.

In these four species, *Dialium lopesense*, *Pseudospondias microcarpa*, *Diospyros polystemon*, and *Uvariastrom pierreanum*, the number of dispersed seeds increases exponentially as fruit production increases (Standardized β , $p < 0.05$). Surprisingly, none of these species are considered “well dispersed” under the SDI_{sp} , and one species, *Diospyros polystemon*, is poorly dispersed. This species has the lowest c of any species, indicating that gorillas have a low baseline “preference” for this species relative to others (i.e., ignoring it when fruit abundances are close to zero). Then, as its relative abundance increases, gorillas increasingly (and exponentially so) consume and disperse it. Since this species begins to ripen during the last months of the high fruit availability (Jan-March), continuing to produce ripe fruits into the long dry-season (a period when other species have waned in terms of ripe fruit), it appears that gorillas concentrate increasingly on *D. polystemon* in order to fill a widening gap in their fruit diet. If this were true, I would expect it to be of a lower quality than simultaneously fruiting species from the month of March.

Gorillas consume and disperse certain species whenever even the slightest levels of fruit are present. Then, there are species that become important only later (and exponentially so), after their relative fruit abundances in the environment increases beyond some level. This threshold level is expected to vary in both time and space and depends upon the simultaneously fruiting neighborhood in sympatric gorilla food species.

Using the dynamic seed dispersal index, gorillas do not disperse seeds relatively more for species that have, on average, higher relative fruit abundances (β does not correlate with mean relative SA_{sp} levels: Spearman’s $\rho = 0.246$, $p = 0.235$, $N = 25$; Fig. 4.5-A). Similarly, densities are not correlated to higher level of seed dispersal (β did not correlate with Ln-density: Spearman’s $\rho = 0.293$, $p = 0.1555$, $N = 25$, Fig. 4.5-B). Dispersal, however, does increase (relatively more) the longer a species bears ripe fruit (β correlates with mean $R_{c,rf}$: Spearman’s $\rho = -0.566$, $p = 0.0037$, $N = 25$, Fig. 4.5-C). However, no relationship is observed between fruiting synchronicity and seed dispersal (β does not correlate with mean proportion of individuals fruiting: Spearman’s $\rho = 0.134$, $p = 0.5234$, $N = 25$, Fig. 4.5-D).

Figure 4.4. Distribution of seed dispersal indices (SDI) for 25 large-seeded species dispersed by gorillas at SEGC.



Dispersal increases relatively more for species that bear ripe fruit close to their expected mean dates (β correlates with R_{reg} : Spearman's $\rho = -0.4754$, $p = 0.0163$, $N = 25$, Fig. 4.5-E), suggesting that changes in availability in the *simultaneously* fruiting environment may have a significant effect on the effectiveness of dispersal by gorillas (for a species). The same trend is not observed, however, in species having more regular inter-cycle intervals, between ripe-fruiting events (β is not correlated with ripe-ripe fruit CV: Spearman's $\rho = 0.1661$, $p = 0.4379$, $N = 24$, Fig. 4.5-F).

Combined, these results indicate that gorillas do not disperse more seeds as production increases in species having a lower proportion of synchronously fruiting trees; however, they do disperse more seeds the longer a species bears fruit. Regularity within the simultaneously fruiting neighborhood, affects seed dispersal by gorillas, suggesting that gorillas closely track fruiting cycles, and reliability in fruiting food species may directly affect their ability to do so.

Unsurprisingly, higher mean fruit (seed) availabilities and stem densities do not lead to a dynamic response in gorilla-mediated seed dispersal services. Finally, the propensity for gorillas to disperse a significant number of seeds in species, c , is inversely related to the gorilla's dispersal response to

increases in fruit/seed production (c is correlated to β : Spearman's $\rho = -0.527$, $p = 0.0076$). This is not surprising since c , the “baseline” dispersal of seeds (when availability is close to zero), and β , the increase in dispersal as availability increases, are likely associated with a different sets of factors. In the first case, I propose that c is associated with factors that make dispersal possible (i.e., predispositions to gorilla dispersal), such as a threshold level of preference in the diet, a seed that is small enough to be swallowed, and a seed that is not easily detached from the flesh during fruit processing; while β is associated with factors that determine the relative preference for a food within a continuously changing (dynamic) fruiting neighborhood.

Microsite compositional analysis

The subsample to compare microsites contains 330 dung samples across 33 months (only months with at least 10 samples are included in a random draw of ten per month). Twenty-five species seeds are in the subsample. Results of the comparisons of seed combinations between microsites differ depending on whether abundance of composition is considered. Using the abundance of seed species deposited by gorillas, nest and trail sites are significantly different during the months of January-March (Table 4.8). In contrast, there is no difference in the numbers of seeds dispersed to different microsites for any other time of the year. Comparisons based on the composition of seed species exhibit differences between trail and nest-sites only in the case of January (group 1).

Considering only the combinations of seeds in dung that received one of the five, most often, dispersed species, nest-sites receive a greater number of seeds than trail sites in dung containing the seeds of *Cola lizae*, though species composition does not differ between sites. The abundance of seeds are not different between microsites in dung containing *Uapaca* spp., but species composition is different. Finally, in dung containing seeds of *Dialium lopense*, both the abundance and composition of seeds differ between trail- and nest-deposited dung. Microsites receiving dung containing the seeds of either *Ganophyllum giganteum* or *Monanthotaxis congolensis* exhibited no differences in abundance or composition.

Figure 4.5 (A-F). Dispersal effect (responses), measured by the increase in dispersed seeds (standardized beta) to increases in (A) mean relative abundance in fruit, (B) species density (Ln-transformed), (C) fruiting duration, (D) mean proportion of individuals bearing fruit, (E) regularity in mean ripe fruit date, and (F) interannual regularity in ripe-ripe fruit intervals (CV). Asterisks next to letters indicate significant relationships between gorilla responses and the covariate tested.

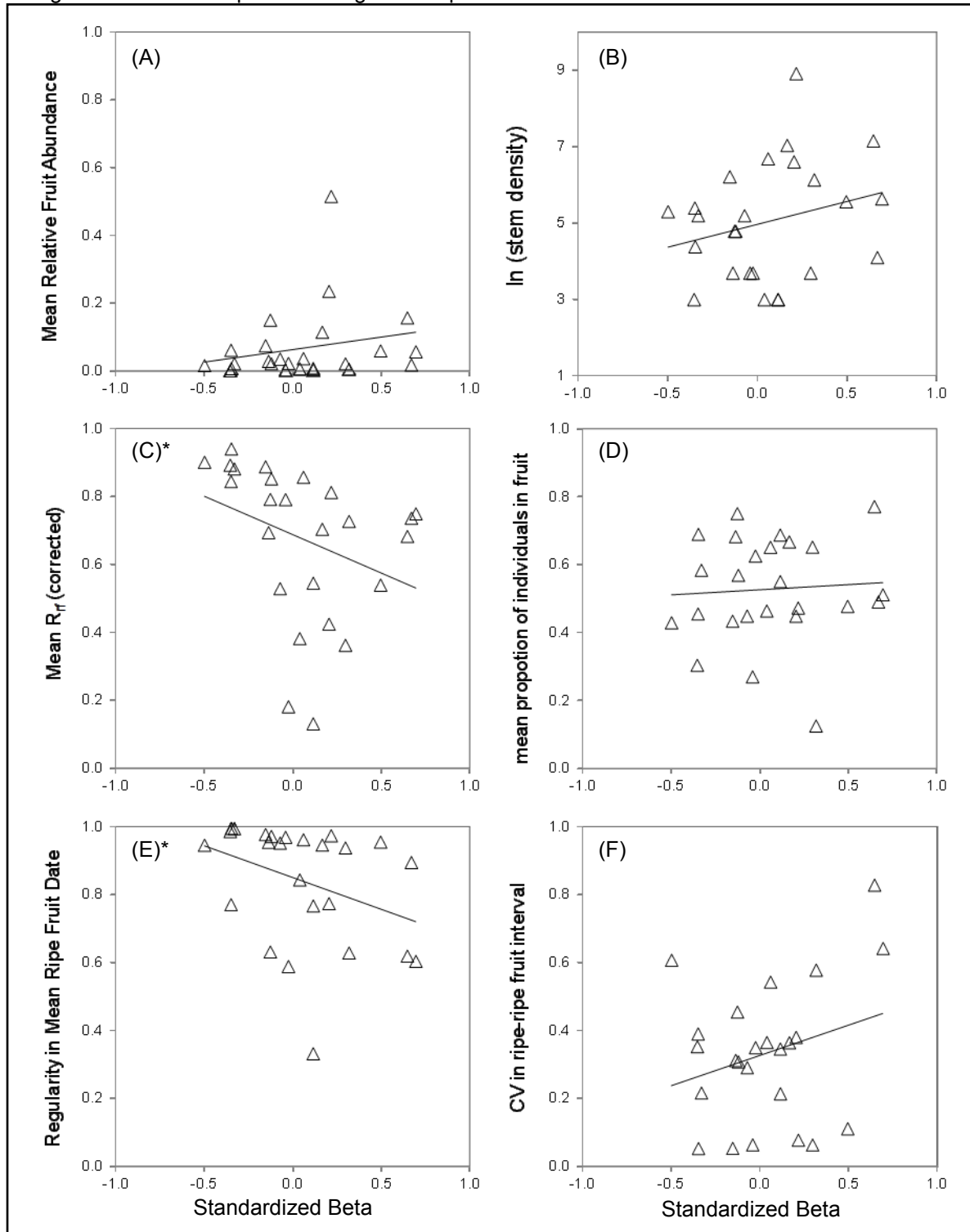


Table 4.8. ANOSIM (R and P values) results for comparisons between trail and nest microsites based on abundance and presence/absence (composition) data of all large-seeded species found in gorilla dung. Significant effects ($p < 0.05$) are highlighted in bold.

Co-dispersed see group	Months	Year	Combinations			
			Abundance		Composition	
1	Jan	1994	R= 0.105	P= 0.032	R= 0.104	P= 0.024
2	Feb-Mar	1994	R= 0.075	P= 0.023	R= -0.013	P= 0.635
3	Apr-Jul	1994	R= 0.073	P= 0.114	R= 0.053	P= 0.172
4	Jun-Aug	1994	R= 0.023	P= 0.219	R= 0.015	P= 0.268
5	Sep-Dec	1993	R= 0.010	P= 0.096	R= 0.005	P= 0.219
species*						
<i>Ganophyllum giganteum</i> (1)		1994	R= 0.066	P= 0.125	R= 0.057	P= 0.112
<i>Cola lizae</i> (2)		1994	R= 0.070	P= 0.037	R= -0.017	P= 0.711
<i>Dialium lopense</i> (3)		1994	R= 0.095	P= 0.014	R= 0.219	P< 0.0001
<i>Monanthotaxis congolensis</i> (3/4)		1994	R= -0.078	P= 0.883	R= -0.096	P= 0.986
<i>Uapaca</i> spp. (5)		1993	R= 0.016	P= 0.114	R= 0.028	P= 0.017

*Values in parentheses are the corresponding co-dispersed seed group. Analyses are on samples randomly selected from seed group subsets.

DISCUSSION

Plant-disperser interactions are dominated by generalist frugivores that consume and disperse a wide variety of plant species. In the megadiverse tropical forests of the Central African Biome, primates generate a complex pattern of multi-specific seed rain. Although dispersal by frugivores can lead to strongly clumped patterns of seed deposition (Schupp et al., 2002; Levine and Murrell, 2003), with some sites receiving many and others none, mechanisms of variability in the abundance and composition of seed rain are poorly understood.

Gorillas disperse a great number of seeds from a diversity of fruit species. Sixty-five percent of dung deposited by gorillas, to two microsites, contained 33 large-seeded species. Dung can be very crowded, with up to 699 large seeds in a single pile. Some species benefit more in terms of “gorilla acquisition”, with 78% of all dung having at least one seed from just four trees, and one climbing-shrub. The co-dispersal of species, in “taxonomic contagions”, is a common trademark in gorilla-mediated seed dispersal, with 54.4% of large-seeded dung containing two or more species (35% of all dung).

Species associations are not random in dung, and not all combinations of (seed) species are likely (or even possible). Dung can be grouped into at least five discrete (and statistically significant) groups of co-dispersed species, which correspond loosely to turnover in the ever-changing, simultaneously fruiting environment. Although dung mass is positively correlated to the number of seeds and species, dung is heaviest during the severe dry season, a period when dung, unsurprisingly, contains the lowest seed densities.

The co-dispersal of large-seeded species in dung is more common between January and March than during any other time of the year, corresponding to the period of greatest ripe fruit abundance (see Fig. 3.9). Dung in January also has the greatest abundance of seeds (mean of 42 seeds/100 grams of dung). If competitive exclusion exists among seeds and seedlings at deposition sites, it should be greatest during the period of highest fruit abundance.

Microsites, broadly speaking, differ in terms of their environmental factors, including available moisture, available sunlight, and protection from trampling (Voysey, 1995). They also differ in the combinations of seeds that arrived to them. Dung deposited around nests has, on average, a greater

mass, and more seeds than trail dung. Differences in the combinations of seeds arriving to different microsites are, in large part, due to variation in seed abundances during the period of highest fruit availability (January -March). However, in dung containing the seeds of certain (preferred) species, deposition sites can differ, in both the number and the composition, of seeds they receive. Thus, for some species, the species with which its seedlings must compete may be less than the total possible combinations, depending on the microsite to which it is dispersed. This variation may lead to different outcomes for recruitment of individual species.

The number of large seeds dispersed by gorillas depended on a number of factors. First, species above a certain seed size threshold were, though their fruits were commonly consumed, unlikely to be dispersed. These species included *Klainedoxa* spp. and *Diospyros mannii* in the sample analyzed here. Second, gorillas dispersed some species in direct proportion to fruit availability. Third, the seeds of some species were dispersed relatively more, the more their fruit became available. This varied in relation to electability for a fruit in the gorilla diet, and to their importance in the fruiting neighborhood relative to other species. Generally, gorillas responded positively (i.e., dispersing more seeds), to species that had longer development times, and those that fruited predictably at the same time of the year.

Schupp (1993) decomposes seed dispersal into quantity and quality, terms that relate to dispersal benefit to an individual tree. For example, in terms of quantity, the most important factors determining the number of dispersed seeds are (1) the number of visits a frugivore makes to a tree, and (2) the number of seeds removed per visit. Both the importance of fruit in the diet, and the reliability of visitation to a plant, influences the number of visits. "Disperser reliability includes a temporal component, the pattern of daily plant visitation, and a spatial component, in which a reliable disperser will dependably visit all individuals of all populations throughout the range of the plant species," (Kaplin and Lambert, 2002:352).

Gorillas appear to demonstrate a high consistency in fruit preference over time, which may translate into visitor reliability for a given species. However, there are few quantitative data on the reliability of visits to individual fruiting trees. Gorillas should be reliable visitors to species with large fleshy fruits that provide a relatively nutritious meal. The exact level of dispersal depends on a host of factors including the electivity of gorillas for a fruit species, the combinations of fruit species available in the

simultaneously fruiting neighborhood, the length of time a species has fruit, and its regularity in the timing of ripe fruit production. From my results, I suggest that the dispersal index (SDI) is good proxy for the reliability of gorillas in dispersing seeds away from any one plant, based on its relationship to abundance in the environment. Though not a tree-level index, it effectively ranks species according to the proportion of the (population-level) fruit crop that can be removed by gorillas.

Dispersers are typically deficient in at least one quantitative trait. Based on avian frugivore studies, Schupp (1993) suggested that the number of visits by a disperser serves as a better predictor of the quantity of seeds dispersed than does the number of seeds removed per visit. Gorillas are expected to make fewer visits to an individual fruiting tree than most avian frugivores; however, groups of gorillas can remove large proportions of fruit crops, often staying in with a fruiting tree for over an hour (Williamson, 1988). Given this feature of gorilla feeding behavior, I expect the number of seeds removed per visit (more than number of visits) to be strongly correlated with the number of seeds dispersed.

In this chapter, I demonstrate that the temporal distribution of phenological patterns greatly influences the seed rain mediated by gorillas. Certain characteristics of phenologies determined the dispersal responses of gorillas; these included the duration of fruit availability and the regularity with which a species maintained a mean fruiting date. Additionally, variation in the combination of seed species dispersed by gorillas depended on the species being dispersed, the neighborhood of simultaneously fruiting species, and the location of the microsite where dung was deposited. In Chapter Five, I analyze the factors that relate to spatial arrangement of gorilla nest-sites, a microsite important in the growth and survival of gorilla-dispersed seeds.

CHAPTER V:
**THE SPATIAL ECOLOGY OF GORILLA NESTING BEHAVIOR: IMPLICATIONS FOR GORILLA-MEDIATED
SEED RAIN AND SEEDLING ESTABLISHMENT**

INTRODUCTION

Wild gorillas, like all great apes, construct nests to pass the night. Typically each night, weaned individuals build a nest, either on the ground or in a tree. The degree of construction varies from minimal to extensive, and the raw material used from woody to herbaceous plants. In Chapter Two, I outline the importance of nest-sites to seed germination and seedling establishment, a topic that has been researched by Voysey (1995) and Rogers et al. (1998). Additionally, understanding the ecological correlates to the nesting behavior of gorillas is important to gorilla conservation. How gorillas utilize their range for food and other resources, such as for nest construction, is a key element to designing effective monitoring programs.

Despite research at SEGC on the importance of gorilla nest-sites to seed dispersal (Rogers et al., 1998; Voysey et al., 1999a,b), the spatial ecology of gorilla nest building has not yet been described for this population. Modeling the important environmental variables that underlie nesting behavior in gorillas (and the possible interaction between nest-sites), will provide a clearer perspective on the consequences of gorilla-mediated seed dispersal to tree species. The groundwork for this type of analysis has been laid by Funwi-Gabga (2011). In this chapter, I analyze a dataset of nest-site locations at SEGC following the methods of Funwi-Gabga (2011), and develop (long-term) nest-site probability maps in order to assess the degree of dispersal limitation in seeds dispersed to nest-sites by gorillas.

Spatial point process modeling

Natural phenomena often occur as point patterns in two-dimensional space (i.e., the plane). The manner in which these points are arranged may provide information on the very objects of study. These objects may include the locations of a wide range of natural occurrences, such as plants, burrowing sites,

the position of animals, fires, earthquakes, etc. Extracting important information from their arrangement is often difficult to detect, extract, and quantify (Turner, 2009).

A point process (e.g., Poisson, Cox, Strauss), is any stochastic mechanism that generates a set of random points in different dimensional spaces (usually either time or geographical space). In the standard jargon of spatial point processes, an *event* refers to actual observations of points, while the *region* (W) is the window of observation (Baddeley and Turner, 2006; Baddeley, 2008). Point processes are well studied in probability theory and are the subject of powerful modeling and analyzing tools that seek to describe and explain the patterns inherent in a point dataset. Modeling a point process is analogous to regression modeling in classical (i.e., non-spatial) statistics, and can be applied to a wide range of fields including forest science (Mateu et al., 1998; Yang et al., 2007; Turner, 2009), epidemiology (Diggle, 2003 ; Bivand et al., 2007), plant ecology (Law et al., 2009), and wildlife ecology (Mayrhofer, 2006; Funwi-Gabga and Mateu, 2012). “Point process models are important not only to understand the effect of different factors on point distribution, but also to predict point occurrence for other areas where point distribution is unknown” (Funwi-Gabga, 2011:4).

The initial step in spatial point process modeling is to summarize the first- and second-order effects within the pattern. First-order effects describe the global spatial trend and compare variations in intensity to the mean value of the process. Second-order effects describe the spatial dependency in the point process. Characterizing and comparing these two effects allows the analyst to test for the most basic of tests in spatial statistics, namely that events are randomly distributed, otherwise known as Complete Spatial Randomness (CSR). A rejection of CSR warrants modeling the aggregations (or inhibitions) in the data by incorporating spatial covariates (i.e., spatial trends), event-event interactions, or both.

Currently, popular GIS software vendors, such as ESRI and its ArcGIS platform, only permit some basic parametric analyses of spatial point data, such as spatial regression analyses (with averaged, lagged, or spatially correlated predictor and/or response variables). Additionally, one may summarize point patterns using the diagnostic properties of first- and second-order statistics, testing them against the assumption of a stationary Poisson process. Out of reach in these analyses, however, are goodness-of-fit

tests for non-stationary Poisson process models, as well as non-Poisson processes incorporating third order (or higher) interactions between events. These must be constructed in a software platform such as R (Baddeley and Turner, 2005).

Specific research questions

My general objective in this chapter is to build predictive models that characterize the placement of nest-sites by gorillas. These models can then be used to describe seed dissemination patterns that result from the directed dispersal of seeds to the immediate vicinity of nest-sites. Specific questions include:

- Are gorilla nest-sites randomly distributed, or are their densities dependent upon geo-environmental gradients within gorilla habitat?
- In addition to environmental covariates, does the distribution of nest-sites conform to models that include (higher-order) interactions between nest-sites?
- Given the best-fit predictive models to nest-sites, are seeds that are distributed in dung around gorilla nests likely to experience significant dispersal limitation, i.e., the preferential arrival of seeds to certain sites, over their arrival to other sites of suitable and similar quality?

METHODS

Gorilla nest-site data

I use 464 nest-site locations collected by researchers in Lopé National Park between 1991 and 2000 for analysis. The XY coordinate locations were obtained from the SEGC and the Wildlife Conservation Society project in Gabon. These data were collected during a period of intensive daily gorillas tracking in the northeastern sector of the park. Researchers followed gorilla trails until they arrived at the site where the gorillas built their nests. In addition, nest-sites were located and recorded opportunistically. The number of nests per site were recorded and commonly differed between sites, usually totaling more than one. Only one GPS waypoint or mapped position was taken at each site. It is

therefore important to emphasize that this analysis is based on nest-site locations and not on the distribution of nests at a particular location.

Nests were constructed by multiple gorilla groups in the area. Nests are not classified according to the gorilla group that created them, since in most cases group identity was unknown. For the purposes of this analysis, only the environmental covariates that best explain the placement of nest-sites are of interest. In analyzing each of the above questions, I was also interested in differences in nesting behavior throughout the year (Table 5.1). I therefore fit models to datasets that were partitioned into three temporal periods, i.e., the 1st wet season (defined here as between January and May), the severe dry season (June-August), and the 2nd wet season (defined here as between September and December).

Table 5.1. Categories of nest-site datasets.

Dataset	Sample size	Description
All nest-sites	458 nests	The entire nest-site dataset
Dry season nests	149 nests	Constructed between June and August
Wet season (1) nests	226 nests	Constructed between January and May
Wet season (2) nests	79 nests	Constructed between September and December

Environmental covariates (predictor variables)

Eight environmental covariates or predictor variables are considered in this study, and my intent is to determine if and how these covariates explained gorilla nest-site locations. I limit the covariates to reflect the factors most expected to influence the choice of nest-site location by gorillas. The covariates are as follows:

Elevation is considered important in the placement of nest-sites due to its influence on vegetation, moisture, and incident heat, and had a demonstrated effect on nest-site locations in Cameroon (Funwi-Gabga and Mateu, 2012). I use a 30-m resolution digital elevation model (DEM) obtained from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation

Model Version 2 (GDEM V2) database available free of charge from <http://earthdata.nasa.gov/>. Elevation values are entered into models as a continuous variable (meters).

Three additional covariates were derived from the DEM, namely slope aspect, slope position, and heat index. Slope aspect and slope degree are calculated using the surface analysis function in the ArcGIS *Spatial Analyst* toolbox (ESRI, 2011). I categorize aspect into four categories, (1) northeast, (2) southeast, (3) southwest, and (4) northwest. Slope degree was categorized into six slope positions, (1) valley, (2) Toe slope, (3) flat, (4) med slope, (5) upper slope, and (6) ridge. The toolbox also has the ability to calculate the Heat Load Index (also known as Beer's aspect) which is a measure of the potential heat incident at a location in the study area. The formula of heat load is: $Heat\ Load = 1 + \cos((45^\circ - \text{slope aspect}) / \text{slope degree})$. I include heat index as a continuous covariate, naturally ranging between 0 (the warmest point) and 2 (the coolest point).

The presence of water has been shown to influence habitat use in gorillas. For example, gorilla density is known to be three times higher in flooded habitats than in a region of primary forest in the Republic of Congo (Blake et al., 1995; Bermejo, 1999), and the combination of Marantaceae forests which provide year-round herbaceous foods, and hydromorphic forest clearings, which afford mineral-rich water plants, correspond to the highest densities known for the species (Magliocca et al., 1999; Magliocca and Gautier-Hion, 2002; Poulsen and Clark, 2004). For this reason, I predict distance from a water channel might influence the distribution of gorilla nest-sites. Distances are Euclidean (in meters) and included as a continuous variable.

Paths throughout the study area have been created and maintained by both wildlife and humans, and are used by both wildlife and researchers for easy navigation through the thick vegetation. I therefore included the distance from the network of paths at SEGC as a factor that might influence nest-site placement. My rationale was that distance from path might be a proxy indicator to bias in observer-detection of gorilla nest-sites. Since paths are commonly used by researchers to reach gorilla core areas, a disproportionately high number of nest-sites next to paths might indicate a human error rather than an ecological correlate. Euclidean distances away from any trail are included as a continuous variable (in meters).

Vegetation type has been shown to influence nest-site placement in Lopé. For example, Tutin et al. (1995) demonstrated that nesting in forested areas is associated with an abundance of ripe fruit in the neighborhood. It appears that gorillas might nest in areas having a sub-optimal abundance of nesting material (open understories), including forests growing on poor or rocky soils, colonizing forests near the savanna/forest interface, and mature forests, when fruit is abundant, rather than travel out of these areas to find herbaceous plants for nesting. Corroborating this, Schaller (1963) and Groves and Sabater Pi (1985) found that gorillas tend to simply "sleep close to their last feeding site in the evening" (Tutin et al., 1995:70). Since vegetation type is strongly associated with the composition of fruit resources, I predicted that vegetation type would strongly influence the placement of gorilla nest-sites in the study area.

To incorporate broad-scale vegetation types into the models, I defined types according to White et al. (1995) and White (2001). In the descriptions that follow, I include the tree species that are commonly associated with each type, and the numbers in parentheses indicate the season they bear ripe fruit if important in the gorilla diet (1= wet season 1, 2= wet season 2, and 3= dry season). I also include generalizations on the densities of ground herbs belonging to the families Marantaceae (arrowroot) and Zingiberaceae (gingers) which provide important food items and nest building materials to gorillas. The degree of canopy cover in each case is broadly defined.

Mixed Marantaceae forest, has a highly closed canopy cover (95%), and relatively high species diversity and evenness. Species include *Cola lizae* (1), *Aucoumea klaineana*, *Scyphocephalum ochocoa*, *Santiria trimera* (1/2), *Irvingia* spp. (1/2), *Dacryodes* spp. (1), *Desbordesia glaucescens*, and *Strombosiopsis tetrandra*. Densities of herbaceous ground cover are less than Marantaceae forest but still abundant as canopy cover increases.

Marantaceae forest has a discontinuous canopy (~85%) that allows light to penetrate to the forest floor. This type has a notably low stem density in the middle story. Dominant tree species are *Cola lizae* (1) and *Aucoumea klaineana*. Other common species include *Xylopia* spp. (3/2), *Diospyros* spp. (1), *Pentaclethra* spp., and *Pycnanthus angolensis*. The understory is covered with dense herbaceous growth.

Rocky forest type has rock outcrops associated with thin and short (10-20 m high) forests characterized by *Diospyros* spp. (1), *Dichapetalum* sp., *Scottellia coriacea*, *Hylodendron gabonense*, *Trichilia prieureana*, *Cassipourea congensis*, and *Monanthotaxis congoensis* (1). Herb densities are low to intermediate, depending upon the vegetation type, colonizing or Marantaceae forest, with which this type is associated. Canopy cover can be highly discontinuous.

Monodominant forest is dominated (>75% of basal area) by one or more of a few species, including *Aucoumea klaineana*, *Lophira alata*, and *Sacoglottis gabonensis*. Herbs are slightly more abundant than in the next category. Additional species, such as *Klainedoxa gabonensis* (2), occur in low densities. Ground vegetation is sparse, but some herbs may become established, notably *Aframomum longipetiolatum* and *Megaphrynium* spp.

All other forest types are pooled due to their low areal coverage (4.5% of the analysis window). Some types are known to influence nesting behavior during different periods of the year and are important, in terms of surface area, in certain areas outside of the analysis window. **Colonizing forest** is recently colonized savanna dominated by *Aucoumea klaineana*, *Lophira alata*, and *Sacoglottis gabonensis*. Common gorilla foods here are *Xylopia* spp. (2/3), *Klainedoxa gabonensis* (2), and *Uvariastrum pierreanum* (1). Canopy cover is discontinuous between 30-70% (White et al., 1995).

Marantaceae swamps, and other types that are associated with water, are scattered throughout the study site. These are associated with some important gorilla fruit species including *Nauclea vanderghuchtii* (2), certain *Uapaca* spp. (2), *Myrianthus arboreus* (1), and *Pseudospondias microcarpa* (1/2). Swamps become very important during the dry season when overall fruit availability is low, and gorillas consume the keystone herb, *Marantochloa cordifolia* (3). **Savanna** (*Psidium* spp. (1/3)) and **Cyperaceae swamps** are included but are uncommon habitats for gorilla nesting. These types have very open canopies, and intermediate to low densities of Marantaceae ground herbs. Much of the ground vegetation is dominated by grasses.

Certain habitats important to gorillas at Lopé occur on much smaller scale than that of the vegetation categories above, and are dispersed throughout the study area. These include marshes, light gaps, and disturbed or secondary forests. In order to capture the effect that small-scale canopy structure

might have on gorilla nesting behavior, I calculated the degree of canopy texture (modeled as the standard deviation) across a 3 x 3 moving window passed over the reflectance values from the NIR spectral band (band 5 $\lambda = 1,580-1,750$ nm) of an image captured by the SPOT XS sensor (20 m resolution). Infrared spectral bands are often used in texture analysis and pattern recognition of forested areas to quantify canopy structure (Riou and Seyler, 1997), with forested areas having a higher texture than grasslands. Texture analysis was implemented in ERDAS Imagine 11.0 (Leica Geosystems, Atlanta, Georgia, USA).

Prior to use in the models here, I wished to verify whether canopy structure, as measured by texture, could identify large-scale vegetation types. A Tukey's Honest Significant Difference (HSD) test between texture and vegetation type confirmed that texture could be used as a signal to canopy continuity, with higher texture values being associated with more closed-canopied vegetation types. Texture could be applied on a much smaller scale (20-60 m) than the broad-scale vegetation categories above, and could therefore be expected to model, with moderate certainty, light gaps, marshes, or disturbed forests should they exist in the analysis window.

Summary statistics for each environmental covariate are found in Table 5.2. The window of analysis (3.7 km^2) is the area containing the core search area of nest-sites between 1991 and 2000.

Characterizing spatial patterns in gorilla nest-sites

The first step in spatial point analysis is to visualize the long-term pattern in nest-sites by “smoothing” the datasets. I characterized the nest-site intensities at a location (i.e., the first-order properties) by applying a smoothing kernel to each of the four datasets, producing a visual tool for observing differences in the spatial structure of nest-site occurrences (Diggle, 2003; Møller and Waagepetersen, 2003). The kernel-smoothed intensity measures the mean number of nest-sites per unit area at a general location within the study area. They do not, however, “provide any information on interaction between events in the point pattern, but yield a general idea about their spatial distribution; that is they only provide information on the global spatial trend of point distribution,” (Funwi-Gabga, 2011:11). For a general location (s) and a given dataset (X), the kernel-smoothed intensity is given by:

$$\lambda_b(s) = \frac{1}{C_b(s)} \sum_{i=1}^n K_{ib}(s - x_i)$$

where $K_b()$ is a kernel with band $b > 0$, and $C_b()$ is an edge correction factor (Diggle, 2003; Yang et al., 2007, Funwi-Gabga, 2011).

Table 5.2. Summary statistics of the environmental covariates in modeling the distribution of gorilla sleeping nest-sites.

Continuous	Spatial scale (m)	Summary statistics		Z-units
Elevation	30	$\mu = 283.6, \sigma = 21.75$	{214.7, 385.3}	meters
Distance to water	10	$\mu = 116.1, \sigma = 105.66$	{0, 617.7}	meters
Distance to trail	10	$\mu = 68.4, \sigma = 62.23$	{0, 403.1}	meters
SD (SPOT SWIR band)	20	$\mu = 24.7, \sigma = 8.47$	{2.51, 60.26}	DN's
Beer's aspect	30	$\mu = 0.98, \sigma = 0.71$	{0, 2}	unitless
Categorical		Proportion of coverage		
Aspect	30			
NE		0.239		
SE		0.179		
SW		0.233		
NW		0.349		
Slope position	30			
Valley		0.111		
Toe slope		0.161		
Flat		0.153		
Mid slope		0.278		
Upper slope		0.172		
Ridge		0.125		
Vegetation type	10			
mixed Marantaceae forest		0.493		
Marantaceae forest		0.257		
rocky forest types		0.073		
monodominant forest		0.131		
all other types		0.045		

In addition to first-order properties, second-order characteristics provide information on small-scale spatial correlations in the nest-site data. Second-order properties statistically present the distributional dependencies inherent in point patterns (Illian et al., 2008). These properties can be characterized by Ripley's K function (Ripley, 1977), which is defined as:

$$K(r) = \frac{E(\text{mean number of events within a distance } r \text{ of an arbitrary event})}{\lambda}$$

where λ is the intensity, or the mean number of points, per unit area. The empirical estimate of K can be compared to K-curves from independent simulations of the complete spatial randomness (CSR), which is $K(r) = \pi r^2$. Deviations between the empirical and theoretical K-curves can then be used to determine whether a point pattern is regular or clustered, with $K(r) < \pi r^2$ indicating a regular (i.e., inhibition) distribution of points, and $K(r) > \pi r^2$ indicating a spatial clustering of points (Yang et al., 2007; Funwi-Gabga and Mateu, 2012). The larger the difference between $K(r)$ and πr^2 , the greater the clustering (or regularity) in the point pattern dataset. To test for deviations from CSR, I use the critical pointwise K values from 199 Monte Carlo simulations of the null model (Baddeley and Turner, 2005). This test has an exact significance level of $\alpha = 2/(1 + \text{number of simulations})$; equivalent to $p = 0.01$ in one-sided tests.

Spatial point process modeling

Homogeneous Poisson Process (HPP)

The first models fit to the datasets are null models that assume a uniformly random distribution of nest-sites within the study area (W). These models are considered to be both stationary and isotropic (Bivand et al., 2007), where the occurrence of any nest-site is independent of the occurrence of another, and the estimated intensity (λ) is invariant across space. Their second-order properties only depend on the relative positions of nest-sites, and not on the environment (or Cartesian coordinates) at their locations (Illian et al., 2008; Funwi-Gabga, 2011).

Inhomogeneous Poisson Process (IPP)

If the empirical K-curves from the datasets are inconsistent with the assumption of a uniform nest-site intensity, I assume their occurrences are influenced by stochastic dependencies in selected environmental covariates and/or Cartesian coordinates (Funwi-Gabga and Mateu, 2012). All combinations of the eight environmental covariates were fitted, resulting in 255 candidate models. Models were fit using the Maximum Pseudolikelihood Estimation (MPLE) method (Baddeley and Turner, 2005), which approximates the maximum likelihood estimation (MLE) and is recommended for point process modeling (Funwi-Gabga and Mateu, 2012). The Berman-Turner algorithm is used to fit models using MPLE (Berman and Turner, 1992; Baddeley and Turner, 2000), wherein models are formulated in terms of their Papangelou conditional intensity, $\lambda(u, x)$, which is the probability of an even occurring at point u given that the rest of the process coincides with the point pattern X (Baddeley and Turner, 2000; Yang et al., 2007; Funwi-Gabga, 2011).

In practice, the conditional intensity is modeled through a log-linear regression model:

$$\log \lambda(u, x) \sim \theta_0 + \theta_1 \beta(u) + \theta_2 \beta(u)^2$$

where the spatial trend term $\beta(u)$ represents the value of an environmental covariate or a Cartesian coordinate at location u (Baddeley, 2008); and theta are the fitted parameters representing the constant effect (θ_0), and the effects of the first (θ_1) and second (θ_2) degree terms of the spatial covariate or coordinate considered. As recommended by Yang et al. (2007), I model all continuous spatial covariates as quadratic functions to ensure convergence in the likelihood estimation.

Environmental covariates are considered in models without the addition of Cartesian coordinates, which in turn were included only when the best-fit covariate models are deemed inadequate to explain the spatial trend in nest-site occurrences. The inclusion of Cartesian coordinates to the intensity formula is equivalent to including any trend variables that are not available (Yang et al., 2007; Baddeley, 2008; Funwi-Gabga, 2011), but are presumably important in nest-site distribution. Such factors may include climatological (i.e., temperature and rainfall) and ecological variables (i.e., the composition of gorilla food items in the immediate vicinity of nest-sites).

Non-Poisson models

If the models including environmental covariates and/or Cartesian coordinates are deemed inadequate to describe the distribution of nest-site intensities, I then explore non-Poisson models that incorporate a stochastic interaction between nest-sites. In these models, an interaction term, $C(u, x)$, is added to the Papangelou conditional intensity function from above:

$$\log \lambda(u, x) \sim \theta_0 + \theta_1 \beta(u) + \theta_2 \beta(u)^2 + \theta_3 C(u, x)$$

where θ_3 is the fitted parameter on the interaction term, and $C(u, x)$ depends on both the location of u and the configuration of x (Yang et al., 2007).

Numerous interaction models are available to fit to point data, including the Strauss process (Strauss, 1975) and the Geyer saturation process (Geyer, 1999; Turner, 2009). Following Funwi-Gabga (2011), I chose the area-interaction model over other models in order to lend my results to comparisons with his results from Cameroon, and because, unlike other models, it is not based on a simple pairwise interaction but on a much more complex structure of interactions (Baddeley, 2008; Illian et al., 2008).

The area-interaction process is defined as a point pattern process with probability density given by:

$$f(x_1, \dots, x_n) \sim \alpha k^{n(x)} \eta^{-A(x)}$$

where x_1, \dots, x_n are the points in the point pattern, k is the intensity parameter, η is the interaction parameter, $A(x)$ is the area of the region created by the union of discs of radius r centered at the points x_1, \dots, x_n , and α represents a normalizing constant (Baddeley and van Lieshout, 1995). The interaction parameter η is < 1 in an inhibitive distribution, > 1 in a clustered distribution, and $= 1$ in a distribution that exhibits no interaction (i.e., a Poisson process). In the rare case where $\eta = 0$, then no points are observed within the hardcore distance (r) of any point in the point process (Baddeley and van Lieshout, 1995; Funwi-Gabga, 2011).

Estimation of the interaction radius (r)

In area-interaction models, the interaction radius is a constant, and must be determined prior to model fitting. Baddeley and Turner (2000) proposed that r be obtained by maximizing the profile log-pseudolikelihood for the data. Thus, for each dataset, I iteratively fit area-interaction models using a range of interaction radii, from 10-300 m, in 2-meter intervals. The upper value of 300 m is based on the maximum inter nest-site distance used in K function estimates. For each dataset, therefore, 146 interaction models were fit, and the radius that corresponds to the maximum log-pseudolikelihood is used in as the interaction radius in Area-interaction models.

Model selection

From the 255 competing candidate covariate models for each nest-site dataset, the best-fit model must be chosen. For this, I use Akaike's Information Criterion (AIC). The AIC is a useful method of selecting the best-fit model because it minimizes the effect of increased number of parameters in selecting the better model (Akaike, 1974). Among competing models, the model with the smaller AIC is considered to fit better the data.

I use residual analysis to determine whether a fitted point pattern depended on, or was improved by, the inclusion of tested covariates. I use a technique called the lurking variable plot to investigate the presence of spatial trend in the data, wherein the Pearson residual measure for any sub region is plotted against each continuous covariate (or Cartesian coordinate) (Baddeley et al., 2005). If a model is good fit, then the cumulative Pearson residuals should approximate to zero and, when plotted against a continuous variable, should fall within 2σ error bands.

To test for goodness-of-fit of model assumptions to fitted models, I computed generalized K-functions, as suggested by Baddeley et al. (2000). This technique evaluates second-order patterns after weighting the first-order effects using the tested model. If the model assumptions are reasonably sound, then the generalized K-curve from the data should fall within the envelope created by 199 simulations of the trend from the fitted model.

Cumulative Pearson residual plots and generalized K-function simulations are not useful in detecting interactions between nest-sites. To validate the interaction terms in a point process model, Baddeley (2008) suggests plotting the distribution of the residuals in a Q-Q plot. A Q-Q plot of smoothed residuals from a fitted point process model is a useful way to check for assumptions of nest-site interactions, while the systematic part of the model (i.e., spatial trend, covariate effects, etc) should be assessed using lurking residual plots.

The choice of analysis window is a key decision in spatial point analysis and is often overlooked. I chose to define the study area as the smallest rectangle that encloses the majority of the nest-site locations. This results in excluding some isolated nest-sites far from the core area that may have otherwise great influence second-order summary statistics. A rectangular window, oriented in the X and Y directions, was achieved by rotating the nest-site pattern, which ran along a SW-NE line, by 45° in a clockwise direction. This created a window that is orthogonal to the x and y axes (Fig. 5.1), making computations in fitted models drastically more efficient, especially in interaction models.

I built a GIS database in the Universal Transverse Mercator (UTM) Zone 32S from geo-referenced data collected in the field, and from the SEGC library of shapefiles. Meandering trails and rivers were either meticulously logged using a Garmin® 60CSX handheld in the field, or plotted in the GIS from a high resolution SPOT XS (20-meter) satellite image, which I geo-referenced using anchor points throughout the study site. From the GIS, nest-sites and all covariate data were exported into R and rescaled to one-tenth their original resolution, from 1-meter to 10-meter grids, a scale I consider appropriate since it is close to the scale of individual nests within a nest-site, as well as the inherent error in a handheld GPS.

All spatial data were managed or derived using ArcGIS 10 (ESRI, 2011). All analyses were performed in the R programming language (R Core Team, 2012). Spatial point models are fitted and diagnosed using the “spatstat” package (Baddeley and Turner, 2005).

RESULTS

First-order characteristics of gorilla nest-site distributions

I estimate the long-term trend and the uniform intensity values (mean number of nest-sites / square meter) for each dataset by applying a smoothing kernel. The greatest issue in applying a kernel is the choice of the “smoothing parameter” or sigma (σ). Following the suggestion of Turner (2009), I set sigma equal to $0.05 \times |W|^{1/2}$ where $|W|$ denotes the area of the window of observation, or 5% of the edge length of the square equal to the same area as W .

Kernel-smoothed intensity plots (Fig. 5.2.A-D) for all nest-site datasets reveal obvious deviations from the primary assumption of a homogeneous Poisson process (i.e., uniform intensity). In each dataset, “hot” and “cold” regions can be observed, suggesting that nest-sites are not randomly distributed, and thereby follow some other process.

Second-order characteristics will verify whether nest-sites are distributed according to CSR. In Figure 5.3, envelopes computed from 199 simulations of the null hypothesis are used to test for CSR. Simulated envelopes of the K-function reveal that nest-sites do not conform to the assumption of CSR for all nest-site datasets. Among nest-site locations across 10 years, and all seasons (Wet or Dry), for example, the empirical K functions are greater than the CSR theoretical K-curves, that is $K(d) > \pi d^2$, at distances greater than 20-50 meters, indicating a clear departure from CSR toward spatial clustering.

From these results, the null hypothesis of CSR is rejected in all datasets, and I conclude that gorilla nest-site distributions exhibit some evidence of clustering. Further modeling of the data is needed to verify whether nest-sites are arranged according to heterogeneity in environmental factors.

Fitting point process models

Models of homogeneous Poisson processes

I fitted stationary Poisson process models to the four nest-site datasets. This set of models, hereafter referred to as null (M_0) models, are used as references against which subsequent models are compared. The AIC values for each null model are in Table 5.3. The null model for the “all nests” dataset

has a constant intensity of $1.258 \times 10^{-4} / \text{m}^2$ over the entire region between 1991 and 2000. This can be interpreted as an average of 125.8 observed nest-sites per square kilometer in the study window over the 10-year study period.

The assumption of uniform intensity of gorilla nest-sites across the study area makes it possible to estimate approximately the observation (or discovery) rate of nest-sites during data collection. For example, assuming an average density of 1 gorilla / km^2 in the study area (White, 1992; Voysey, 1995), and an average group size and home range of 10 individuals and 10 km^2 , respectively, I am able to estimate an “all nest-site” observation rate of 0.34 over the entire 10-year period. Rates for the other datasets are included in Table 5.3.

Table 5.3. Constant intensity values in stationary Poisson models (M_0) fit to the four nest-site datasets. These models assume a uniform (Poisson) distribution of nest-sites.

Nest-site pattern	Uniform Intensity (points per m^2)	AIC	number of parameters	number of nests	observation rate
H_0 all nest-sites	1.258×10^{-4}	5032.67	1	468	0.3447
H_0 wet season 1	6.236×10^{-5}	2821.44	1	232	0.4100
H_0 dry season	4.086×10^{-5}	1977.77	1	152	0.4478
H_0 wet season 2	2.150×10^{-5}	1144.58	1	80	0.1767

Models of inhomogeneous Poisson processes

Having ruled out the assumption of complete spatial randomness in the placement of gorilla nest-sites, the next step is to test whether environmental gradients influence the placement of nests by gorillas. I fit models to all possible combinations of the eight environmental covariates (Fig. 5.4), resulting in 255 competing inhomogeneous Poisson models (hereafter M_1 models) for each of the four nest-site datasets. Models within 2 AIC values of the best model (i.e., lowest AIC) are in Table 5.4. For each nest-site dataset, AIC values from inhomogeneous models are an improvement over the homogeneous Poisson models (M_0) from Table 5.3.

In the case of “all nest-sites”, slope position, distances from rivers and paths, vegetation types, and the standard deviation in the SPOT SWIR sensor, are identified as predictor variables. Cumulative Pearson residuals, plotted against each of the continuous covariates and for each of the best-fit M_1

models, demonstrate that M_1 models are largely adequate to explain the distribution of nest-sites at SEGC, at least with respect to the chosen covariates. However, there is a violation of the 5% significance bands in cumulative Pearson's residuals when plotted against Cartesian coordinates in three out of the four datasets (Fig. 5.5), implying the presence of some remaining residual spatial trend after inclusion of environmental covariates. The exception, the case of the "wet season 2" dataset, lurking variable plots indicate that the covariates are adequate in capturing the spatial trend.

I perform goodness-of-fit tests by plotting generalized second-order K functions for each M_1 model (Fig. 5.6). These plots indicate there is either residual spatial trend, an interaction between nest-sites, or both, remaining in the data.

Figure 5.1. Gorilla nest-sites showing UTM zone 32S Cartesian coordinates and analysis window. Image to the right demonstrates the 45° clockwise rotation around the anchor point (latitude=9,975,596 m, longitude=787,826 m (UTM 32S)). Cross-hatches represent nest-site locations.

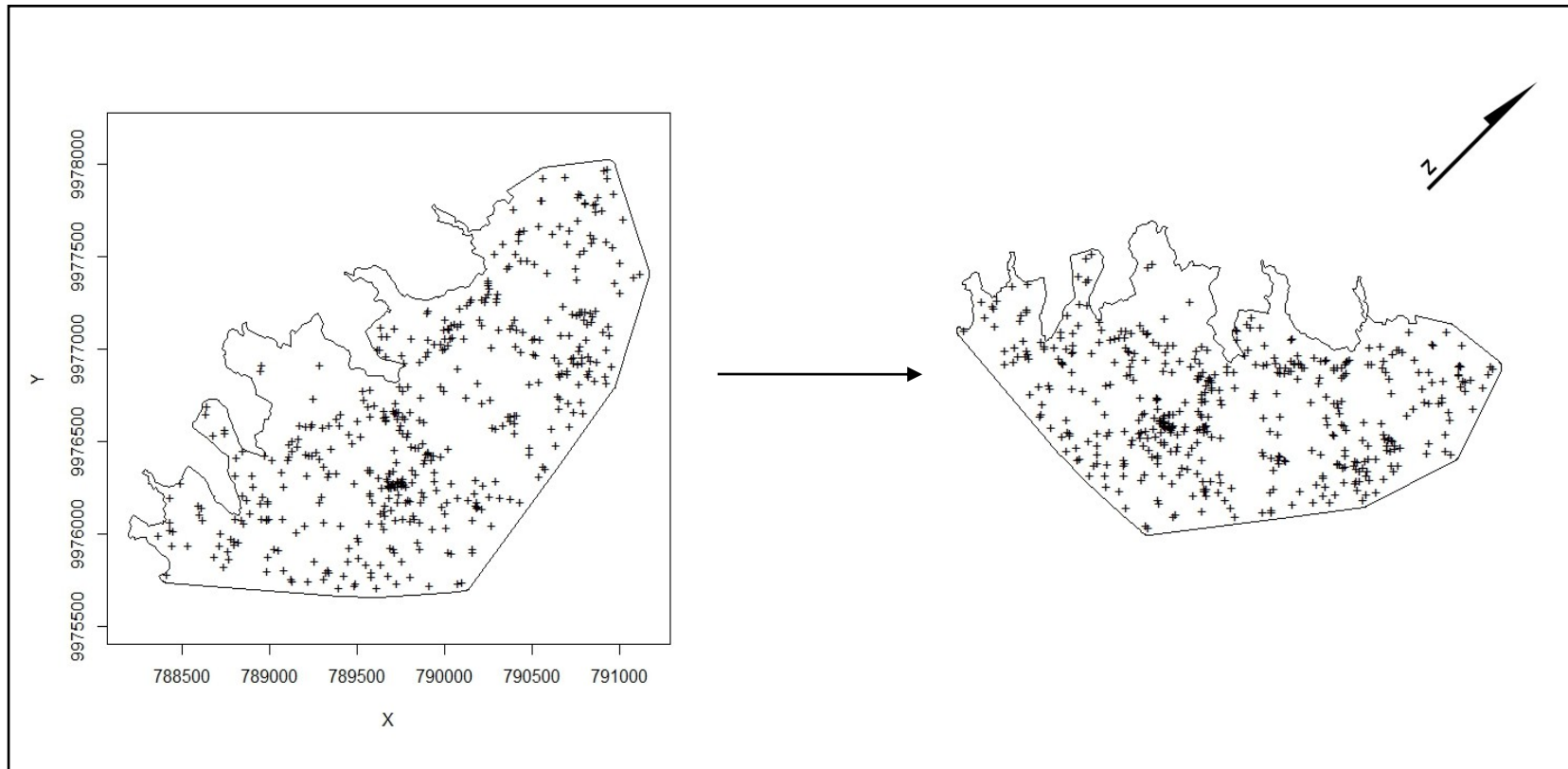


Figure 5.2. (A-D). Kernel-smoothed intensities of nest-site datasets. Cross-hatches represent the observed nest-site locations. The smoothing bandwidth parameter (σ) is set to 5% of the square root of the window area.

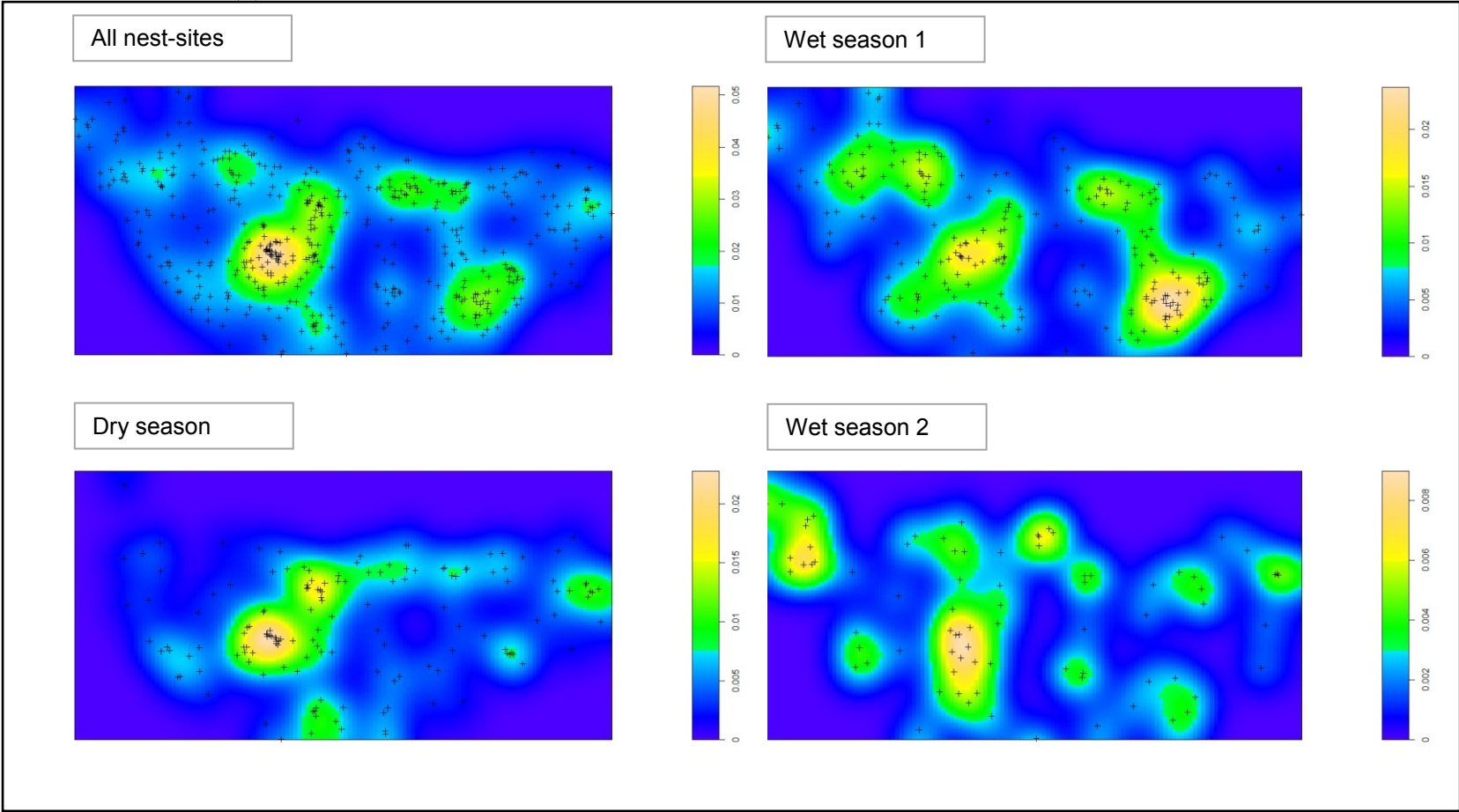
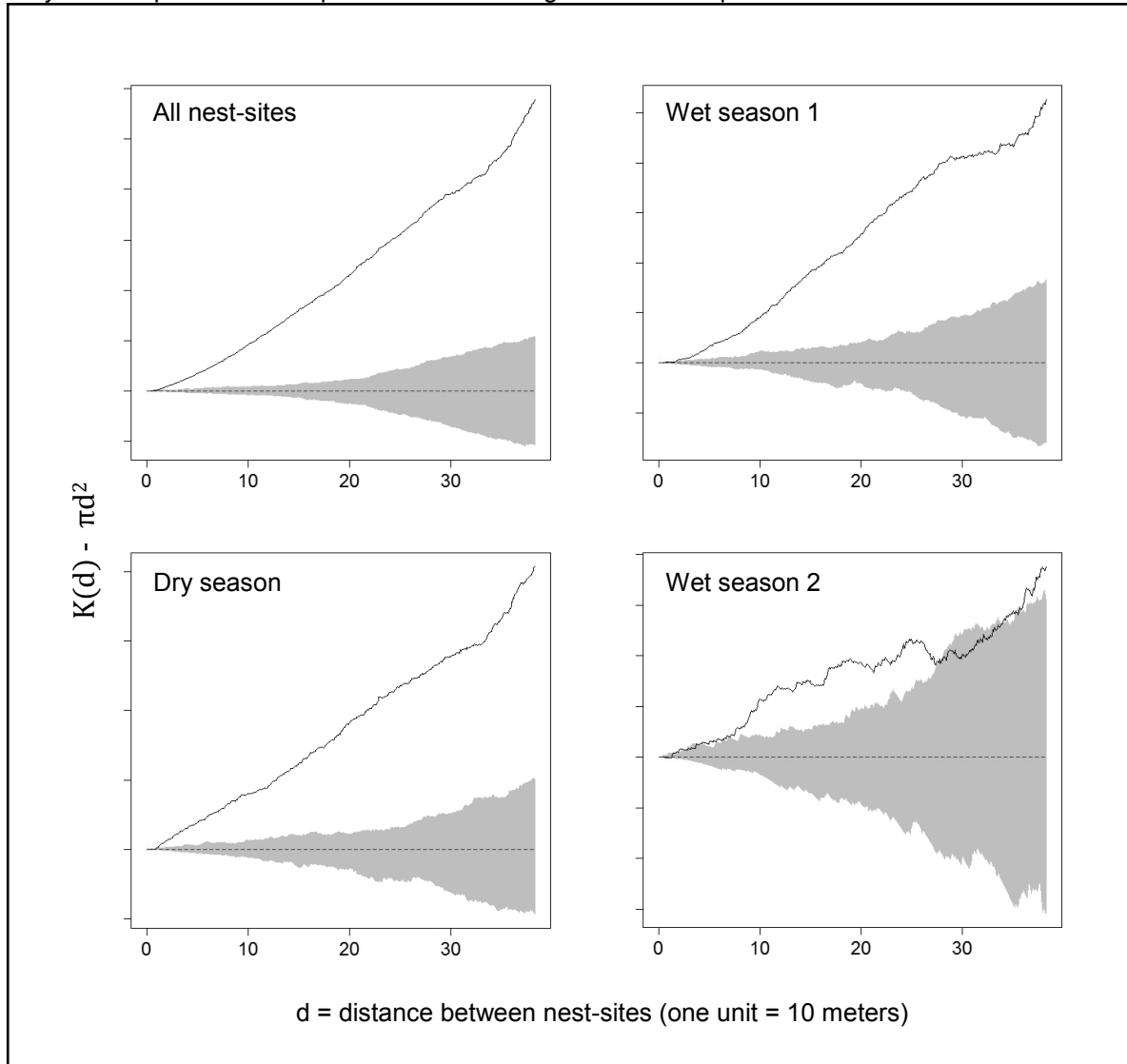


Figure 5.3. Second-order K-function at fixed inter-nest-site distances of empirical nest-site patterns. $K = \lambda^{-1}(E = \text{expected number of nest-sites within a distance, } d)$. The value πd^2 is subtracted from the K to get a more readable plot. The shaded region indicates envelopes from 199 simulations under the assumption of complete spatial randomness (CSR). The solid line is the empirical K curve. Values of $K(d) - \pi d^2$ above the envelope indicate nest-sites that are closer to each other than expected from a homogeneous Poisson (i.e., random) pattern, while those below indicate regularity (i.e., inhibition). The test has an exact significance level of $2/(1+199) = 0.01$. The scales of the ordinal axes are not displayed since only the comparisons of empirical values with significant envelopes are relevant.



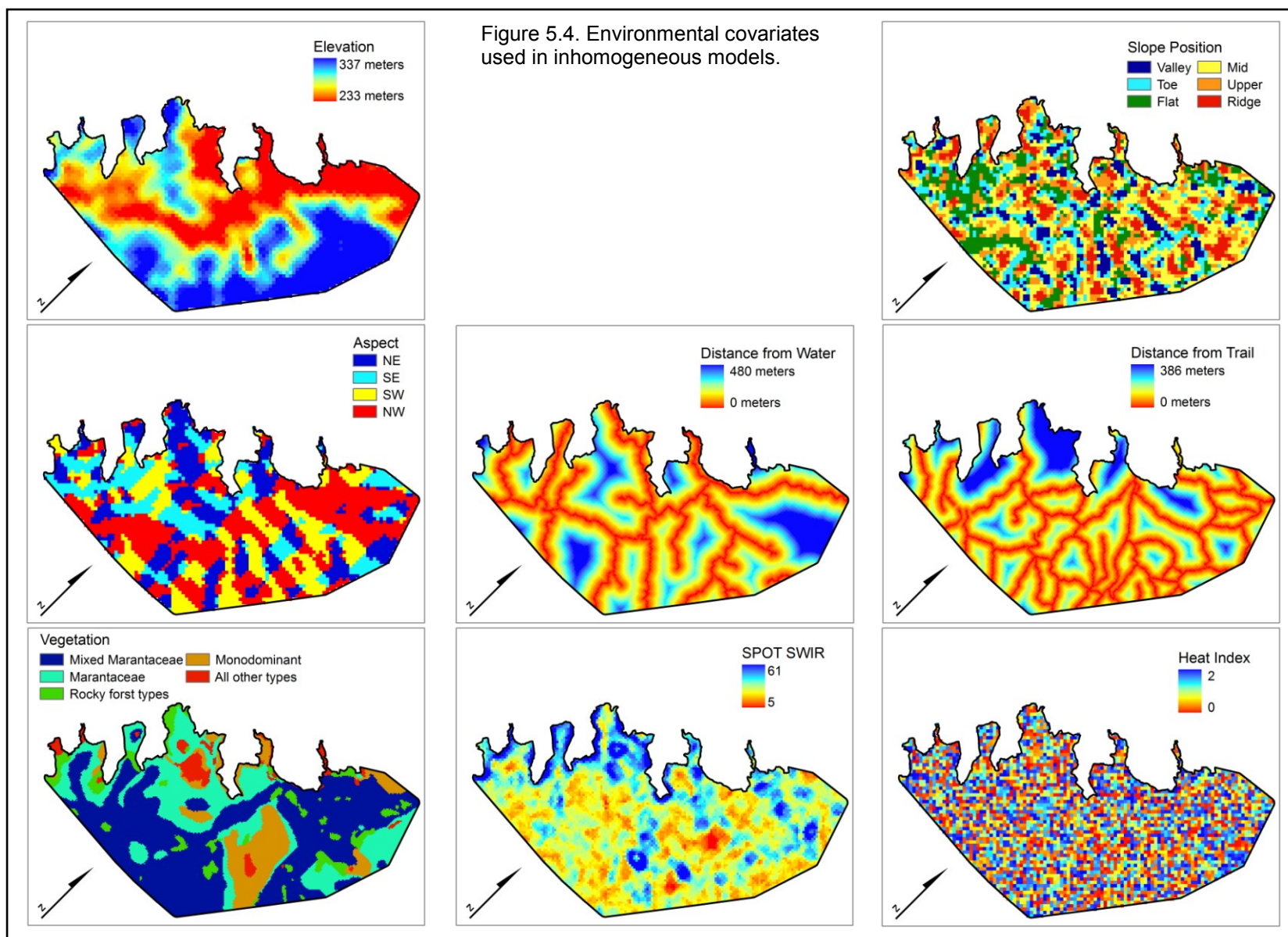


Table 5.4. The intensity functions for inhomogeneous Poisson point process models that only include spatial covariates (M_1) fitted to the four nest-site datasets. For each dataset, all models (out of 255 competing models) within 2 AIC units of the “best-fit” model are listed. The best-fit model is in bold.

Model	AIC	No. of parameters	Formula
All nest-sites	4908.8	16	$F(D_2) + P(D_{4,2}) + P(D_{5,2}) + F(D_6) + P(D_{7,2})$
	4910.6	18	$P(D_{1,2}) + F(D_2) + P(D_{4,2}) + P(D_{5,2}) + F(D_6) + P(D_{7,2})$
Wet season 1	2746.8	16	$P(D_{1,2}) + F(D_2) + P(D_{4,2}) + F(D_6) + P(D_{7,2})$
	2747.0	18	$P(D_{1,2}) + F(D_2) + P(D_{4,2}) + F(D_6) + P(D_{7,2}) + P(D_{8,2})$
	2748.0	14	$F(D_2) + P(D_{4,2}) + F(D_6) + P(D_{7,2})$
	2748.4	16	$F(D_2) + P(D_{4,2}) + F(D_6) + P(D_{7,2}) + P(D_{8,2})$
	2748.5	19	$P(D_{1,2}) + F(D_2) + F(D_3) + P(D_{4,2}) + F(D_6) + P(D_{7,2})$
	2748.7	21	$P(D_{1,2}) + F(D_2) + F(D_3) + P(D_{4,2}) + F(D_6) + P(D_{7,2}) + P(D_{8,2})$
Dry season	1929.6	13	$P(D_{1,2}) + P(D_{4,2}) + P(D_{5,2}) + F(D_6) + P(D_{7,2}) + P(D_{8,2})$
	1929.9	11	$P(D_{1,2}) + P(D_{4,2}) + P(D_{5,2}) + F(D_6) + P(D_{7,2})$
	1930.0	11	$P(D_{1,2}) + P(D_{4,2}) + P(D_{5,2}) + F(D_6) + P(D_{8,2})$
	1930.3	9	$P(D_{1,2}) + P(D_{4,2}) + P(D_{5,2}) + F(D_6)$
	1930.7	18	$P(D_{1,2}) + F(D_2) + P(D_{4,2}) + P(D_{5,2}) + F(D_6) + P(D_{7,2}) + P(D_{8,2})$
Wet season 2	1137.8	9	$P(D_{4,2}) + P(D_{5,2}) + F(D_6)$
	1138.2	7	$P(D_{5,2}) + F(D_6)$

D_1, D_2, \dots, D_8 denote the spatial covariates: elevation (m), slope position, aspect category, distance to water channel, distance to trail, habitat category, SPOT[®] satellite sensor band 5 variance, and Beer's aspect.

P denotes the order of polynomial; F denotes a factor.

Figure 5.5. Lurking residual plots of the best-fit M_1 models to nest-site datasets. Models include environmental covariates (i.e., inhomogeneous Poisson process models).

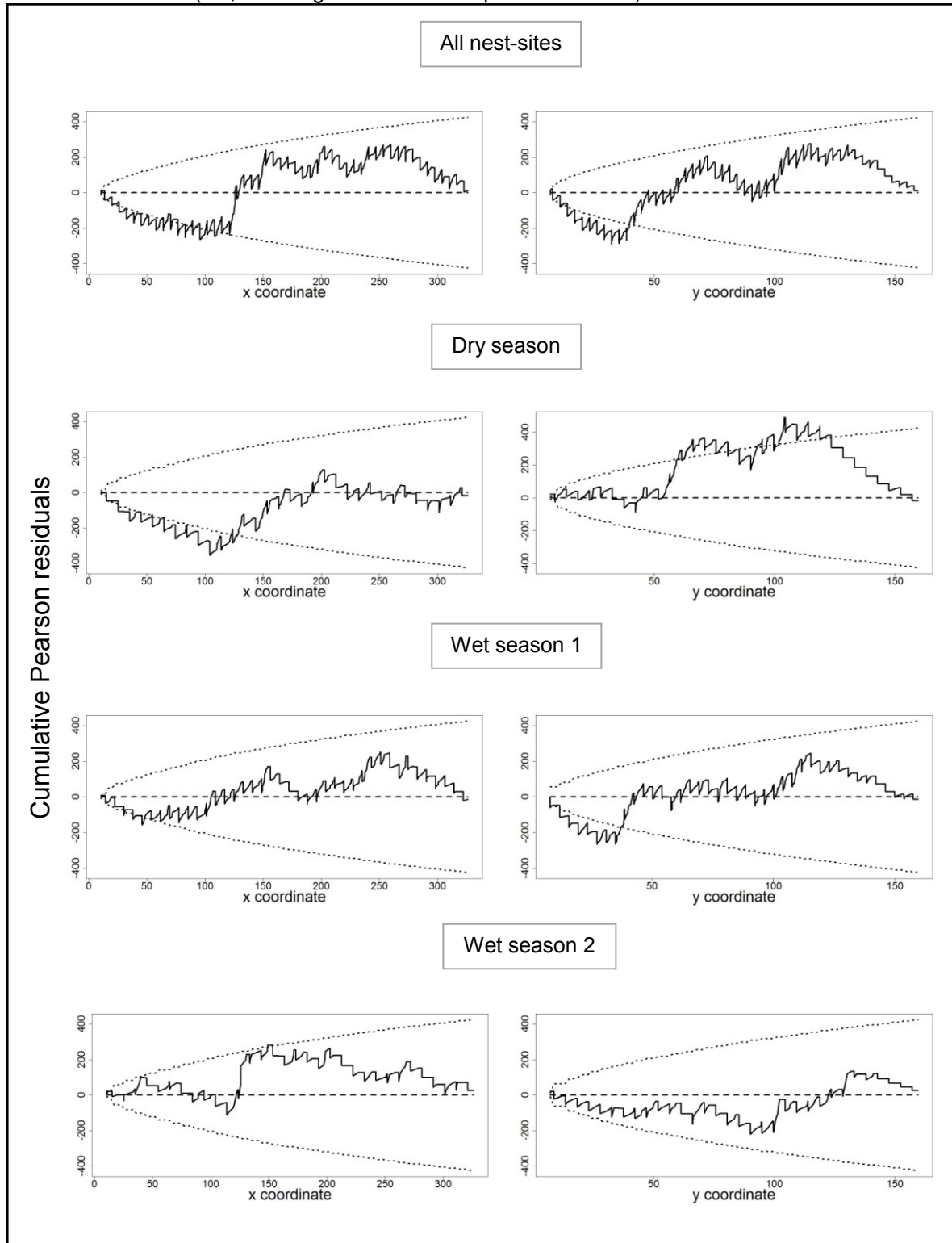
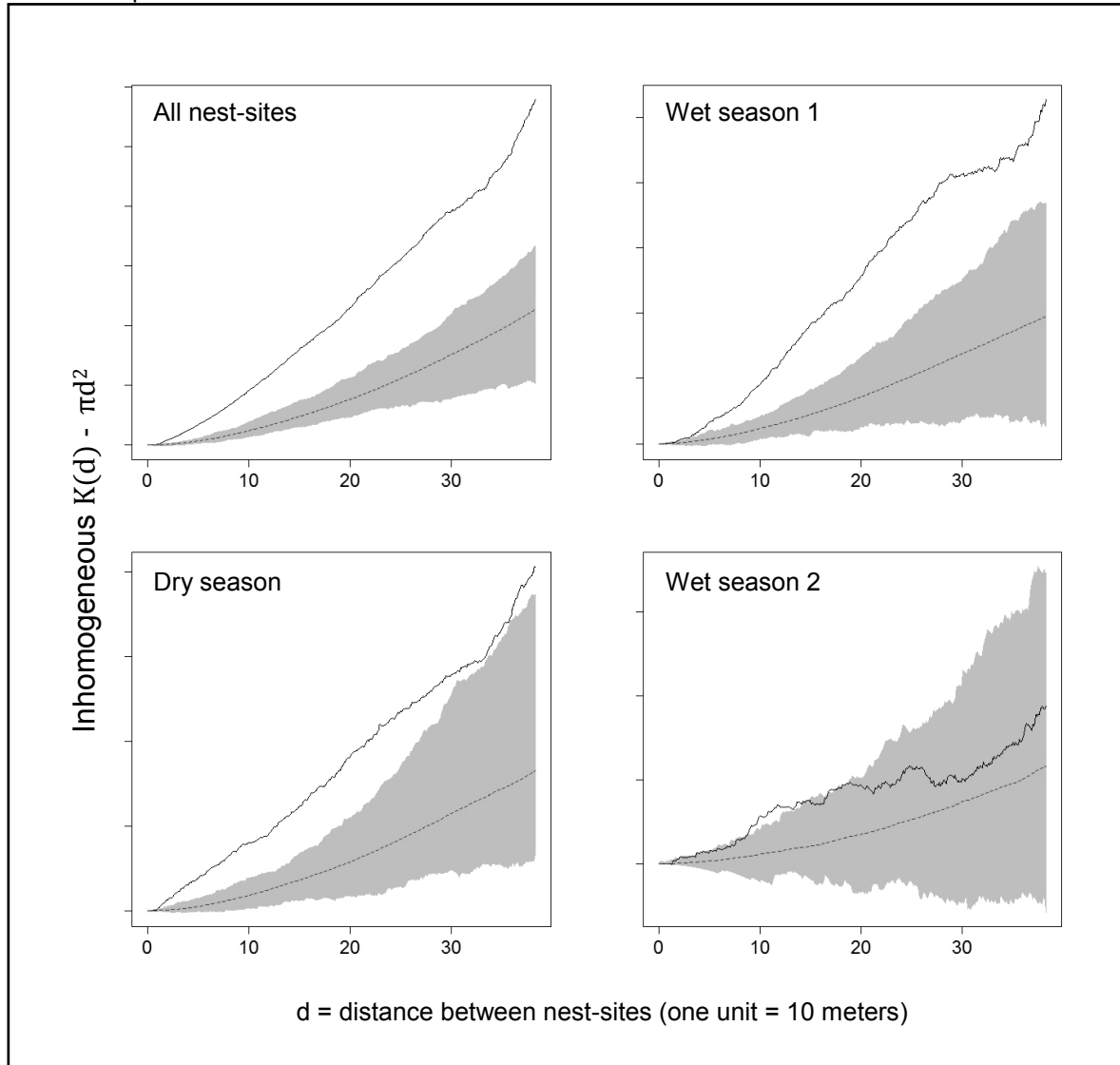


Figure 5.6. Generalized second order K-functions ($-\pi d^2$) at fixed inter-nest-site distances of the empirical nest-site patterns against 199 realizations of the best-fit, inhomogeneous models that incorporate spatial covariates (M_1). The solid line is the empirical K curve. Values of $K(d)-\pi d^2$ above the envelope indicate nest-sites that are closer to each other than expected from a homogeneous Poisson (i.e. random) pattern, while those below indicate regularity (i.e. inhibition). The test has an exact significance level of 0.01. The scales of the ordinal axes are not displayed since only the comparisons of empirical values with significant envelopes are relevant.



The next step is to add Cartesian coordinates to the best-fit M_1 models and see if these new models could better describe nest-site distributions. These models, denoted by M_2 models, have AIC values that are lower than M_1 models, demonstrating a clear improvement in three of the four nest-site datasets (Table 5.5). “Wet season 2” nest-sites already has an adequate fit from its M_1 model (covariate-without-Cartesian-coordinate model). Lurking residual plots against Cartesian coordinates also show improvements in M_2 over M_1 models (Fig. 5.7), indicating they are adequate to describe nest-site distributions. To confirm the goodness-of-fit of M_2 models to the assumptions of an inhomogeneous Poisson process, the empirical generalized K-curve should lie within the envelopes built from 199 ($p=0.01$) simulations of the spatial trends (intensities) incorporated in M_2 models. Figure 5.8 shows the corresponding inhomogeneous K functions. From these plots, it is clear that even after accounting for the effect of spatial trend, there is still a certain degree of clustering. This raises the question of whether some type of interaction between nest-sites exists, which cannot be fit with covariates alone.

Q-Q plots of the smoothed residuals, with pointwise 5% critical envelopes from 100 simulations of the best-fit M_2 models (Fig. 5.9) indicate that inhomogeneous Poisson models might not be the most appropriate (or adequate) model to describe gorilla nest-site patterns.

Table 5.5. The intensity functions for inhomogeneous Poisson point process models that include spatial covariates and Cartesian coordinates (M_2) fitted to the four nest-site datasets.

Model	AIC	No. of parameters	Formula
All nest-sites	4858.8	21	$F(D_2) + P(D_{4,2}) + P(D_{5,2}) + F(D_6) + P(D_{7,2}) + P(x,y,2)$
Wet season 1	2706.7	21	$P(D_{1,2}) + F(D_2) + P(D_{4,2}) + F(D_6) + P(D_{7,2}) + P(x,y,2)$
Dry season	1889.4	18	$P(D_{1,2}) + P(D_{4,2}) + P(D_{5,2}) + F(D_6) + P(D_{7,2}) + P(D_{8,2}) + P(x,y,2)$
Wet season 2	1142.6	14	$P(D_{4,2}) + P(D_{5,2}) + F(D_6) + P(x,y,2)$

D_1, D_2, \dots, D_8 denote the spatial covariates: elevation (m), slope position, aspect category, distance to water channel, distance to trail, habitat category, Spot[®] satellite sensor band 5 variance, and Beer's aspect.

x and y indicate Cartesian x- and y- coordinates.

P-indicates the order of polynomial used, and F-indicates a factor.

Figure 5.7. Lurking residual plots of the best-fit M_2 models with intensity functions including environmental covariates + Cartesian coordinates (Inhomogeneous Poisson process models) to nest-site datasets.

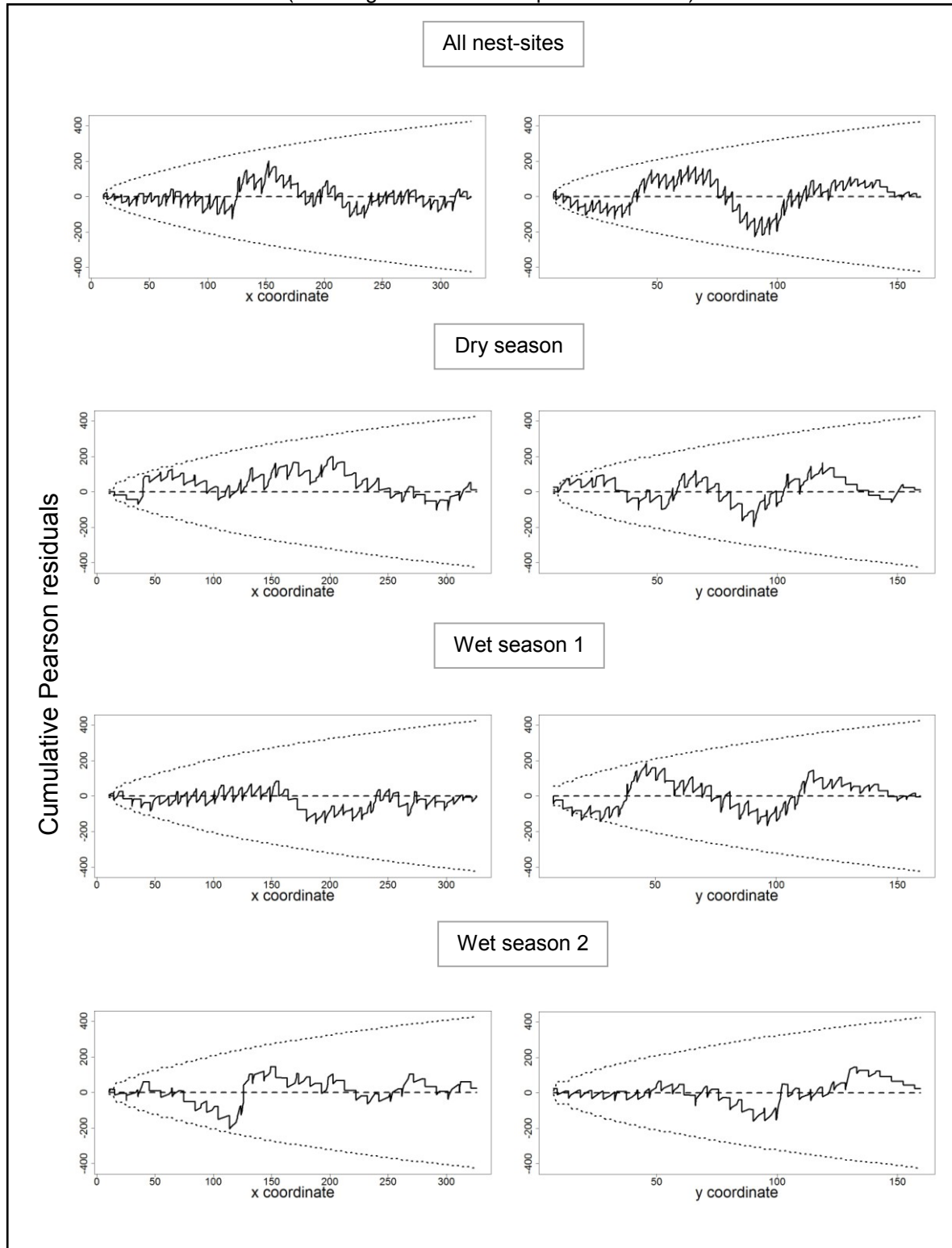


Figure 5.8. Generalized second order K-functions ($-\pi d^2$) at fixed inter-nest-site distances of the empirical nest-site patterns against 199 realizations of the best-fit, inhomogeneous models that incorporate spatial covariates and Cartesian coordinates (M_2). The solid line is the empirical inhomogeneous K curve. Values of $K(d)-\pi d^2$ above the envelope indicate nest-sites that are closer to each other than expected from an inhomogeneous Poisson Process with intensity function as in M_2 models, while those below indicate regularity (i.e. inhibition). The test has an exact significance level of 0.01. The scales of the ordinal axes are not displayed since only the comparisons of empirical values with significant envelopes are relevant.

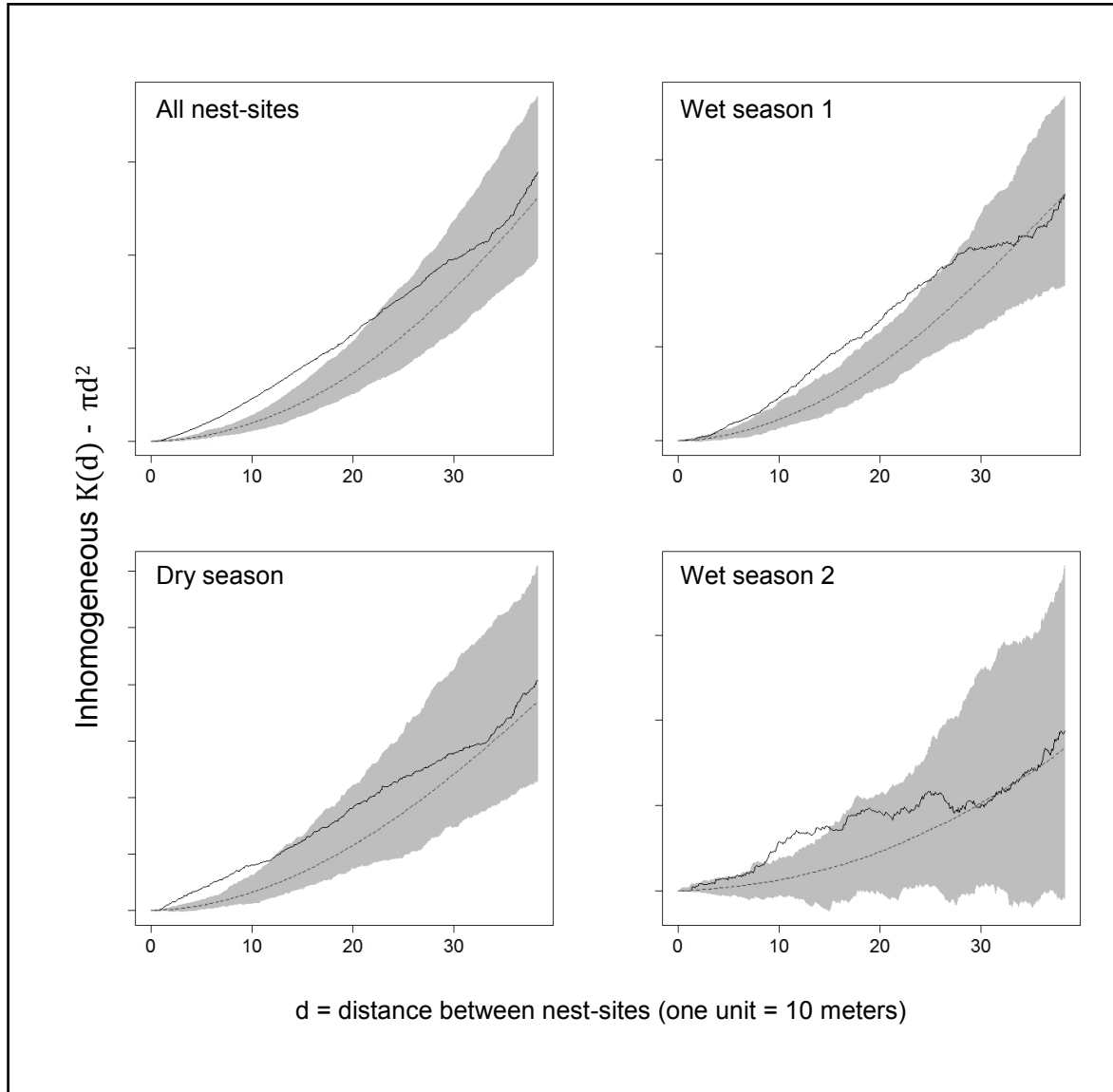
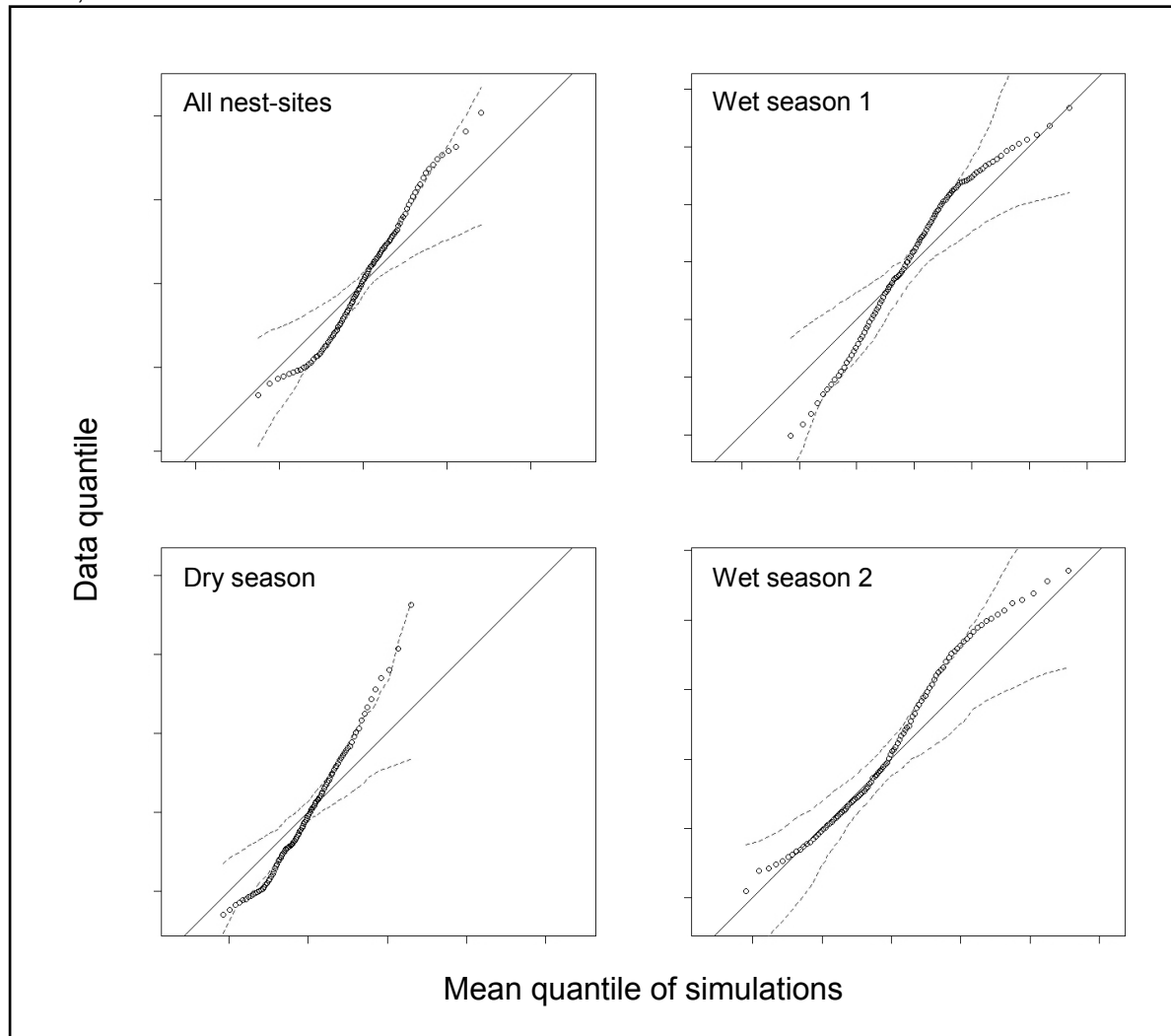


Figure 5.9. Pearson residuals of M2 models. Dotted lines show the 2.5 and 97.5 percentiles, over the 100 simulations, of the “mean” of Pearson residuals.



Accounting for nest-site interactions (non-Poisson models)

The residuals, goodness-of-fit tests, and Q-Q plots indicate that gorilla nest-sites have a tendency to attract to each other. Thus, I attempt to model this interaction by means of the Area-interaction model (Baddeley and van Lieshout, 1995). In the case of the Area-interaction model, the function is given above, but with the constant k replaced with the trend function from the best-fit M_2 models. Prior to implementing these models, there are two important parameters that must be estimated from the data, namely the interaction radius (r) and the interaction parameter (η). I estimate the appropriate interaction radius parameter by fitting 146 models of varying radii (10-300 m, in steps of 2 m) and extract their

corresponding log-pseudolikelihoods. Plots of the resulting values for each nest-site dataset are shown in Figure 5.10, and Table 5.6 lists the “optimal” interaction radii and interaction parameters, η . The interaction parameters were all greater than one, indicating a significant “attraction” between nest-sites, resulting in clustering.

Using these estimates, I then fit inhomogeneous area-interaction process models (hereafter M_3) that include environmental covariates, Cartesian coordinates, and an interaction term. In the case of the “wet season 2” dataset, Cartesian coordinates were omitted in the trend formula. Parameter coefficients and AIC values for M_3 models are shown in Table 5.7, and AIC values are the lowest of any of the previous models tested.

As with previous models, I simulate 199 point pattern datasets from the intensity functions in each M_3 model, and compare their K functions to those of the empirical generalized K functions from each datasets. If the assumption that nest-sites are arranged according to an inhomogeneous Area-interaction process is valid, then the empirical curves should lie within the critical envelopes. Figure 5.11 shows the corresponding K functions and envelopes. From these, it appears that an inhomogeneous, area-interaction process might be appropriate to describe each of the nest-site datasets. However, a small degree of aggregation still exists in the “all nest-sites” case at inter-nest-site distances of 70-200 meters.

Finally, to test whether M_3 models account completely for any inter-point interactions in the datasets, Q-Q plots are run. M_3 models appear to account for all the apparent inter-nest-site interactions (Fig. 5.12) except again in the case of “all nest-sites”, where some interaction is still unaccounted for by the model.

Figure. 5.10. Pseudo-likelihood profiles of the Area-interaction range (r) for nest-site datasets (Area-interaction with log-quadratic trend from the best-fit M_2 models). The spatial trend from the M_1 model is used in the case of the “wet season 2” dataset. Dashed lines show the radii (r) values at which the pseudo-likelihood is maximized. One radius unit equals 10 meters.

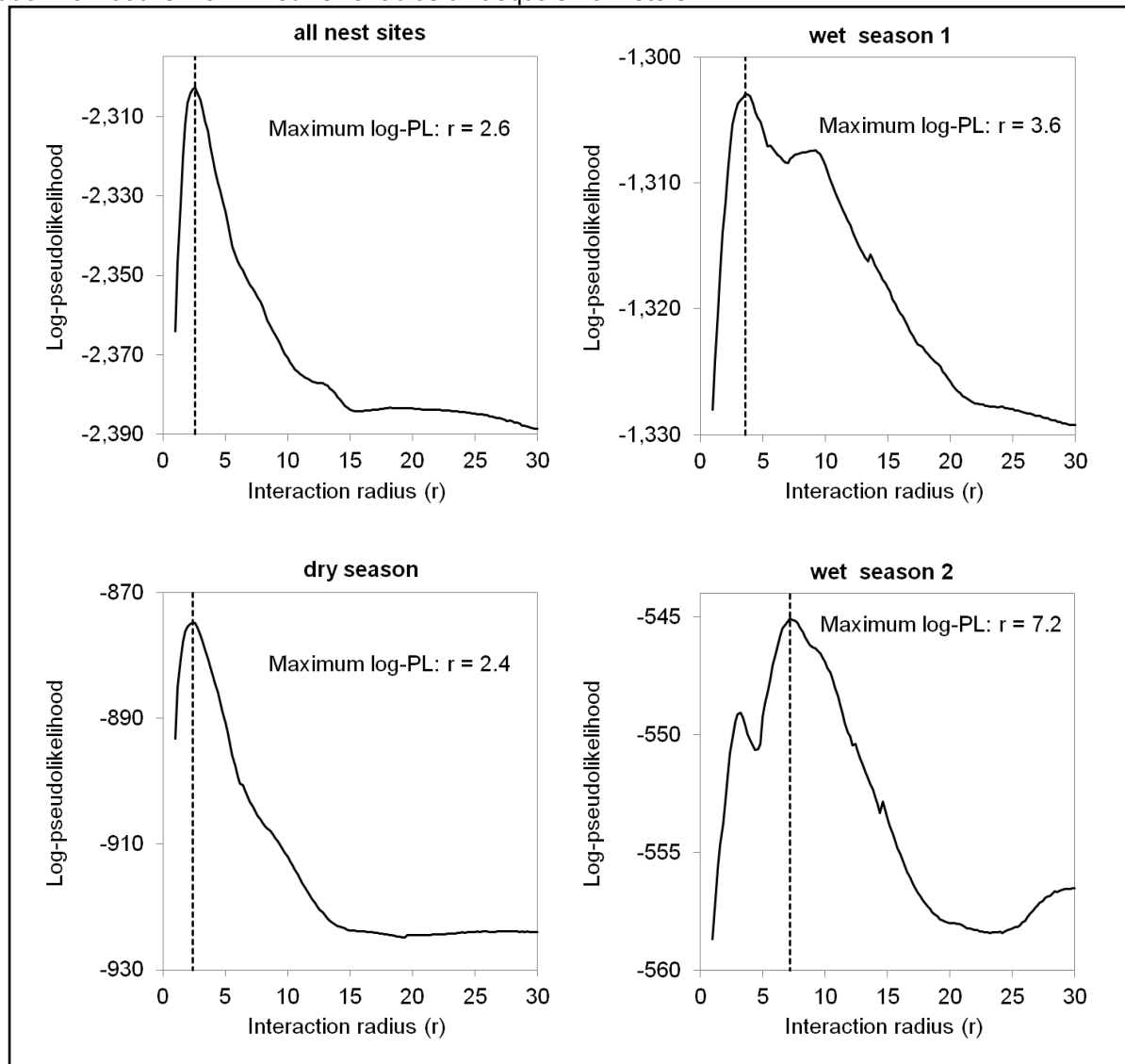


Table 5.6. Area Interaction parameter estimates in M_3 models (Covariates + Cartesian coordinates + Interaction).

Dataset	Interaction radius (r) in meters	Interaction parameter (η)
All nest-sites	26	8.7643
Wet season 1	76	5.3475
Dry season	24	19.0395
Wet season 2	36	6.9203

Table 5.7. Regression coefficients for the log conditional intensity function of nonstationary (i.e., non-Poisson), Area-interaction process models (M_3) to gorilla nest-site locations.

Model environment				
observations	458	149	226	79
number of parameters	22	19	22	10
AIC	4649.94	1787.72	2649.97	1110.31

Covariates	Nest-site dataset			
	All nests	Dry season	Wet season 1	Wet season 2
intercept	-6.75425	-36.25882	3.27501	-7.46951
D ₁ ² elevation		0.21078	-0.09909	
D ₁ ²		-0.00039	0.00019	
D ₂ : valley	0 (n/a)		0 (n/a)	
D ₂ : toe slope	-0.32046**		-0.37964*	
D ₂ : flat	-0.25219		-0.45405*	
D ₂ : mid slope	-0.38487***		-0.55596***	
D ₂ : upper slope	-0.49480***		-0.81185***	
D ₂ : ridge	-0.57007***		-0.82410***	
D ₃ : NE				
D ₃ : SE				
D ₃ : SW				
D ₃ : NW				
D ₄ dist. from water	0.00227	-0.00137	0.00370	-0.00087
D ₄ ² course	-0.00001	-0.00001	-0.00001	0.00000
D ₅ dist. from path	0.00164	0.00032		0.02930**
D ₅ ²	-0.00001	-0.00001		-0.00021***
D ₆ : mixed Marantaceae	0 (n/a)	0 (n/a)	0 (n/a)	0 (n/a)
D ₆ : Marantaceae	-0.04614	0.15744	-0.17957	0.28751
D ₆ : rocky forest	-0.01271		0.09668	-0.07479
D ₆ : monodominant	-0.56917***		-1.03622***	0.14591
D ₆ : all other	-2.94096***	-0.56675**	-3.13476***	-1.73573*
D ₇ texture	0.03184	0.07726	0.07740	
D ₇ ²	-0.00038	-0.00094	-0.00109	
D ₈ heat index		-0.66688		
D ₈ ²		0.35047		
Cartesian coordinates included?	Yes	Yes	Yes	No

Area interaction				
disc radius (r) (meters)	26	24	36	76
eta (η)	8.7643	19.0395	5.3475	6.9203
interaction β	2.17069***	2.94652***	1.676620***	1.934460***

D₁, D₂, ..., D₈ denote the spatial covariates: elevation (m), slope position, aspect category, distance to water channel, distance to trail, habitat category, SD SPOT satellite sensor band 5, and heat index.

*** Indicates the z-test is rejected at 1% significance, ** at 5%, and * at 10%.

Figure 5.11. Generalized second-order K-functions ($-\pi d^2$) at fixed inter-nest-site distances of the empirical nest-site patterns against 199 realizations of the best-fit, inhomogeneous M_3 models (spatial covariates + Cartesian coordinates + Area Interaction). The solid line is the empirical inhomogeneous K-curve. Values of $K(d) - \pi d^2$ above the envelope indicate nest-sites that are closer to each other than expected from the M_3 model, while those below indicate regularity (i.e. inhibition). The test has an exact significance level of 0.01. Scales on the ordinal axes are not displayed since only the comparisons of empirical values with significant envelopes are relevant.

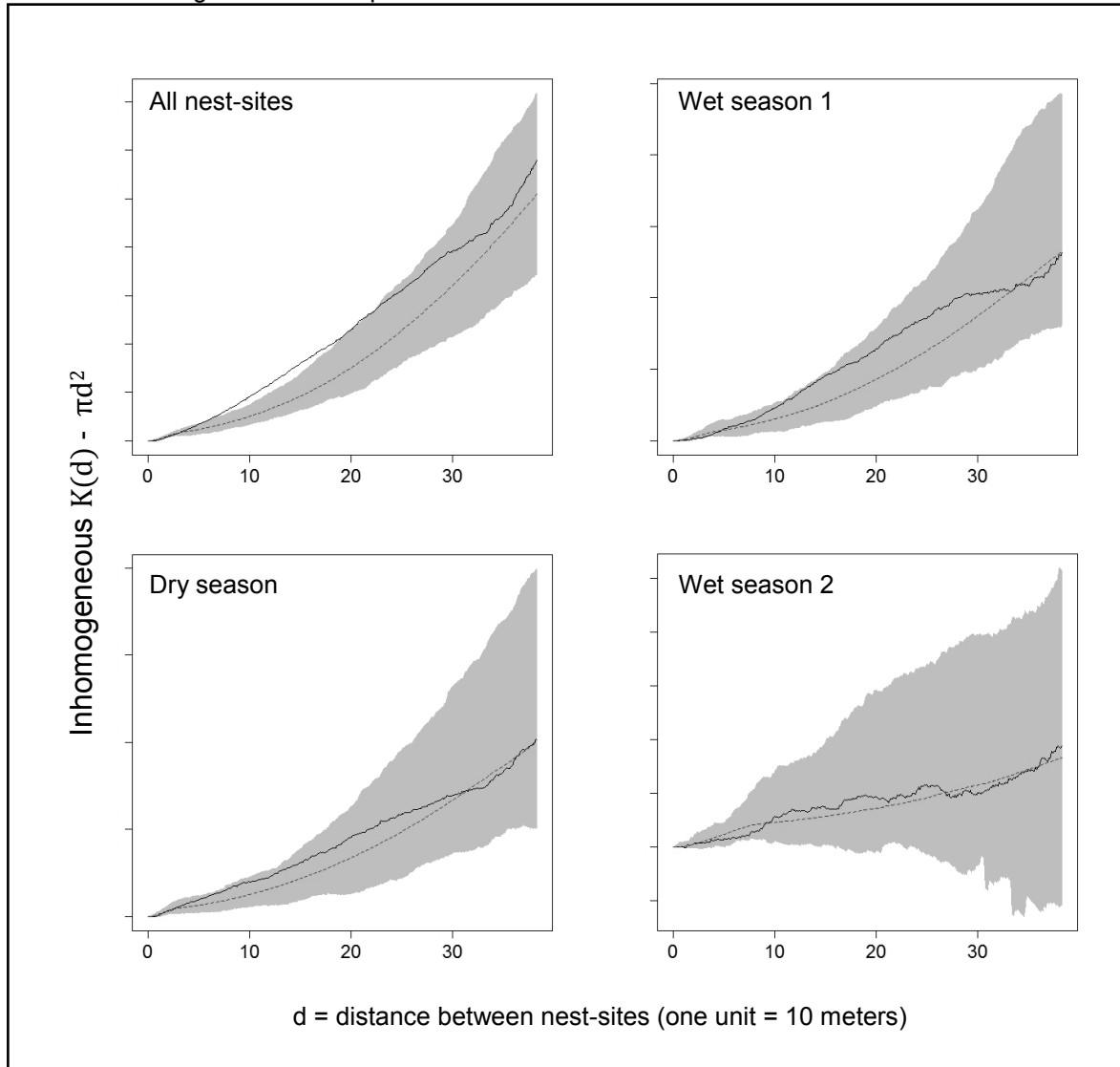
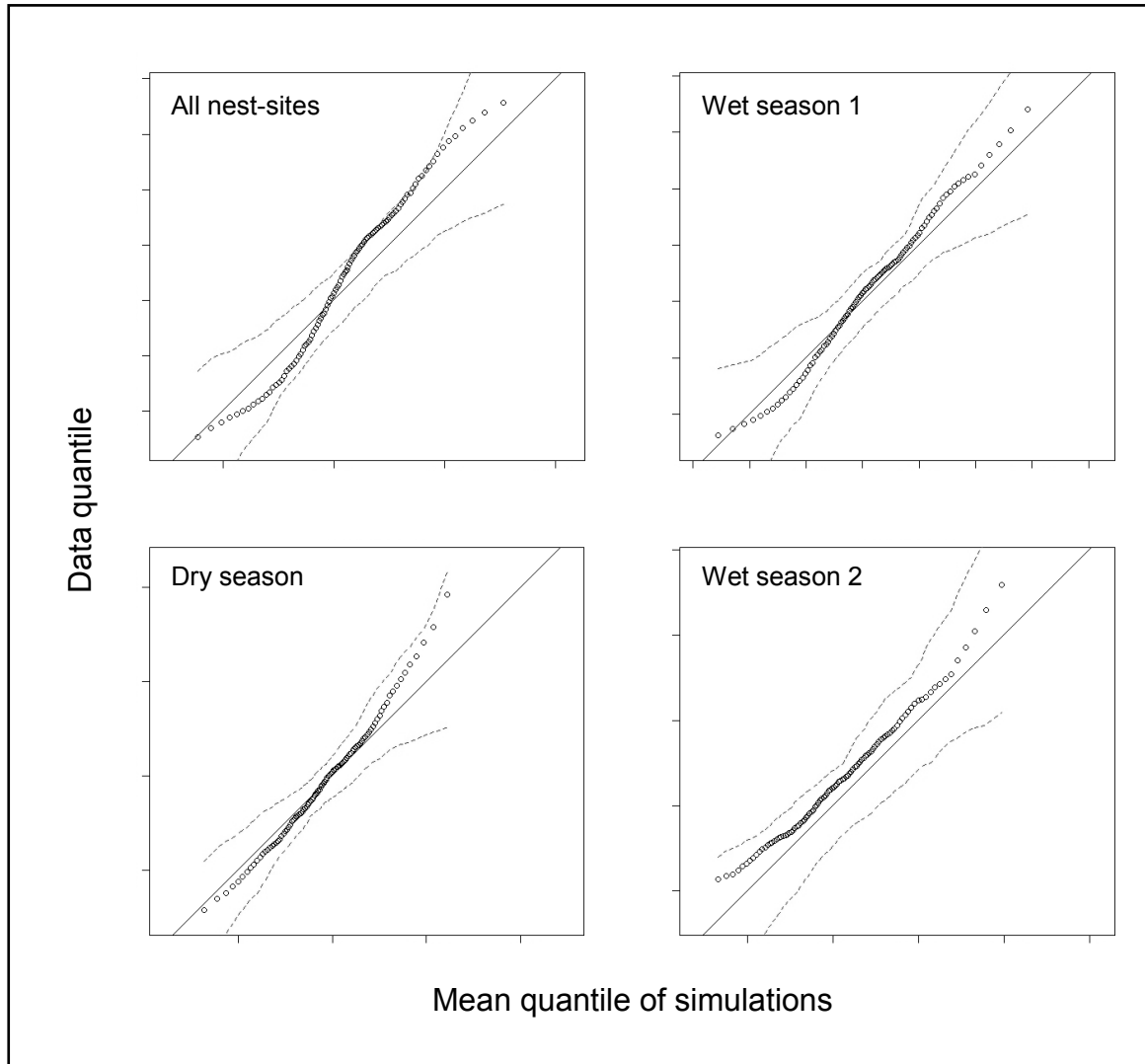


Figure 5.12. Pearson residuals of M_3 models. Dotted lines show the 2.5 and 97.5 percentiles, over the 100 simulations of the “mean” of Pearson residuals.



The effects of environmental factors on gorilla nest-site distributions

The coefficients of the best-fit Area-interaction models (Table 5.7) provide quantitative information on how environmental factors affect gorilla nesting behavior. The sign and value of the coefficients obtained for each covariate suggest the direction and magnitude of their influence. Positive coefficients indicate a positive effect on nest-site density while negative ones have a negative effect. In continuous variables, the log-intensities of nest-sites are modeled as quadratic functions. Using the estimated

coefficients, it is possible to derive the contribution of these variables to nest-site locations in each of the respective nest-site datasets.

The effect of elevation on nests-sites is generally non-significant. This result should be considered in context. Unlike regions in the south and west of Lopé National Park, which has a great range in elevation, the study area at SEGC has little variation, with elevations ranging between 233 and 337 meters. It is not surprising, therefore, that a significant effect in elevation is not found in this analysis. Indeed, a negative elevation effect on nest-site locations was observed in a region of great topographic relief in southwest Cameroon (Funwi-Gabga and Mateu, 2012), and gorillas in the more mountainous areas of Lopé National Park, where elevations reach 850-900 meters, may be affected by elevation or related factors.

Slope position is significant in the distribution of “All nests” and “Wet season 1” nest-sites. In general, valleys, toe slopes, flat regions, mid slopes, upper slopes, and ridges, are in decreasing order of importance in terms of nest-site densities. In both datasets, valleys received the greatest number of nest-sites. Relative to valleys, nest-sites decrease in intensity between -22 to -43% in “all nests”, and -31 to -56% during the 1st wet season, as position on the slope moves upward. The influence of slope position is not observed in either “Dry season” or “Wet season 2” datasets.

Aspect does not have an observed effect in any of the datasets. Once again, this is not surprising given the low degree of topographic relief in the study area. Distance to the nearest water channel approaches significance in only one dataset, the “all nests” dataset. In this case, the contribution to log-intensity increases from 0.000 to 0.118 as the distance to a water channel increases from 0 to 100 meters, it then decreases as distance increases beyond 100 meters.

Distance to the nearest trail, which was intended to test whether observer bias (i.e., the bias associated with search effort) influenced the data, is significant (and highly so) in the “wet season 2” dataset. In these data, log-intensities increase from 0.00 to 1.01 as distance to nearest trail increases from 0 to 70 meters, then decreases slightly as distance increases beyond 70 meter. I will comment more on the inferences from this covariate below.

The influence of vegetation type is evident in all datasets, with the highest nest-site densities occurring in mixed Marantaceae forests, Marantaceae forests, and rocky forest types. The coefficients associated with these forest types are not significant because their contributions to the log-intensities are not different from the mixed Marantaceae category (dummy code= 0). Near-significant cases were observed in Marantaceae forests during the two wet seasons, with lower log-intensities over mixed forests during the 1st wet season (a decrease of 0.18), and higher intensities during the 2nd wet season (an increase of 0.29). Unsurprisingly, the least important vegetation types are monodominant forests and all other forest types (a category that includes colonizing forests). Overall, the influence of vegetation type on gorilla nesting behavior is strongest during the 1st wet season, moderate in the 2nd wet season, and weakest during the dry season.

With respect to forest structure, the only dataset to exhibit a near-significant effect in terms of the standard deviation in the SPOT XS SWIR band is “wet season 1”. The contribution to log-intensity from SWIR variation increases from 0.00 to 1.37, as variation in forest structure increases from zero (similarity in structure) to a mid-range value; it then decreases as texture increases (dissimilarity in structure), suggesting that gorillas prefer areas of moderate heterogeneity in forest structure over those with the lowest and highest degrees of variation. The smallest contribution to nest-site intensities occurs in forests having the least amount of spatial heterogeneity in forest structure. These areas coincide with such types as monodominant forests.

Lastly, the heat index (Beer’s aspect) is influential in the case of dry season nest-sites only. Its effect is difficult to interpret, however, with the lowest contribution occurring in mid-range and greatest contributions at values of zero (i.e., the warmest areas) and two (i.e., the coolest ones).

In addition to the effects of environmental variables on nest-site densities, the best-fit models indicate that gorillas tend to construct nests in areas where nests have been previously constructed. The “attraction” between nest-sites occurs on relatively small spatial scales, 0.18 hectares in the dry season, and 1.81 hectares in the 2nd wet season, for example. Using the coefficients on the interaction parameter, the tendency to revisit nest-sites appears to be greatest during the dry season (beta= 2.947, interaction

radius= 24 meters, η = 19.04) and weakest during the 1st wet season (beta= 1.677, interaction radius= 36 meters, η = 5.35).

Nest-site probability maps

From the fruiting plant's perspective, it is more useful to think of space as a surface of nest-site probabilities over time than as one of nest-site intensities. Spatial intensities calculated from the best-fit M_3 models can be interpreted as nest-site occurrences. These in turn, can be used to calculate probabilities to create a spatio-temporal surface where the value at any given point in space is a probability that a nest-site is constructed.

In order to produce probability surfaces, I divide the study region into 1-hectare grid cells (100 x 100 m), and calculate a normalized nest-site density (λ) surface for each dataset using the fitted coefficients from the M_3 models above (Table 5.7). Units in these surface maps are: number of nest-sites / 10 x 10 m cell / decade. Given the temporal scale at which a fruit tree's total reproductive output typically occurs (i.e., decades), and the low probability of seedling establishment and adult recruitment relative to the number of seeds produced during a tropical tree's lifetime, I redefine nest-site probability as the probability of at least one nest-site occurring within a 1-hectare cell over one decade. Following Yang et al. (2007), I calculate this from the Poisson probability density function as

$$P(x \geq 1) = 1 - P(x = 0) = 1 - e^{-\lambda*100}$$

where x is the number of nest-site occurrences in a 1-hectare cell. The calculated nest-site occurrence probability surfaces for each nest-site dataset are in Figure 5.13.

From these maps, it is evident that space is not uniformly (nor randomly) used, in terms of the probability of a nest-site occurring, and the amount of space available to gorillas for constructing nest-sites may be limited. Space is utilized differently depending on the season, with less space available for nest-sites during the dry season than in either the two wet seasons. These results may be related to the stronger attraction between nest-sites during the fruit-scarce dry season. The spatial trend component of the dry season intensity function is nearly devoid of significant environmental effects. It is unclear whether

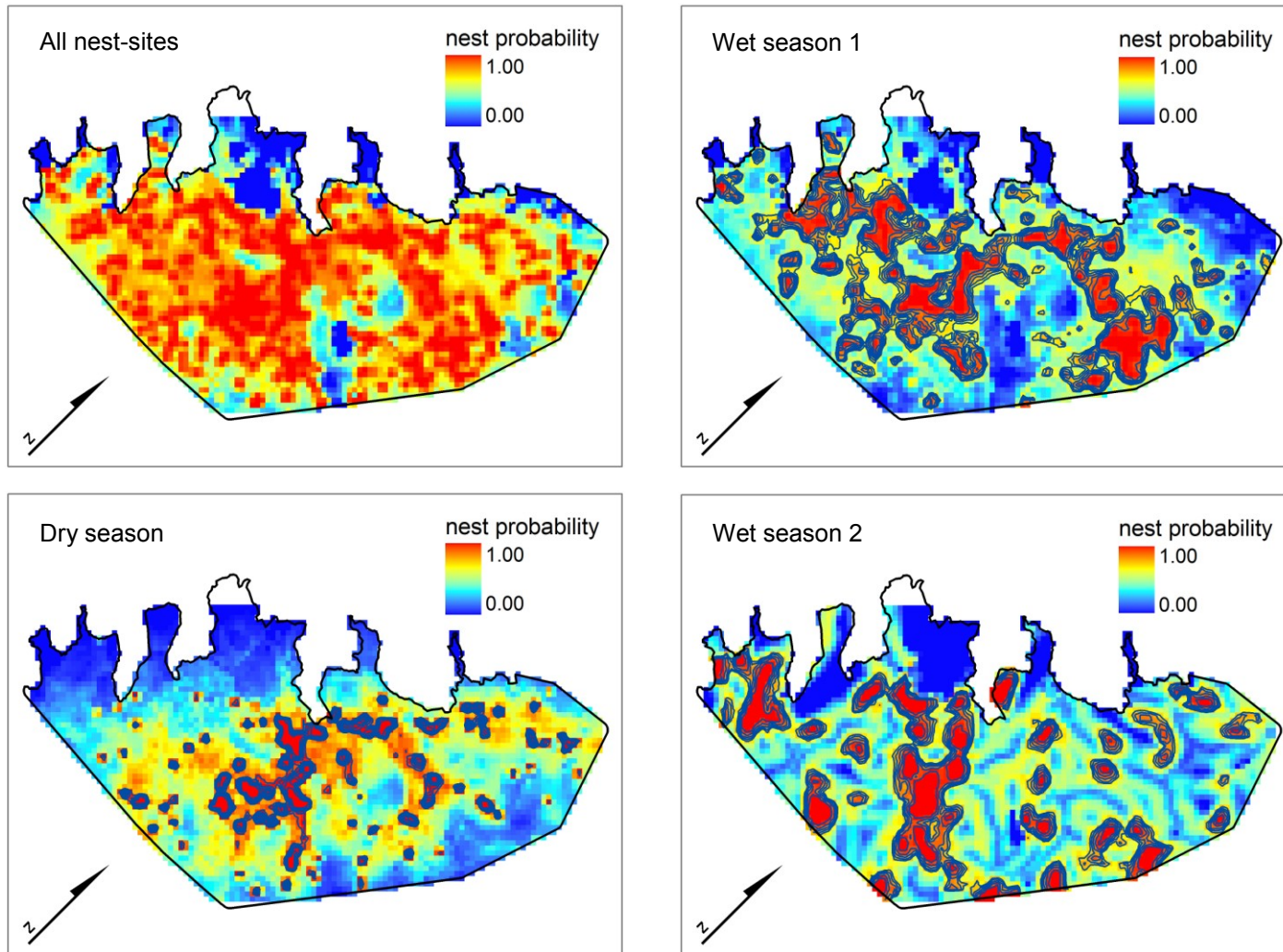
some unknown variable is responsible for the clumped nature of dry season nest-sites, though the inclusion of Cartesian coordinates greatly improves the fit to the dry season dataset, indicating that some spatial trend exists. The absence of significance among the trend variables tested here is unsurprising. Gorillas reduce daily path lengths and forage on ubiquitously dispersed food plants during this period. Variation in terrestrial vegetation is less likely to co-vary with the spatial covariates tested here than is variation in the fruiting environment.

Since gorillas are selective in their choice of fruit resources, and do not travel far from their last feeding site (in a day) to construct their nests (Schaller, 1963; Williamson, 1988; Tutin et al., 1995), it is not surprising that vegetation has a strong effect on nest-site intensities.

The greater degree of nest clustering in the dry season coincides with reductions in daily path lengths and home ranges at Lopé. Daily path lengths and home ranges are lower during the non-fruiting seasons than during the fruiting season. This is due to a combination of factors, including a digestive ecology and physiology that allows for fibrous, herbaceous foods to sustain the gorilla's bulk during times when the easily digestible sugars of fruits are rare. Since these spatially ubiquitous "fallback foods" are available year-round, gorillas need not expend much energy in searching for them; thus, reducing their ranging patterns when fruit is in abundance results in highly localized nest-sites exhibiting a strong inter-nest-site attraction.

Gorillas range more widely and with a greater degree of dietary selectivity as they track fruit resources during the fruiting ("wet") seasons. Using the models I present here, I suggest that differences in gorilla ranging behaviors throughout the year, and particularly during the wet seasons, can result in longer dispersal distances, and more importantly, a complex pattern of densely aggregated seeds, directed to a limited number of sites.

Figure 5.13. Grid surface maps of estimated nest-site occurrence probability, defined as the probability of having at least one nest-site occurrence for the given 1 hectare cell over a decade. Contours indicate .05 probability intervals above the 0.75 level (excluded in the 'All nest-sites' case).



DISCUSSION

Tropical forest trees, and particularly large-seeded trees, are commonly dispersed by large mammals, and often exhibit clumped distributions (see Chapter Six). The results I present in this chapter shed some light on an important mechanism in gorilla-mediated seed dispersal and may help to explain the maintenance of these clumped distributions, and co-existence (i.e., diversity) of tropical forest plants. By evaluating the spatial ecology of the location of gorilla nest-sites in terms of first-, second-, and higher-order processes, I am employing a powerful methodology to understanding how gorilla behavior is linked to the spatial demography of the fruiting species consume.

Researchers who have studied the ecological correlates to gorilla ranging behavior indicate that gorillas selectively visit a mosaic of habitats affected by natural (Williamson, 1988; Tutin. 1996; Doran et al., 2002) and anthropogenic (De Vere et al., 2011) environmental gradients. Funwi-Gabga and Mateu (2012), for example, found clusters in Cross River gorilla nest-sites (*Gorilla g. diehli*) in Cameroon, resulting from a combination of environmental variables and attraction between nest-sites. Gorilla nest-sites at Lopé are also clustered, explained in part by both spatial trends in environmental variables and attractions between nest-sties. Gorillas tend to construct their nests in places where nests have previously been constructed. By looking into the composition of clusters, I found they are comprised of nests that have been constructed over the course of long periods (i.e., years, not months), long after any previous nest-sites might be evident to gorillas. This might indicate that something else, yet unknown, about the environment in favorable nest-sites, is attracting gorillas to these locations, and site “preferences” should not be ruled out.

By partitioning the nest-site data into finer temporal scales (one low fruit, and two high fruit seasons), I am able to investigate the relative effects of different covariates on nesting behavior, as well as the resulting template of co-dispersed fruit species.

Nest-sites in relation foraging behavior

Gorilla food resources, and in particular their fruit trees, are not randomly distributed across vegetation types at Lopé. Fruiting species have individual habitat preferences that result in specific

associations of plants within these types. Unsurprisingly, habitat use by gorillas is not uniform (nor random) across vegetation types, and depends on the season and the phenologies of the food species they track.

Mixed Marantaceae forest is the most common vegetation assemblage in the study area (49%) and contains many of the fruit species (and important herbaceous plants) that gorillas find attractive (White et al., 1995). Since 40% of nests (N= 2435) were constructed from herbaceous terrestrial herbs (Tutin et al., 1995), this vegetation type contains both important food resources and nest-construction materials. Gorillas preferred to construct ground nests over tree nests in Lopé (64% versus 34.5%; Tutin et al., 1995), especially wherever herbs are available, and one can expect a higher rate of ground (over tree) nests when gorillas are using this vegetation type.

Marantaceae forests have a similar floristic assemblage to mixed Marantaceae forest, and a slightly higher density of terrestrial herbs. Therefore, I would expect higher rates of ground nests here. In the best-fit model for the 2nd wet season data, higher nest-site densities are predicted in Marantaceae forests over mixed forests.

Rocky forest types receive slightly more (though not significantly) nest-sites than either mixed Marantaceae or Marantaceae forests during the 1st wet season. This could be due to fruiting in the highly preferred genus *Diospyros*, a group that is found in high densities on rocky soils. Three species in particular, *Diospyros zenkeri*, *D. dendo*, and *D. polystemon*, have ripe-fruit mean dates of the 23rd of February, and the 12th and 23rd of April, respectively (see Table 3.1), dates that fall in the 1st wet season dataset. Together, these species form an important cluster of gorilla foods available late in the first wet season and early in the dry-season (i.e., the end of a period of fruit abundance; see Fig. 4.2, and Table 4.4). The tracking of these fruit resources by gorillas, results in increased nest-site intensities in rocky forest types over mixed forest types.

The stronger attraction between dry season nest-sites does help to explain why few environmental covariates are significant in predicting nest-site distributions. Gorillas during this period fall back onto ubiquitously distributed resources, such as *Celtis tessmannii* (Cannabaceae) leaves, barks, the young shoots of Marantaceae and Zingiberaceae families, and the marsh plant, *Marantochloa cordifolia*.

Variation in these resources likely exists on a smaller scale than that of most of the variables I consider here. If these resources cannot be approximated by the spatial covariates tested here, the covariates will be of minimal importance in predicting either gorilla foraging or nesting behavior. The tendency of gorillas to eat large amounts of aquatic plants during the dry season (Rogers et al., 1988; Tutin et al., 1991b) is interesting, since the best M_3 model indicates a near-significant effect for the distance from a water channel, with densities decreasing the farther away from a water channel. Given the importance of aquatic vegetation during this season, the correlation is not surprising.

The monodominant forest (as well as all remaining forest types) receives significantly fewer nest-sites than any other vegetation type. This again, is unsurprising given its marginal importance to gorillas in terms of numbers of food species it has. Of particular interest, however, is the lack of significance observed for monodominant forests relative to the mixed Marantaceae category, and only during the 2nd wet season.

The influence of sympatric mammals on nest-site locations

Distance to nearest path is a significant influence on nest-site placement during the 2nd wet season. Paths at SEGC are a combination of old logging roads and elephant traveling/feeding paths. Today, they are maintained by elephants, other wildlife, and researchers (mostly by the trampling of vegetation). They are most commonly elephant feeding trails (White, 1992). Between September and December, elephants at SEGC reach their highest densities (5225 kg / km², or 2-3 individuals / km²). Indeed, this figure may be the highest density ever recorded for Africa (White et al., 1993; White, 1994c). The potential for gorilla-elephant interactions is, therefore, greatest at this time.

At Lopé, elephants (*Loxodonta cyclotis*) and buffalo (*Synerus caffer nanus*) are cathemeral, being active both day and night, and both feed on the same herbaceous plants favored by gorillas for nest construction. Tutin et al. (1995) reported, on at least one occasion, a gorilla interaction with elephants, and suggested that while mutual avoidance is practiced, silverbacks will display at elephants if they approach. In addition, gorillas have been known to abandon nest-sites if disturbed by elephants during the night (Tutin et al., 1995). The authors proposed that nesting in trees might offer some protection from

elephants. However, unless the trees are large, this strategy is unlikely to be very effective, since elephants are reported to push over trees where gorillas had recently nested up to 25 cm DBH easily.

From 23 months of data, no correlation was found between the proportion of gorilla nests constructed in trees and elephant densities (White, 1992; Tutin et al., 1995). However, in results I present here, there are significantly more tree nests during the 2nd wet season (44.6%) than in either the 1st wet season (39.5%; $\chi^2= 4.139$, simulated $p= 0.044$) or the dry season (30.2%; $\chi^2= 29.582$, simulated $p= 0.0005$; Table 5.8), suggesting that elephants may be a factor in determining where in the vertical strata nests are constructed. I propose that another successful strategy in avoiding elephant disturbances is moving nests away from the paths that elephants use (for both feeding and traveling) during the period of greatest elephant densities.

Table 5.8. Distribution of ground and tree nests across seasonal nest-site datasets.

	Ground	Tree
1st wet season	822	537
dry season	584	253
2nd wet season	302	243

Methodological advances in censusing gorillas

Incomplete sampling/monitoring of animal populations is done in conservation biology to understand trends and inform natural resource management, since the amount of resources (time and money) required to census the entire population is often not available. Indirect measures of gorilla abundance, including nest counts and dung piles, are most often used to survey gorilla populations (Tutin et al., 1995; Fay, 1997; Kuehl, et al., 2007; Todd et al., 2008). In the case of nest count data, researchers often fall short of attaining estimates having high confidence, because of sample sizes that are too small. Despite the often great effort, these small sample sizes often result from over-sampling areas of low nest densities, and/or under-sampling areas of high nest densities.

Development of long-term monitoring programs for endangered populations demands that survey designs “achieve statistical rigor and are efficient but remain flexible to inevitable logistical or practical

constraints during field data collection” (Theobald et al., 2007:134). Point pattern process models are ideal for developing probability-based survey designs that are both spatially balanced and efficient. They allow sampling effort to be modified according to factors that are known to influence the behaviors of the animals being sampled. In a rigorous probability-based survey design, the location of samples is specified by models that are constructed using data from the targeted population, enabling inferences from the survey to better apply to the entire population (Theobald et al., 2007). Here, I advocate that a pilot study of nest-sites in a localized area, followed by a careful modeling of locations (employing spatial point processes), can be used to develop more efficient, site-specific surveys to estimate gorilla densities.

Gorilla nesting behavior and dispersal limitation

Gorilla nesting behavior can be explained in terms of environmental covariates, but nest-site clusters also occur on a very small scale. Just as the effects of geo-environmental covariates on nest-sites are not constant throughout the year, small-scale clustering is not stationary. For plant species with seeds dispersed by gorillas, the greatest level of dispersal limitation is expected in those species bearing fruit during the dry-season. Though dispersal limitation is still high in the 1st wet season, seeds deposited around nest-sites between January and May should experience greater dispersion.

In the next chapter, I evaluate the spatial dispersion of extant trees, and assess whether aggregation tendencies in wind-, small vertebrate-, and ape-dispersed species persist into the adult population.

CHAPTER VI:
SPATIAL AGGREGATIONS OF FRUIT TREES AT LOPÉ: RECRUITMENT LIMITATION IN GORILLA-
DISPERSED SPECIES

INTRODUCTION

Seed dispersal is critical because it lays down the initial spatial template from which seeds germinate and all subsequent tree demographic processes occur (e.g., “template of offspring dispersion”, *sensu* Russo et al., 2006). Within this template, the majority of tropical trees rely on fruit-eating animals to deliver their seeds to possible establishment sites (Herrera, 2002). Thus, the nature of this template depends on the biological characteristics of dispersers, including disperser richness, abundance, physiology, and behavior (Clark et al., 2005; Russo et al., 2006). Most vertebrate-dispersed tree species have many dispersers (polychory) that scatter and clump (Howe, 1989) seeds, both near and far from the parent tree, creating a complex pattern of seed rain. The final adult distribution of vertebrate-dispersed species is the sum effect of processes that aggregate seeds, and post-dispersal processes that alter the initial dispersion of dispersed seeds through non-random survival (Russo and Augspurger, 2004).

“Despite highly diverse coterie of mutualistic frugivores dispersing seeds, critical long-distance dispersal events might rely on a small subset of large species” (Jordano et al., 2007:3278). These rare, long-distance dispersal events (outside the local neighborhood) are disproportionately more important to gene flow, recruitment, colonizations, range expansions, and speciation mechanisms, than the overwhelmingly common, distance-restricted dispersal events (Clark et al., 1998b; Cain et al., 2000; Nathan and Muller-Landau, 2000; Fagan and Lutscher, 2006).

Among the community of disperser-frugivores in the African forest, gorillas are not typical. On the contrary, Tutin (1998:228) remarks, “they are an extreme case: the largest bodied arboreal frugivore in Africa.” Aspects of their behavior greatly increase their effectiveness as dispersers over sympatric primates, as well as other vertebrate frugivores. They reliably visit a substantial proportion of trees (in some species), and swallow a large numbers of fruits and seeds (Voysey et al., 1999a). In addition, they

deposit seeds in a matrix of natural fertilizer, and often to sites that are favorable to seedling establishment such as nest-sites, which have greater long-term seedling survival rates than “trail” deposition sites, or sites containing dropped/scattered seeds. (Voysey et al., 1999b). If gorillas are effective in influencing gene flow and demography in the species of seeds they disperse, the dispersion of seeds must be demonstrably correlated to the spatial patterns of adult trees, beyond mere germination benefits, and high seedling survival (Voysey, 1995).

Recruitment limitation is the failure of a plant to recruit at a given site (or to recruit at less than maximum density) due to (1) the failure of seeds to arrive (seed limitation), and (2) the lack of suitable conditions for establishment (Nathan and Muller-Landau, 2000). Seed limitation is further decomposed into (1) factors that limit the number of seeds available for dispersal, such as source limitation, and (2) factors that limit the arrival of seeds to a site, such as dispersal limitation (Clark et al., 1998a,b).

Establishment limitation is the sum effect of processes associated with distinct mortality factors, including predation, parasitism, and disease (Nathan and Muller-Landau, 2000). Deficiencies in suitable conditions at seed deposition sites result in plants establishing at less than their maximum.

Specific research questions

Gorillas at Lopé extensively disperse a great numbers of large seeds throughout their home ranges. Due to complex patterns of post-dispersal mortality, recruitment patterns can differ drastically from seed dissemination patterns, potentially decoupling the influence that seed dispersal has on the adult tree distribution. In this chapter, I investigate the abundance and dispersion in seven fruiting tree species at Lopé, the seeds of which are dispersed by different dispersal vectors, including wind, birds, and primates. I enumerate the extant distributions in two wind-dispersed species (*Aucoumea klaineana* and *Lophira alata*), two bird/monkey-dispersed species (*Xylopia aethiopica*, and *X. quintasii*), and three ape-dispersed species (*Diospyros dendo*, *Diospyros polystemon*, and *Cola lizae*).

Enumerating the extant density and dispersion of individual trees, enables me to make inferences related to the long-term, ecological consequences of different dispersers guilds (particularly the gorilla guild) in shaping tree distribution patterns. I use spatial pattern analysis to evaluate the consequences of

dispersal and post-dispersal processes to the aggregated patterns so often observed in tropical tree species. Specifically, I address two fundamental questions concerning these patterns:

- Do the different patterns of dispersion observed in tree species, and at different spatial scales, reflect the expected patterns of seed dissemination (i.e., seed rain) occurring from different dispersal vectors?
- Using extant distributions in DBH classes, do aggregation tendencies in small-sized cohorts persist into large-sized cohorts, in putatively gorilla-dispersed species?

I assume that the spatial extents of local-scale aggregations in trees reflect distance-restricted dispersal, whereas separation of local aggregations the long-distance, and potentially directed, dispersal events (Kraft et al., 2002). I predict that ape-dispersed species (*Cola lizae*, *Diospyros polystemon*, and *D. dendo*) will exhibit a greater overall tendency to aggregate, and at larger spatial scales, than the smaller-seeded, polychorous, bird- and monkey-dispersed species, due to the greater spatial scale at which ape ranging behaviors and defecation (clump-dispersal) occurs. I expect wind-dispersed species to exhibit the greatest distance-restricted recruitment, and at small spatial scales. I expect the scale of distance-restricted patterns (local aggregations) to increase as seed size increases across species, since larger seeds are associated with disperser-specific behaviors that remove seeds only a short distance from the tree for processing.

Aggregations of individual trees across spatial scales result from environmental factors, interactions between environmental factors and species-level traits (i.e., dispersal ability), or simply species-level traits (Clark et al., 1998b; Réjou-Méchain et al., 2011). In the latter case, these traits will confer an endogenous effect on tree distribution patterns irrespective of the environmental context (Réjou-Méchain et al., 2011). Assuming, as other researchers have, that environmental processes take over from species-level traits in influencing dispersion patterns as spatial scale increases (Levin, 1989, 1992; Wiens, 1989), I expect aggregated patterns to fade as spatial scale and cohort age increase. Random distributions in late-adult stage trees (and at large spatial scales) would suggest an effacing of the seed deposition patterns, mediated through non-random, density-dependent survival in recruitment processes.

METHODS

Enumeration of dispersion in fruiting trees

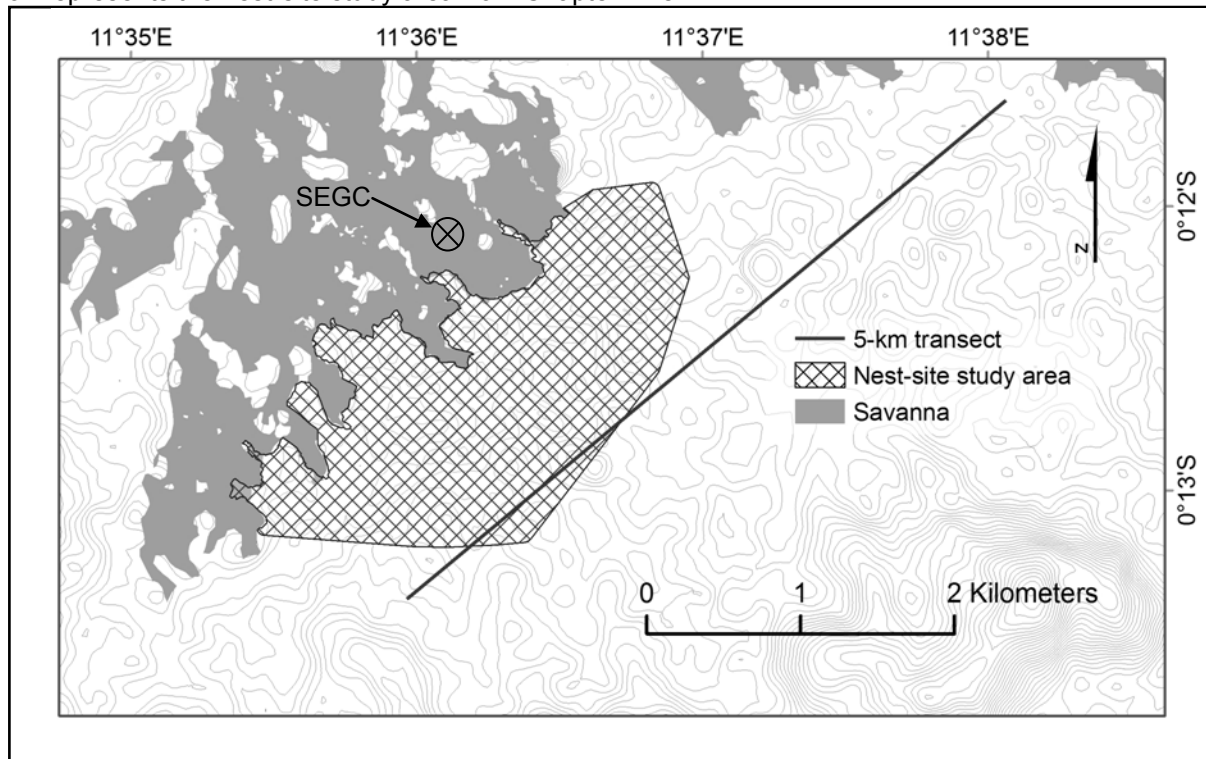
Locations of individual trees were recorded along an established 5-kilometer transect at the study site in Lopé National Park in 1989 (White, 1992; see Fig. 6.1). Individuals of all trees greater than 10 cm DBH were identified and measured along a 5-meter wide strip (2.5 meters on either side). The transect was positioned at a 225° bearing, roughly one kilometer from, and running parallel to, the savanna-forest interface (Fig. 6.1). Most species in tropical forests are rare, and many species have fewer than 10 individuals along the transect. Since parameterizing aggregation tendencies, using the methods presented here, requires larger sample sizes than those of most of the trees sampled, I set the lower limit on sample sizes to 19 individuals, a number that might be low for reliable use in spatial statistics. Nonetheless, seven species met this criterion, and six of these had sample sizes greater than 29, a much more statistically acceptable number. In Table 6.1, I list tree species and characteristics that I analyzed in this chapter.

Study tree species

The wind-dispersed species, *Aucoumea klaineana* and *Lophira alata*, have winged fruit. High densities of terrestrial herbs from the Marantaceae and Zingiberaceae families inhibit their germination and regeneration. They are light-demanding, shade-intolerant, pioneer species responsible for colonizing areas that were formerly savannas in the Lopé ecosystem. The fruit in *Lophira alata* is a two-winged, conical capsule (3 x 1 cm) containing a single, green seed. When the ripe fruits are released in late January to March, the long wings (12-18 cm) cause the fruit to spin for a prolonged time in the air, dispersing the seed several hundred meters on windy days (White and Abernethy, 1997).

Xylopia is a genus common in island-groves ("bosquets") and gallery forest at SEGC, though it is also relatively abundant in Marantaceae forests and disturbed areas. It bears ripe fruit during the long dry season and is therefore particularly important to many bird and small primate species, which feed on the arils during this normally, fruit-scarce period. The arils are firmly attached to the seeds, which are small enough to be swallowed whole and dispersed by many bird and small mammal species. The two species

Figure 6.1. Map of 5-kilometer transect in the forested study area (from White, 1992). The cross-hatched region represents the nest-site study area from Chapter Five.



I analyze here are *Xylopia aethiopica* and *X. quintasii*, due to their abundance on the transect line. Clark et al. (2001) claimed that large frugivorous birds are the primary dispersers of *X. aethiopica*, while *X. quintasii* is defecation-dispersed by monkeys. Though gorillas and chimpanzees sometimes feed on fruits of this genus, they rarely disperse the small seeds of *Xylopia* spp.

Most species in the genus *Diospyros* prefer thin rocky soils at SEGC, and they all produce fruits consumed by all of the resident frugivorous primates (Williamson et al., 1990; Tutin and Fernandez, 1993a). The majority of species flower after the long dry season, and their fruits ripen after the spring equinox. The thin, white pulp around the seeds of *Diospyros* is difficult to remove, encouraging animals, particularly primates, to swallow the seeds whole. The two species that I analyze are *Diospyros dendo* and *D. polystemon*. Since the fruits of *D. dendo* and *D. polystemon* do not absciss, it is unlikely that non-arboreal frugivores disperse many of its seeds. From an extensive study on the ecologies of elephants and apes in Lopé, White (1992) considers these two species to be dispersed only by chimpanzees and

gorillas, and to a limited extent, elephants. In samples of chimpanzee dung collected between 1989 and 1998, 6.5% and 6.7% contained at least one intact seed of *D. polystemon* and *D. dendo*, respectively, whenever fruit was available. Seeds of these species were in less than 1% of elephant dung piles sampled (White, 1992).

Cola lizae is a medium-sized canopy tree (height= 35m) that is only found in central Gabon. Relatively new to science (Hallé, 1987; Williamson, 1988), it is the most important tree in the study area, with up to 7,000 stems per square kilometer in the northeastern sector of the park. Large individuals rarely reach sizes greater than 70 cm DBH. Phenology records since 1986 show that the majority of reproductive individuals flower in most years, but fruiting is less predictable, and occasional failures in fruit set are common (Voysey, 1995). Fruiting in this species occurs during a four-month period between January and April. Fruits are widely eaten by all diurnal monkeys and both ape species at Lopé (Tutin et al., 1991b; Ham, 1994; Voysey, 1995), however, most of these species are incapable of dispersing the large seeds (2.8 x 1.9 cm) more than a short distance since they rarely swallow the seeds whole. Gorillas are the only frugivores that swallow the seeds of *Cola lizae* with reliability and in great quantities, whenever fruit is available.

Table 6.1. Characteristics of species in the analysis of tree dispersion patterns (≥ 10 cm DBH).

Disperser syndrome / species	Mean ripe fruit date	Seeds in gorilla dung ¹	Habitat specialization	Recruitment strategy	Adult height (DBH)	Characteristics, fruit (f); seed (s)	Seed dispersal ²
Wind-dispersed							
<i>Aucoumea klaineana</i>	Jan-Mar	n.a.	colonizing savanna	Pioneer; large gaps	45 m (120 cm)	f: winged; s: 0.098 grams	wind
<i>Lophira alata</i>	Jan-Mar	n.a.	colonizing savanna	Pioneer; large gaps; Full sun, "lie in waiting"	60 m (150 cm)	f: winged, 12 – 18 cm; s: 1.6 grams	wind
Bird-, monkey-dispersed							
<i>Xylopia aethiopica</i>	7-Aug	n.a.	Marantaceae forest; forest-savanna; disturbed	scatter-dispersed; shade-intolerant	>30 m (75 cm)	f: 0.5 – 1cm, aril small; s: <0.5 cm	bird-def
<i>X. quintasii</i>	28-Aug	n.a.	Marantaceae forest	scatter-dispersed; shade-intolerant	15-30 m (50 cm)	aril nearly covers seed ; s: ~0.5 cm	dropped, bird-regurgitated, monkey-def
Ape-dispersed							
<i>Diospyros dendo</i>	12-Apr	5.6%	rocky forest, Marantaceae forest	clump-dispersed; shade-tolerant	15 m (30 cm)	f: berry, 1.3 x 1.1 cm; s: 0.7 x 0.4 cm	primate-preyed, dropped, def
<i>D. polystemon</i>	23-Apr	26.7%	Marantaceae forest; thin soils (rocky)	clump-dispersed; shade-tolerant	15-35 m (70 cm)	f: berry, 2.5 x 2.3 cm; s: 1.5 x 0.8 cm	primate-preyed, dropped, def
<i>Cola lizae</i>	18-Feb	61.6%	Marantaceae forest	clump-dispersed; shade-tolerant	35 m (70 cm)	f: capsule; s: 2.8 x 1.9 cm	primate-preyed, dropped gorilla-def

¹ Percentage of dung containing whole seeds, when ripe fruit is available. Percentage was calculated from dung samples collected during the presence of ripe fruit; for *Cola lizae* this included the seed group #1 (N= 177 dung), and for *Diospyros* spp. this included only April – May of seed group #5 (N= 90 dung).

² In all vertebrate-dispersed spp., seeds are commonly drop-dispersed by frugivores that process the fruit prior to swallowing the pulp, creating seed shadows that are close to the parent trees.

Data Analysis

Measuring patterns of tree aggregations

I evaluate the spatial patterning in seven tree species by examining neighborhoods around individual trees. To test for spatial gregariousness, I use the second-moment measure of random placement, Ripley's K (Ripley, 1976; Diggle, 2003), adapted to the 1-dimensional case, and compare the observed K-curves with those predicted under the assumption of random placement.

If adult trees are placed randomly according to a Poisson-process with intensity λ , then the expected number of conspecifics within a circle of radius d is simply $\lambda\pi d^2$. As in Chapter Five, Ripley's K quantifies the departure the random situation, with larger values indicating clustering and smaller ones indicating regularity. Specifically, given a point-process on the plane, Ripley's K-function is defined as:

$$K(d) = \lambda^{-1} \mathbb{E} \left(\begin{array}{c} \text{number of extra events within a given} \\ \text{distance } d \text{ from an arbitrary event} \end{array} \right)$$

Data that are arranged in 1-dimensional space, such as along a transect, pose difficulties for analyzing processes that operate on two or more dimensions. Fortunately, developments in the mathematics of spatial statistics have addressed some of these issues (e.g., Cowling, 1998). To test for deviations from complete spatial randomness (CSR) in the dispersion of adult trees along the transect, I collapse tree positions to fall along the line, then employ a K-function modified for the 1-dimensional case (Diggle, 2003; Russo and Augspurger, 2004).

Given a particular arrangement of n trees along a transect of length, L , sampled from area A_0 , the edge-corrected estimator of K is given by Russo and Augspurger (2004):

$$\text{linear}\hat{K}(d) = \frac{|L|}{n^2} \sum_{i=1}^n \sum_{j=1, i \neq j}^n c_{i,j} I_d(d_{i,j})$$

where $d_{i,j}$ is equal to the distance between the i^{th} and j^{th} tree ($i \neq j$), and $c_{i,j}$ is an edge-correcting modifier that equals 2 when the distance between the i^{th} and j^{th} point is greater than the distance to the

nearest endpoint, and equals 1 otherwise. The indicator function, $I_d(d_{ij})$, is 1 if $d_{ij} \leq d$, and 0 otherwise.

The linear K-function calculates the density of neighboring conspecifics as a function of distance from an average individual. This aggregation index is a biologically meaningful measure of clumping in trees, because it evaluates the conspecific population density in the neighborhood surrounding each tree.

K-values mean little without comparing them to values generated from random placement of events. In order to test for random placement of trees, I compare the observed $\hat{K}(d)$ to the maximum generated from 199 Monte Carlo simulations of a Poisson-process along the transect. If $\hat{K}(d)$ is larger than the maximum simulated envelope for a given distance, I conclude at the 1% confidence level that the species is clustered (Diggle, 2003). Values falling below all simulations indicate regularity. Using this technique, I am able to determine how aggregated tendencies vary at increasing spatial scales, since the linear $K(d)$ -curve is a cumulative measure of tree distribution at fixed distances ($< d$ meters) from an average conspecific tree.

In contrast to temperate forests (Bodziarczyk and Szwagrzyk, 1996; Bodziarczyk et al., 1999), most tropical forest trees, if not rare, are clustered (Condit et al., 2000). In order to rank species having different population densities by their tendency to aggregate, it was necessary to generate a Cramer-von-Mises-type statistic that compiles information from the observed $\hat{K}(d)$ -curves. I adapted this “k-statistic” to the 1-dimensional case, from that of the 2-dimensional case used by Plotkin et al. (2000):

$$k\text{-statistic} = \int_0^{h_{\max}} [\hat{K}(h)^{0.5} - h^{0.5}]^2 dh$$

where h is the distance from an average individual, and $\hat{K}(h)$ is the empirical $K(d)$. This statistic is the integrated squared difference between the square roots of the observed K-function, and those corresponding to complete random placement. In practice, I approximate the integral using a Riemann sum between 0 and h_{\max} using subintervals, Δh , equal to 5 meters.

To compile information on tendencies to aggregate at different spatial scales, I calculate the k-statistic for increasing distances from a conspecific tree, using h_{\max} (= 100, 250, 500, 750, 1000, ..., 2500

meters). Given an observed k-statistic, if a large number of random simulations are done, then the quantile in which k_{observed} falls yields a good index of aggregation (Plotkin et al., 2000), one that is comparable across species. Thus, for each h_{max} , I calculated the k-statistic for 999 simulations of a Poisson process (i.e., random placement) and determined the 0.95th quantile in which the k_{observed} in a species fell, corresponding to a 5 % confidence level. Since the k-statistic calculates the squared differences between the observed and random distributions, both aggregation tendencies and segregations (e.g., gaps formed by processes associated with dispersal limitation) contribute positively to its value.

Poisson Cluster Model

While the k-statistic yields a convenient, single measure of aggregation over a selected scale from the Ripley $K(d)$ -curve, it does not quantify the important parameters behind the underlying processes that create aggregated distributions. To estimate these parameters, I desired a parametric model that described tree placement along the transect. The information to fit such a model is also embedded in the $K(d)$ -curve. Parameters that I wished to estimate from extant aggregated tree patterns are (1) a measure of the number of tree clusters, and (2) a measure of the mean cluster size. One such model, the Poisson cluster process, is well established theoretically (Neyman and Scott, 1958; Plotkin et al., 2000). I chose this model because of its simple probabilistic properties, and its K-function is already defined for the 1-dimensional case (Cowling, 1998; Aldrin et al., 2003).

I use the following definition for the Poisson cluster process:

- “Parents” form a Poisson process with intensity λ . The realization of this process comprises cluster centers.
- Each “parent” produces a random number of “daughters”, drawn independently from a fixed distribution.
- The locations of “daughters” relative to cluster centers follow a radially symmetric Gaussian distribution function, $f(x, y)$. The final pattern consists only of “daughter” events.

The positions of “daughters” are drawn independently from the bivariate probability density function:

$$f(x, y) = (2\pi\rho^2)^{-1} \exp\left(\frac{-(x^2 + y^2)}{2\rho^2}\right)$$

where the mean squared distance from a daughter to its cluster center is $2\rho^2$, and the mean distance is $\rho\sqrt{\pi/2}$. Thus, λ is a measure of the density of tree clusters and ρ is a measure of the size, in distance, of tree clusters. Although the assumption of a Gaussian distribution of daughters within a cluster may be unrealistic for natural distributions, the estimated model does adequately partition conspecific distributions into real clusters that are separated by areas of low density, or gaps.

By choosing this model to describe natural tree distributions, I implicitly imply that clusters of trees arise from local recruitment. In this sense, the Poisson cluster model parameterizes aggregations in trees that result from the sum effects of local seed rain (dispersal) and survival probabilities (establishment). Cluster sizes are certainly caused by a number of abiotic and biotic factors; however, seed dispersal and survival probabilities are prominent among these factors (Plotkin et al., 2000). I do not, however, wish to imply that all daughters in a cluster originate from a single parent “tree”. Indeed, cluster centers do not (necessarily) represent an actual tree. Rather, the Poisson cluster model is useful because it offers a convenient model with which to parameterize spatial characteristics that result from processes that aggregate seeds (dispersal) and those that modify it (mortality).

In order to implement the Poisson cluster model, and estimate the best-fit aggregation parameters from information contained in the observed $K(d)$ -curves, I relied on the equation for the Poisson cluster process ($K^{PCP} | \lambda, \rho, \sigma$) collapsed onto a 1-dimensional transect line. This equation has already been developed by Cowling (1998) and corrected slightly by Aldrin et al. (2003):

$$K_{1D}^{PCP}(d) = 2d + \frac{\left\{ 2\Phi\left(\frac{d}{\rho\sqrt{2}}\right) - 1 \right\}}{2\sqrt{\pi}\lambda\sqrt{\sigma^2 + \rho^2}}$$

where Φ is the distribution function of the standard normal distribution, λ is the intensity of the invisible Poisson-distributed cluster centers, ρ is the standard deviation of a radially symmetric (i.e., isotropic)

Gaussian distribution of “daughters” in distance relative to their cluster centers, and σ is the standard deviation of the detection function away from the transect line. Subsequent to fitting the model, the number of daughters, μ , that each cluster independently produces is Poisson-distributed and found by:

$$\mu = \{E(n)\}/(2\lambda wL)$$

allowing μ to be estimated by substituting $E(n)$ by the observed number of events (n) along the transect. The half-width of the transect line is w , and is equal to 2.5 meters here. I describe λ in units of clumps-per-hectare, and p in units of meters.

Cowling (1998) and Aldrin et al. (2003) developed the 1-dimensional K-function from a theoretical Poisson cluster process for the detection of events (in their case, minke whales) projected onto the transect line in mind. Events are the number of detected animals along a line-transect, which naturally decrease as function of perpendicular distance to the line. The detection function, therefore, defines an anisotropic thinning of the population in the sample data as distance from the line increases. In the case of vegetative surveys, where all individuals within a fixed bandwidth are detected, there is no need to impose such an assumption.

Cowling (1998) incorporated the probability of detecting an individual animal as: $g(x) = g_0 e^{-x^2/2\sigma^2}$, where x is the perpendicular distance from the transect line, g_0 is probability of detection on the line (i.e., $x=0$), and σ^2 is the variance in detection away from the line. In vegetation surveys, $g(w)$ is equal to 1 and $\int_{-w}^w g_0 e^{-w^2/2\sigma^2} dw$ is equal to $2w$, provided that g_0 equals 1, which it does. In the R package “spatstat” (Baddeley and Turner, 2005), the linear-K function calculates the 1-dimensional $K(d)$ from a point pattern that has been collapsed onto a linear network. In fitting a Poisson cluster model to data from a vegetation transect, it is necessary to fix σ to a meaningful value. I found that a value of 0.01 effectively models a $g(0)=1$, and a $g(x>0)\approx 0$. Since the observed $K(d)$ -curves are calculated from data that has been collapsed onto the transect, a zero detection probability away from the line is desirable. In simulations of 2-dimensional cluster processes with known parameters, collapsed onto the

transect, I was able to recuperate known parameters with sigma fixed to 0.01. I therefore determined that fixed $\sigma = 0.01$ was appropriate in model fitting.

Estimating cluster parameters

I fit a Poisson cluster model to each of five tree species (*Diospyros dendo* was omitted since it did not exhibit aggregated tendencies in the $K(d)$ -curve). Estimation of parameters (λ, ρ) in the theoretical $K_{1D}^{PCP}(d)$ from the empirical $\hat{K}(d)$ -curves was achieved by using the minimum contrast method, as suggested by Illian (2008). The estimates for λ and ρ are the values that minimize the function:

$$\int_0^{h_{\max}} \left[\{\hat{K}(h)\}^{c_0} - \{K^{PCP}(h|\lambda, \rho, \sigma)\}^{c_0} \right]^2 dh$$

for some tuning constant c_0 , and the range of distances, $0 \rightarrow h_{\max}$, over which parameterization is to occur. Diggle (2003) discussed the choice of h_{\max} and c_0 based on empirical evidence. He suggested that $c_0 = 0.5$ stabilizes the variance for a Poisson process; however, $c_0 = 0.25$ has been shown to be more effective for aggregated data (Plotkin et al., 2000). Since the species analyzed here exhibit highly aggregated tendencies, I use the latter. Similarly, the upper limit over which the integral is calculated, h_{\max} , can greatly affect parameter estimation. Plotkin et al. (2000) suggested using the greatest distance over which clustering was observed.

To minimize above equation, I needed to specify the initial guesses for λ and ρ , which can also have a dramatic effect on the resulting parameter fit. Following Plotkin et al. (2000), I specified the initial parameters as $(\lambda, \rho) = (1/\hat{K}(\bar{d}), \bar{d}/4)$, where \bar{d} is the distance of the maximum value on the $K(d)_{\text{observed}}-d$, over the range of d from zero to the maximum of the first cluster (associated with the smallest scale in distance from an average tree). I tested for goodness-of-fit in models by plotting $K(d)$ -curves from 100 simulated patterns using the fitted parameters against the observed $K(d)$. If a given model fit reasonable well, then the observed $K(d)$ -curve should fall with the envelope created from the 100 simulated $K(d)$ -curves. Since the choice of h_{\max} can also greatly affect estimated parameters, I

evaluated fitted parameters at 25-meter intervals between 25 and 2500 meters. Although the $K(d)$ -curves in some species fit reasonably well inside the simulated envelopes from more than one fitted model, most candidate models were observed to deviate outside these envelopes at one or more spatial scales. The best-fit model was the model that remained well within simulated envelopes at all spatial scales.

All modeling and calculations are performed using the R language (R Core Team, 2012). Species $K(d)$ -curves and cluster parameter estimates are performed using the “spatstat” package (Baddeley and Turner, 2005).

RESULTS

The relative abundance of individuals across DBH-cohorts along the line-transect are shown in Table 6.2. Recruitment patterns differ between species. In most species, a typical DBH frequency structure is observed, with many small-sized individuals and fewer large-sized ones. Two species, however, exhibited right-skewed age structures; namely, *Aucoumea klaineana* and *Diospyros polystemon*. With *A. klaineana*, it is clear that recruitment (regeneration) into the small DBH classes was limited, presumably due to specific habitat requirements related to shade-intolerance on the part of seedlings. Seedling establishment and recruitment in this species is greatest in large open areas and savannas, due to its light requirements (White, 1992). The more complex vertical structure observed in Marantaceae forest, where the transect was cut, likely reduces the amount of light available to young recruits (seedlings and saplings) in this pioneer species (White, 1996). With *D. polystemon*, the reason for a right-skewed DBH distribution is not entirely clear. White and Abernethy (1997) state that this species is relatively common in mixed forests; thus, the transect is not outside its normal habitat requirements. As with many species in this genus, it prefers thin, rocky soils. Heterogeneity in soil structure along the transect line, may therefore limit recruitment in *D. polystemon*. *Xylopia aethiopica*, had a low density ($N=19$); thus, sampling error may lead to biased interpretations based on its observed $K(d)$ -curve.

Mean densities exhibit a range of values from 11.6 individuals per hectare in *D. dendo* to 72.4 per hectare in *Cola lizae*. These values, however, contain no information on the aggregation tendencies of individuals. For that, I use the second-order K-function.

Table 6.2. DBH frequency distribution of eight tree species along a 5-km transect. Individuals are grouped by DBH-cohorts (N= number of individuals sampled of each species). Frequencies of stems in each DBH-class differed across species.

Species	N	Mean density*	Frequency within DBH-cohorts				
			[10-15)	[15-20)	[20-25)	[25-30)	≥30
Wind-dispersed							
<i>Aucoumea klaineana</i>	61	24 .4	0 .0	1 .6	4 .9	4 .9	88 .5
<i>Lophira alata</i>	59	23 .6	40 .7	20 .3	6 .8	8 .5	27 .5
Bird-, monkey-dispersed							
<i>Xylopia aethiopica</i>	19	7 .6	73 .7	21 .1	5 .3	0 .0	0 .0
<i>X. quintasii</i>	39	15 .6	48 .7	33 .3	17 .9	0 .0	0 .0
Ape-dispersed							
<i>Diospyros dendo</i>	29	11 .6	89 .7	6 .9	0 .0	3 .4	0 .0
<i>D. polystemon</i>	38	15 .2	5 .3	21 .1	13 .2	18 .4	42 .1
<i>Cola lizae</i>	181	72 .4	34 .8	18 .2	16 .0	11 .0	19 .9

*Mean density is number of individuals per hectare.

Second-order characteristics of tree distributions in Marantaceae forest at SEGC

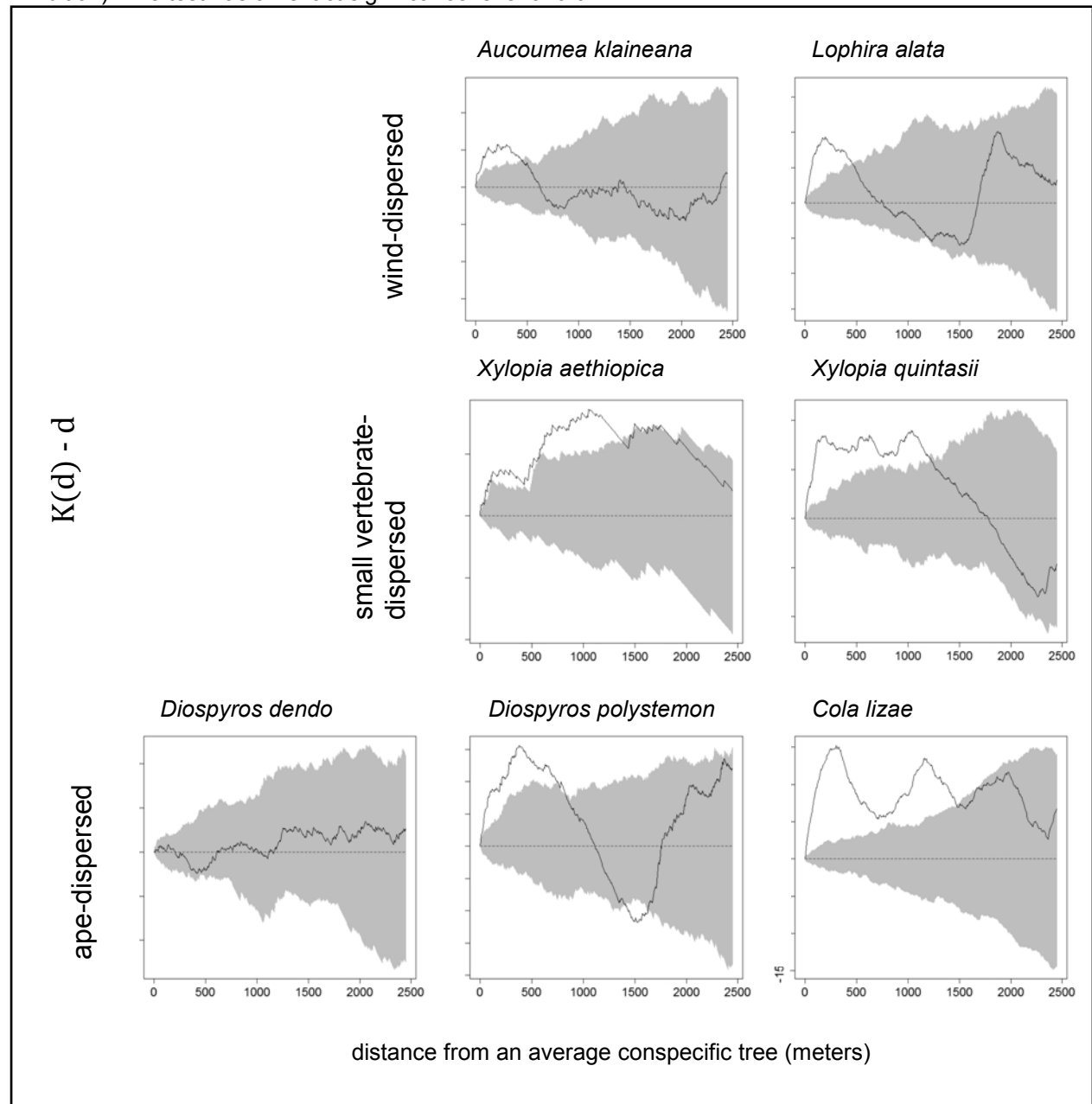
Second-order $K(d)$ graphs exhibit aggregated tendencies at small spatial scales in all but one species, with $K(d)$ values greater than 199 random simulations at distances less than 500 meters from a conspecific tree (Fig. 6.2). Clustering is not observed in *Diospyros dendo* individuals. Since *D. dendo* is dispersed by primates and other medium-bodied frugivores, one might expect clumping at small spatial scales. However, *D. dendo* is a small-stature tree of roughly 15 m in height, and thinning prior to recruitment into the 10 cm DBH-cohort has likely already occurred. In this case, non-random mortality may have already obscured any aggregated tendency that existed in seed, seedling, and young tree distributions in this species. As with *D. polystemon*, *D. dendo* also has a preference to rocky forest types, a habitat not sampled with great frequency along the transect. Thus, heterogeneity in establishment conditions may also help to explain why clustering is not detected in *D. dendo*, at least in sites that are suitable for establishment.

In some species, aggregative tendencies are observed at more than one spatial scale. This is the case in *Cola lizae*, *Xylopia aethiopica*, *X. quintasii*, and to a lesser extent, *Diospyros polystemon*. Caution is warranted in the case of *X. aethiopica*, however, due to its small sample size (N= 19 individuals). *Cola lizae* peaks at regular intervals of 700-1000 meters, while *X. quintasii* has multiple peaks at close range (< 1300 meters), then becomes indistinguishable from random at larger scales. *Diospyros polystemon* is the only species to demonstrate an inhibited (or regular) distribution, at a distance of ~1500 meters. Since this species also has a right-skewed DBH distribution, indicating low regeneration ability, heterogeneity in establishment conditions along the transect is a possible explanation for the inhibited pattern in this species.

Beyond merely qualifying the tendency for individual tree species to aggregate, I wished to rank species across spatial scales. To do this, I compare the species-specific k-statistics to the 0.95th quantile of 999 random simulations. Figure 6.3 shows the results for five species at increasing spatial scales along the 5-kilometer transect. Wind-dispersed species exhibit weaker tendencies to aggregate than vertebrate-dispersed species, and clustering occurs on smaller scales (< 500 meters). In addition, these tendencies dissipate at a faster rate than those of animal-dispersed species (as distance increases), and are indistinguishable from randomly placed individuals at scales greater than 1500 meters. The dispersion of *A. klaineana*, though dominated by large individuals and having very few new recruits, is nearly identical to that of *L. alata*. The magnitude of aggregation in the latter is, however, slightly greater, presumably due to greater numbers of 10-20 cm DBH cohorts.

In the case of the bird/monkey-dispersed, *X. quintasii*, and the ape-dispersed, *D. polystemon*, high tendencies to aggregate at moderate scales are observed, with peaks at 1000 and 1250 meters, respectively. Since the k-statistic squares the difference between the empirical and random K-curves, both clustering and regularity will contribute positively to its value. Both clustering and regularity, will reflect recruitment limitation (i.e., vacancies at suitable sites), and patterns in adult dispersion may be the result of either higher levels of seed limitation (e.g., dispersal limitation) or establishment limitation. Both clustering and inhibition are observed in the extant *D. polystemon* population (see Fig. 6.2), however,

Figure 6.2. Second-order linear K-function of tree locations along 5-kilometer transect. $K = \lambda^{-1}(E = \text{number of extra trees within a distance } d \text{ of an average tree})$. The value d is subtracted from the linear K to achieve a more readable plot. The shaded region indicates envelopes from 199 simulations under the assumption of complete spatial randomness (CSR). The solid line is the empirical K curve. Values of $K(d)-d$ above the envelope indicate trees that are closer to each other than expected from a homogeneous Poisson (i.e., random placement) pattern, while those below indicate regularity (i.e., inhibition). The test has an exact significance level of 0.01.



given its poor regeneration (see Table 6.2), and its propensity toward rocky soils, determining whether clusters (and their separations) are a consequence of seed limitation (failure to arrive) or establishment limitation (failure to survive) is not possible. In contrast, a normally recruiting population in *X. quintasii* (see Table 6.2) coupled with what appears to be multiple small-scale aggregations (see Fig. 6.2) provides evidence to support a distance-restricted dispersal process (as mediated by monkeys) in this species.

An increase in the k-statistic will result from two aspects of aggregated structure, namely, increases in the number of clusters (λ), and decreases in the average cluster size (ρ). In the case of *Cola lizae*, aggregation tendency does not peak until a scale of ~2500 meters is considered. This species maintains a gradual increase in k-value as distance increases up to 2500 meters, indicating that aggregation here is largely due to processes that occur at scales larger than the individual (local) cluster. In other words, it appears that the periodic addition of clusters in *C. lizae* (the neighborhood) accounts for most of its gregariousness as measured by the k-statistic. Lower k-values at smaller scales in *C. lizae*, relative to the other vertebrate-dispersed species, are likely due to its very large cluster sizes (neighborhood size). Only after distances greater than 1000 meters, does the effect of the number of clusters overtake the aggregation index in this species, suggesting that processes associated with the formation of additional (nascent) clusters may be more important than those associated with creating large clusters, in describing the spatial distribution of adult *Cola lizae*.

Estimated clumping parameters

In Table 6.3, I show the fitted parameters from cluster models in six species. The mean distance from an individual to a cluster center is determined by $\rho\sqrt{\pi/2}$, which is a proxy to the mean patch size and is a function primarily of dispersal distances and gap-sizes. The smallest average cluster size is in *A. klaineana* (mean distance= 38.8 meters), a value that is not unexpected given its presumed low dispersal ability, specific habitat requirements, and a presumed thinning that has already occurred prior to the larger DBH classes. Clusters in *L. alata* (mean distance= 49.9 meters) are similar in size to those of *A. klaineana*. Since a “normal” age-class recruitment pattern is observed for *L. alata* (Table 6.2), a small

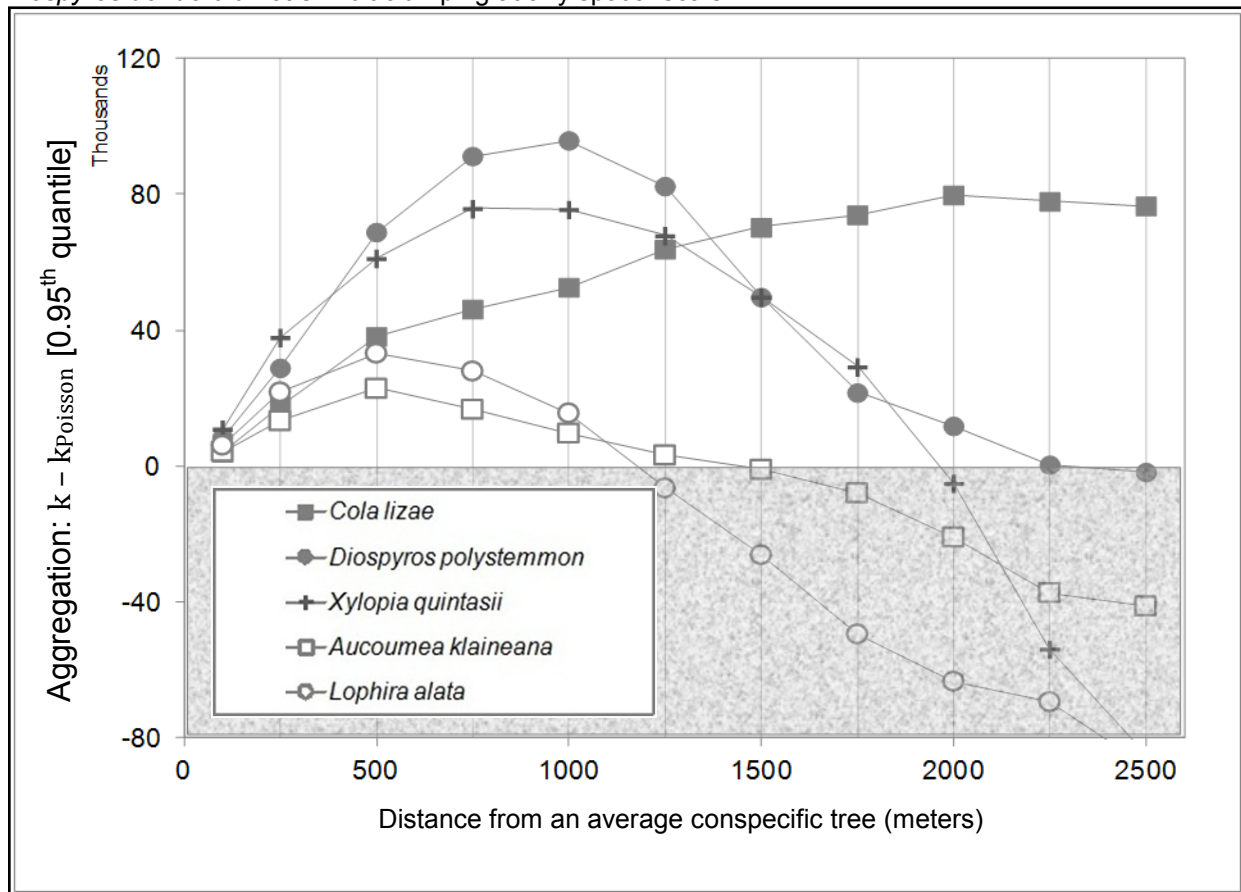
cluster size in this wind-dispersed species could be due to a high degree of distance-restricted dispersal, coupled with weak density-dependent mortality near parent trees.

Cluster sizes among the small-seeded *Xylopia* spp. are similar to each other, with *X. aethiopica* having a mean distance of 60.9 meters, and 51.9 meters for *X. quintasii*. The ape-dispersed species, *D. polystemon* and *Cola lizae*, have the largest clusters of 67.1 and 94.6 meters, respectively. The larger seed sizes in these species nearly guarantee that within-cluster dispersions (i.e., local neighborhoods) are largely mediated by the drop- and spit-dispersal behaviors common in the sympatric monkey community. Cluster sizes in these last two species (and for *Cola lizae* in particular), are consistent with the local dispersion patterns that are expected from scatter-dispersal, and the large-scale patterns expected from clump- (defecation) dispersal (Howe, 1989).

Abundances within clusters are not equal across species, with *C. lizae* being the most populated ($\mu = 549.6$), followed by *D. polystemon* ($\mu = 121.1$), *X. quintasii* ($\mu = 106.1$), *X. aethiopica* ($\mu = 91.1$), *L. alata* ($\mu = 85.0$), and *A. klaineana* ($\mu = 49.8$). The number of clusters per square-kilometer ranged 6-fold, from *X. aethiopica* ($\lambda = 8.3$) to *A. klaineana* ($\lambda = 49.0$), and more than 3-fold if the highly right-skewed, large-sized, *A. klaineana* population is removed.

Since λ is related to the scale of segregation between clusters, it reflects the possible long-distance and directed dispersal of seeds away from conspecific neighborhoods. From the fitted parameters in Table 6.3, it appears that vertebrate-dispersed species are more dispersal-limited (or recruitment-limited) than wind-dispersed species at nearly all scales, and particularly so at scales greater than the size of the local cluster. Severe large-scale dispersal-limitation is observed in the large-seeded *Cola lizae*, which has a relatively low number of clusters per hectare (λ), despite being very locally abundant.

Figure 6.3. Species aggregation ranks at increasing distances away from an average tree along the 5-kilometer transect. Rankings are based on their k -statistic against 999 Monte Carlo simulations of a Poisson-distributed pattern. The y-axis is the observed k -statistic minus the 0.95th quantile of simulations. Values greater than zero indicate non-randomness at the 5% confidence level. Increasing values along the y-axis indicate a greater degree of clustering, with clustering defined as either a greater number of clusters or a tighter average cluster size. The textured box indicates the region where the random placement of individuals could not be rejected. Two species (*Cola lizae* and *Diospyros polystemon*) are distance-restricted in their dispersal by monkeys and defecation-dispersal by apes, with *Cola lizae* dispersed only by gorillas. *Xylopia quintasii* is scatter-dispersed (i.e., dropped) by birds and monkeys, with some contagious dispersal (i.e., defecation dispersal) by monkeys. *Aucoumea klaineana* and *Lophira alata* are wind-dispersed. *Xylopia aethiopica* is not included due to a small sample size ($N=19$), and *Diospyros dendo* did not exhibit clumping at any spatial scale.



The near-random presence of a tree at increasing spatial scales would represent a uniform probability that a site will be occupied by a species. Since vertebrate-dispersed species maintain tendencies for aggregation at far greater scales than wind-dispersed species, I infer that the former species experience greater recruitment limitation than the latter. Additionally, if non-random, density-

dependent mortality in large-seeded tree species, particularly in *C. lizae*, does exist, it is not severe enough to efface the scattered and distance-restricted pattern of seed deposition mediated (locally) by birds and monkeys, nor the long-distance, defecation-dispersal of seeds left ostensibly by gorillas. Estimating the parameters of the Poisson cluster process is accomplished here by minimizing the distance between theoretical (random) and empirical Ripley's K functions for the one-dimensional case. This is essentially a moment estimator that does not have the advantage of likelihood methods, including model selection via the AIC criterion (Skaug, 2006). In lieu of a statistically sound goodness-of-fit procedure between model and data, the important criterion by which to judge these cluster models should be their ability to reproduce the observed distribution of trees along the transect line. Using the estimated parameters (λ , ρ , μ) for each species, I simulate 100 Poisson cluster patterns onto a 5-km x 5-km plane and overlay a 5-km x 5-m transect onto each simulation. For each simulated transect, I then calculate a linear $K(d)$ -curve. If the cluster process from the fitted parameters fits the data reasonably well, then the observed $K(d)$ should fall within the envelope created by 100 simulated K -curves. Figure 6.4 shows a realization of the best-fit models for each species, and $K(d)$ -curves from 100 simulations projected onto a 5-km transect.

Species are ranked in Figure 6.4 by order of increasing cluster sizes. A large window of observation, 25 km², is used to demonstrate differences in spatial patterning among species on two (nested) spatial scales, cluster and inter-cluster. Aggregations are very "tight" in the first couple of species (i.e., wind-dispersed); however, the pattern formed by the clusters themselves (at larger scales) appears random throughout the window. As cluster sizes (and seed sizes) increase, the patterns of associations between clusters appear to retain aggregated tendencies.

This highlights the potential for hierarchical clustering that may emerge, as a consequence of gorilla-mediated seed dispersal behaviors and subsequent seedling establishment probabilities, in which local clusters are themselves clustered at large spatial scales. Although the distribution of cluster centers (λ) is not explicitly modeled as an inhomogeneous parameter (i.e., dependent on heterogeneity of environmental factors) in the models, future research into the aggregated patterns of trees should focus

Table 6.3. Fitted Poisson cluster model parameters. Distribution statistics of mature trees (DBH > 10 cm) in species of varying fruit and seed size, and different dispersal syndromes. No departure from random placement is observed in *Diospyros dendo*.

Species	Density ^a	$\hat{\lambda}$	$\hat{\mu}$	$\hat{\rho}$ ^b	$\rho\sqrt{\pi/2}$	Initial parameters		
		clusters per km ²	individuals per cluster	cluster size (m)	dist. to cluster center (m)	h_{\max} ^c	λ	p
Wind-dispersed								
<i>Aucoumea klaineana</i>	24.4	49.0	49.8	30.9	38.8	225	147.8	31.1
<i>Lophira alata</i>	23.6	27.8	85.0	39.8	49.9	475	72.4	41.9
Bird-, monkey-dispersed								
<i>Xylopia aethiopica</i>	7.6	8.3	91.1	48.6	60.9	225	9.3	268.0
<i>X. quintasii</i>	15.6	14.7	106.1	41.4	51.9	200	43.9	47.9
Ape-dispersed								
<i>Diospyros dendo</i> ^d	11.6	----- Poisson process -----						
<i>D. polystemon</i>	15.2	12.5	121.1	53.5	67.1	350	45.8	89.7
<i>Cola lizae</i>	72.4	13.2	549.6	75.5	94.6	300	77.1	75.4

^a stems per hectare assuming uniform density.
^b offspring distribution around center of cluster following a radially symmetric Gaussian distribution with variance ρ^2 .
^c maximum distance over which the minimizing function was integrated.
^d no observed departure from uniform Poisson process, i.e., CSR.

on modeling cluster centers using to the environmental covariates that are found to be significant in the construction of nests by gorillas (Chapter Five).

Cluster persistence in successive DBH cohorts

The high abundance in *Cola lizae* at Lopé guarantees that sample sizes will large enough to investigate clumping in successive DBH cohorts. The upper pane in Figure 6.5 shows the $K(d)$ -curves in DBH classes for *Cola lizae*. Aggregated patterns exist at both small and medium spatial scales in the smallest of DBH classes (10-15 cm, and 15-20 cm). These patterns subsequently disappear in larger DBH classes (>20 cm), suggesting that some density-dependent thinning of individuals does occur prior to reaching a substantial age. Using average growth rates in DBH-classes reported from White (1996), I calculate that a 10-to-20 cm DHB growth-interval is associated with 50 years in *Cola lizae*, with total age being 50 plus the number of years to enter the 10 cm DBH class. Note that both within- and between-cluster aggregations persist in cohorts less than 20 cm DBH.

In three additional species, it is not possible to place DBH sizes into discrete bins due to small sample sizes. However, it is possible to test for aggregated tendencies above specific DBH thresholds, in these species. The lower pane in Figure 6.5 shows the smallest such threshold for which random placement could not be rejected in the $K(d)$ -curves of *Aucoumea klaineana* (≥ 40 cm) *Lophira alata* (≥ 20 cm), and *Diospyros polystemon* (≥ 20 cm). Once again, using growth rates in White (1996), aggregated tendencies persist for roughly 131 years in *A. klaineana*, and 48 years in *L. alata*. It is not possible to calculate persistence of aggregations in *D. polystemon* due a lack of data on growth rates. However, considering that a closely related congener, the “true” ebony tree (*Diospyros crassiflora*) likely takes 500 years to achieve 50 cm DBH (White, 1996). Persistence of aggregations in cohorts up to 20 cm DBH undoubtedly represents a significantly long period of time in *D. polystemon*.

Figure 6.4. Tree distributions simulated from the Poisson cluster models for six species across three dispersal syndromes. The simulation window is 25 km² (5km x 5km). Species are listed in increasing order of cluster size (ρ). Despite minor discrepancies, linear K(d)-curves calculated from 99 simulations of the best-fit Poisson cluster models, provide visually acceptable reproductions of observed linear K(d)-curves. *Diospyros dendo* is not included since it did not deviate from random replacement.

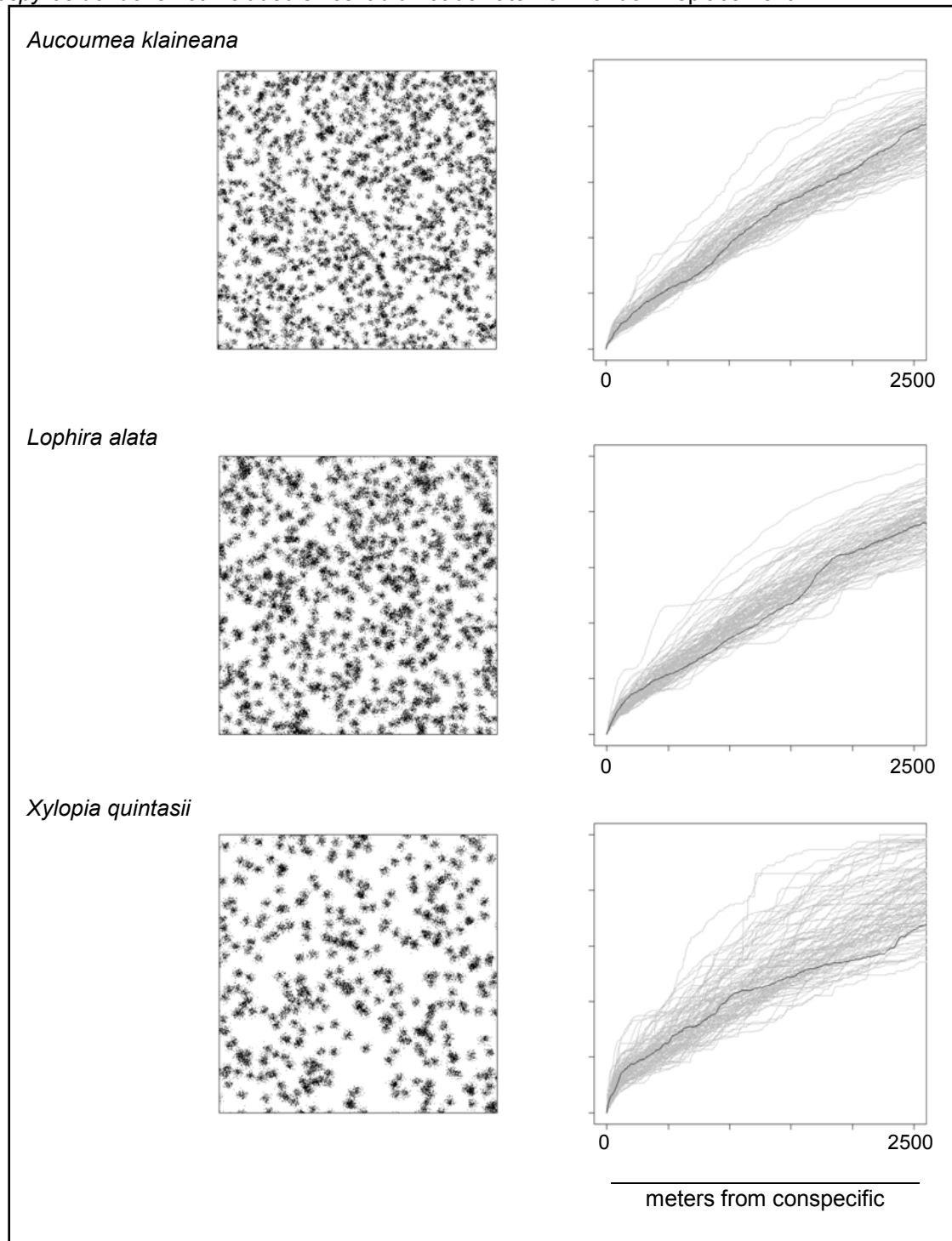


Figure 6.4, continued.

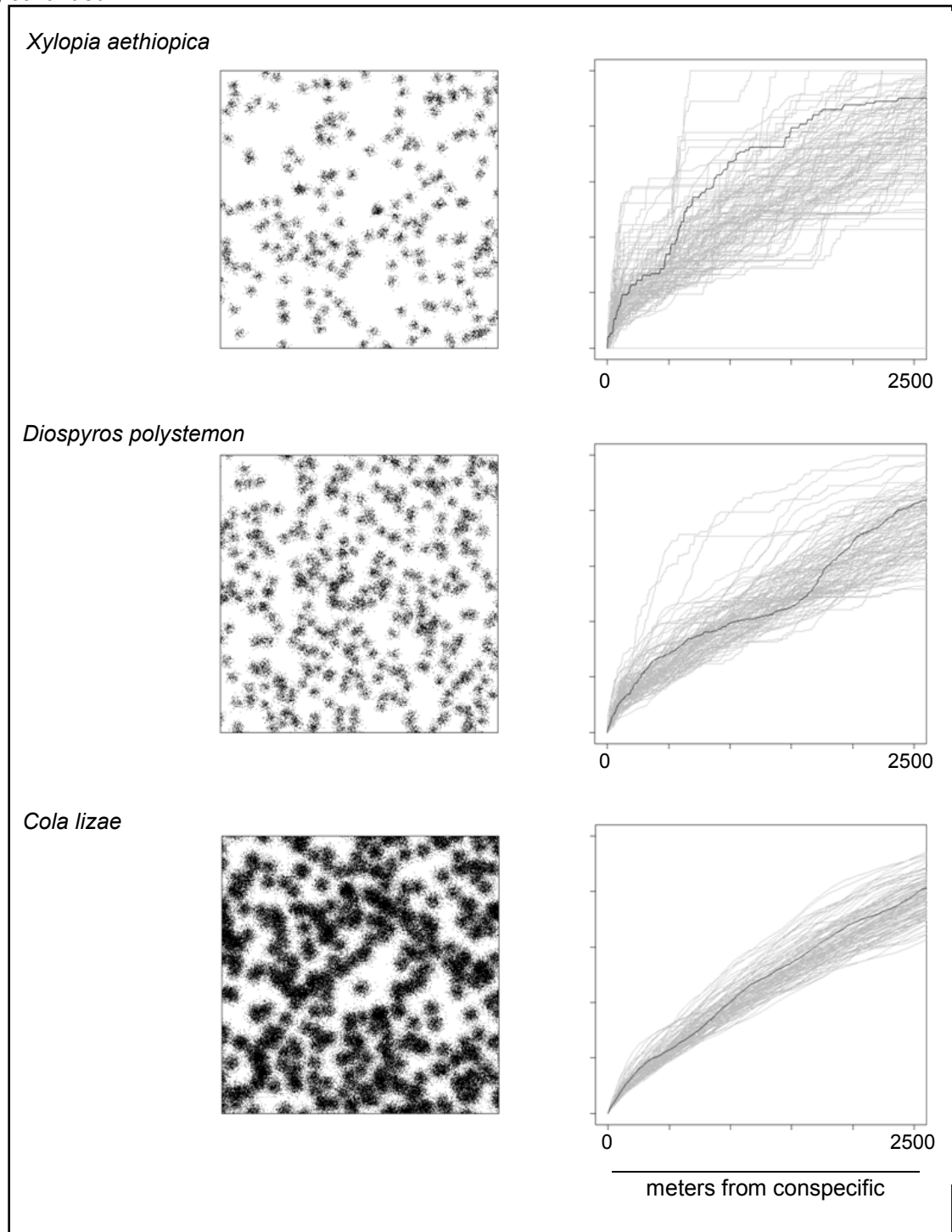
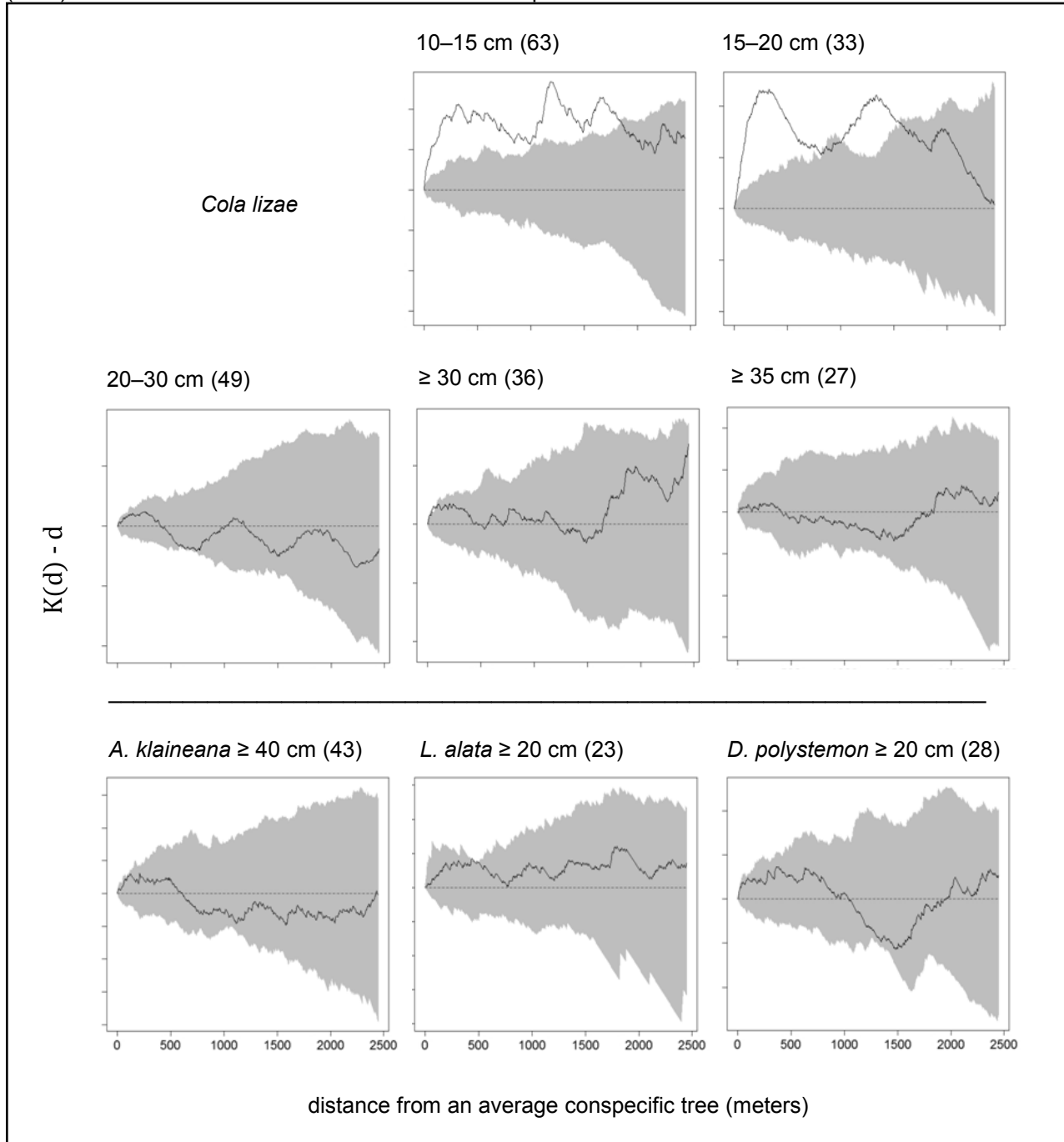


Figure 6.5. Second-order linear $K(d)$ -curves for successively larger DBH classes in *Cola lizae* along 5-kilometer transect (upper panel). The lower panel shows the smallest DBH threshold for which random placement cannot be rejected in the $K(d)$ -curves of *Aucoumea klaineana*, *Lophira alata*, and *Diospyros polystemon*. The value d is subtracted from the linear K to achieve a more readable plot. The shaded region indicates envelopes from 199 simulations under the assumption of complete spatial randomness (CSR). The number of individuals in each cohort is in parentheses.



DISCUSSION

Although processes responsible for the patterns of aggregations and gaps observed here cannot be definitively inferred from spatial point analysis, possible scenarios behind dispersions can be compared to the observed spatial patterns (Kraft et al., 2002). Separation of clusters in *Cola lizae*, at scales greater than 1000 meters, is consistent with the idea of gorilla-mediated, directed, and long-distance seed dispersal events away from local neighborhoods. These events could establish nascent foci from which local dispersal can occur via the short-distance dispersal typical under the seed dropping and spitting behaviors of birds and monkeys.

The uncoupling of seed deposition patterns from later demographic life stages is common in plant recruitment dynamics (De Steven, 1991; Herrera et al., 1994; Wakibara, 2005). Alternatively, some researchers have demonstrated that dispersion patterns among seedlings can persist through later recruitment stages in some species (Rey and Alcántara, 2000; Russo and Augspurger, 2004). If mortality is a random plant-thinning process, independent of distance from conspecifics, there should not be a significant change in the general, aggregated appearance of observed $K(d)$ -curves as cohort age increases. Therefore, if spacing is occurring in successive age-cohorts, it must occur because of mortality among younger cohorts, and this mortality must have a component of distance-, and/or density-dependency.

In results I present here, both persistence and differential mortality can exist within the same tree population, occurring at different temporal periods of life history, and neither should necessarily negate the importance of directed dispersal events in the demographic development of a tree community. I propose that for some species, mortality factors at small spatial scales can be low relative to the high seed deposition densities that might exist prior to the early stages of seedling establishment and recruitment, leading to aggregation tendencies well into advanced tree stages. Evidence for this comes from the aggregated tendencies of trees in observed $K(d)$ -curves at scales < 250 meters. Persistence may be substantial, with patterns associated with seed dispersion maintained for tens, if not hundreds, of years depending on the species.

Six out of the seven species analyzed in this chapter exhibit clustering at spatial scales of less than 100 meters. Aggregations in trees are result in what may be called conspecific neighborhoods. The scale of these neighborhoods is consistent with distance-restricted seed dispersal, and subsequent establishment, often associated with wind- and scatter-dispersal. In species with animal-assisted seed dispersal, the development of neighborhoods is mediated by the dropping and spitting behaviors of small-bodied vertebrates, including birds and monkeys.

All vertebrate-dispersed species tested here, excluding *Diospyros dendo*, exhibit aggregations at both small and medium spatial scales. In the case of *C. lizae*, the distribution of the clusters themselves, are on the same scale as gorilla nesting behavior. Presumably, clumped seed deposition patterns (Voysey, 1999a; Chapters Four and Five) are maintained into both small and medium-sized tree stages (*A. klaineana*: ~40 cm DBH; *L. alata*: ~20 cm DBH; *D. polystemon*: ~20 cm DBH; and *C. lizae*: ~35 cm DBH). Therefore, although Janzen-Connell mechanisms associated with the benefits of escaping the immediate neighborhood of conspecifics (see Chapter One) may cause substantial non-random thinning in seedling and sapling aggregations, these mechanisms do not appear strong enough, in most of the species examined here, to efface the high densities associated with the seed dissemination patterns in the local (near-to-parent) seed rain. Non-random thinning in both wind-dispersed species (*A. klaineana* and *L. alata*) and vertebrate-dispersed species (*D. polystemon*, and *C. lizae*), eventually does eliminate the clumped dispersion patterns in their populations.

The biotic and abiotic factors affecting survival and growth in these trees are not known. Reductions in clumping tendencies in trees may be the result of density- and distance-dependent mortality in later-life stages. In addition to predation and disease, non-random, late-stage thinning processes may result from species-specific regeneration requirements or competitive interactions between species (Grubb, 1977). Despite these yet to be described mortality factors, it is evident that aggregated tendencies seen in *Cola lizae* is a direct result of low mortalities in seeds and seedlings relative to patterns of seed deposition mediated by both small vertebrates (within-cluster) and gorillas (between-cluster). The importance of gorillas in mediating extent distributions in *Cola lizae*, and perhaps other large-seeded species, is defensible. The uniformly-distributed *Cola* tree (≥ 20 cm DHB) must first

survive a highly aggregated neighborhood of conspecifics; a neighborhood that was ostensibly created by gorilla-directed seed deposition processes that aggregated seeds to a suitable establishment site in densities high enough to offset subsequent mortalities. One such site is the location where gorillas construct their nests. The low, though not zero, recruitment in seeds deposited at gorilla nest-sites (Voysey et al., 1999b), I argue here, is the primary, if not the sole, founding process behind the spread of *Cola lizae*.

Jordano et al. (2007) found non-overlapping contributions in seed deposition patterns among frugivores of different sizes. Here, I propose that a gorilla-mediated dispersal syndrome includes large-seeded species such as *Cola lizae* and *Diospyros polystemon*. In these species, dispersal is characterized by a “division of labor”, with small mammals (i.e., monkeys) providing rapid expansion of tree neighborhoods via effective local dispersal, and gorillas providing the occasionally successful long-distance (and directed) dispersal that is necessary for “large leaps” in the population, and the founding of future neighborhoods.

CHAPTER VII

CONCLUSIONS

In this study, I have explored the factors influencing the spatial and temporal patterns of seeds deposited by gorillas, and their consequences to the plant community in Lopé National Park, Gabon. Although I focus on the effects of only a few aspects of gorilla behavior, previous studies have shown these behaviors, namely gorilla foraging choices in a simultaneously fruiting environment, and their tendency to construct nests in places that are (on average) favorable to recruitment, to be fundamental in determining the nature of seed/seedling shadows. The ultimate goal was to examine the strengths of mechanisms mediated by gorillas, at the population level, that affect plant demography and the maintenance of floristic diversity in Central African forests inhabited by gorillas.

CONSEQUENCES OF GORILLA SEED DISPERSAL: IMPLICATIONS FOR COMMUNITY STRUCTURE

In this study, I not only demonstrated substantial temporal variation in fruit availability to gorillas, but also revealed the importance of climatic factors in limiting (source limitation) seeds at the community level (Chapter Three). Large fruits and seeds evolve to increase per capita removal and seed survival rates, but require larger-bodied and reliable dispersers. Gorilla-plant interactions are temporally mediated by the simultaneously fruiting plant community, with seed removal and dispersal greatest during periods of high fruit availability. The physiological requirements to producing large fruits and seeds place constraints on the timing of a plant's reproductive cycle, with earlier flowering necessary to accommodate longer fruit development times.

Although per capita seed survival is strongly dependent upon competition in the co-dispersed clumps of seeds present in gorilla dung, the highest survival and best seedling performances always occurred at a gorilla nest over other sites (Voysey et al., 1999b). Gorillas respond positively, in terms of the number of seeds removed, to species that produce fruit for a longer period and at regular (predictable) times in the year (Chapter Four). Since synchronicity in a fruiting species does not result in

more seeds being dispersed, sequential ripening, both within and between fruiting individuals, is a possible strategy to reliably acquire a visit by gorillas, especially in trees that occur in high densities.

Gorilla defecation patterns and nesting behaviors are strong factors in mediating the spatial variation in seed shadows. Dung deposited at nest-sites contains higher densities, and a greater diversity, of seeds in comparison with dung otherwise scattered by gorillas throughout the day (Chapter Four). Since the numerical size a seed cohort has been shown to be proportional to the seedling population at a later stage (De Steven, 1994; Russo and Augspurger, 2004), future studies should examine the dependency of per capita seedling survival on the size and composition of seed cohorts dispersed in gorilla dung at nest-sites.

The locations of gorilla nest-sites vary in both space and time, depending on environmental factors that include habitat type, slope position, distance to an elephant path, and, to a lesser extent, proximity to a water channel (Chapter Five). In addition, gorillas are attracted to particular locations, and this tendency varies spatially depending on the time of year. Since nest-sites vary in environmental conditions, there may not really be a “typical” nest-site. Future research should attempt to assess the dependence of seedling establishment on the variable environments that occur at nest-sites. Particular attention should be made to the nature of the surrounding vegetation at a nest-site, since some species show better seedling performance in more open locations than others (Voysey, 1995).

For some large-seeded species, which are typically shade-tolerant and may not exhibit strong abiotic limitations on recruitment, gorilla-mediated dispersal to nest-sites containing variable degrees of shadiness may be the principal mechanism by which spatial variation in demography arises. In general, regeneration in long-lived tree species is difficult to study and poorly understood. Susceptibility to natural enemies, such as seed and seedling predators, affects the distribution of seedling and later stages in plant life histories (Janzen, 1970; Connell, 1971; Russo and Augspurger, 2004). In animal-dispersed plants, rates of recruitment into diverse communities are determined by a number of factors. Because vertebrate dispersers, and in particular large-bodied ones such as the gorilla, create spatially restricted patterns of dispersed seeds, dispersers can play a role in mediating species coexistence via dispersal

limitation whereby some species may become established in sites that they “win by forfeit” (Hurtt and Pacala, 1995).

Deposition patterns of seeds dispersed by gorillas can not be easily linked to sapling or adult tree distributions, since natural ecosystems present a shifting mosaic of suitable sites in terms of climate, germination requirements, phylogenetic constraints, and post-dispersal motilities that alter the direct effects of gorillas on the actual distributions of plants. For this reason, second-order statistics can be of greater use, than first-order ones, in characterizing (and testing) the dependencies of extant tree distributions on seed dispersion patterns. The spatial distributions in two gorilla-dispersed species tested here exhibited clustering on a greater scale than those found in other vertebrate- and wind-dispersed species (Chapter Six). Given the gorilla’s tendency to disperse multiple species in the same dung pile, strong evidence for a significant relationship between gorilla-mediated seed dispersal and plant distributions would come from data demonstrating close interspecific proximities among co-dispersed tree species. Using information from the suites of species typically co-dispersed by gorillas that I have identified, future research should attempt to investigate whether gorillas mediate, through their seed dispersal behaviors, associations in the adult tree population in the forests they inhabit.

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APPENDICES

Appendix A. Estimated density and biomass of some of the larger diurnal mammals at SEGC (from White, 1994c).

Species	Density (no. / km ²)		Est. biomass (kg / km ²)
	Groups	Individuals	
<i>Cercopithecus nictitans</i>	1.76	23.7	80.6
<i>Cercopithecus pogonias</i>	0.38	4.8	10.6
<i>Cercopithecus cephus</i>	0.64	6.2	12.4
<i>Cercocebus albigena</i>	0.46	8.6	35.3
<i>Colobus satanus</i>	1.12	13.6	114.2
<i>Mandrillus sphinx</i>	0.01	1.5	15.3
<i>Gorilla gorilla</i>	0.18	1	78.1
<i>Pan troglodytes</i>	0.28	0.7	27.1
Sub-total: diurnal primates			373.6
<i>Loxodonta cyclotis</i>	1.1	3	5225.1
<i>Potamochoerus porcus</i>	0.05	1.6	99
<i>Syncerus caffer</i>	0.1	0.3	71.3
<i>Cephalophus monticola</i>	0.25	0.3	1.2
Red duikers	2.25	2.5	38.8
<i>Cephalophus sylvicultor</i>	0.91	0.9	51
<i>Hyemochus aquaticus</i>		P	P
<i>Neotragus batesi</i>		P	P
Sub-total: ungulates			5486.4
Squirrels			4.2
Total			5864.2

P: present but not recorded

Appendix B. Characteristics of fruit species consumed by gorillas in Lopé National Park, Gabon, analyzed in this dissertation.

Species ¹	life-form ²	Density ³		max dbh ⁴	fruit type ⁵	fruit size ⁶	color	seed size ⁷	seed fate ⁸	import in diet ⁹
		MF	CCF							
ANACARDIACEAE										
<i>Pseudospondias longifolia</i>	MC	*		0.6	DR	M	RED	M	1	3
<i>P. microcarpa</i>	MC	0.6	*	1.0	DR	M	PURPLE	M	1	5
<i>Trichoscypha abut</i>		*	2.0		DR		PINK	L		
<i>T. acuminata</i>	MC	4.6	1.2	0.9	DR	L	RED	L	1	2
ANNONACEAE										
<i>Annickia chlorantha</i>	MC	5.0	2.0	0.7	APO/BE/I	M	RED	M	1	2
<i>Monanthotaxis congoensis</i>	CS					M	RED	M	1	4
<i>Uvariastrum pierreanum</i>	LC	2.6		0.4	APO?	L	YELLOW			
<i>Xylopia aethiopica</i>	MC	4.8	14.4	0.8	APO/CA/D	L	ORANGE	S		
<i>X. hypolampra</i>	UC	4.4	0.4	0.9	APO/CA/D	L	BLUE	M		
<i>X. quintasii</i>	MC	26.6	2.0	0.5	APO/CA/D	L	ORANGE	M		
BURSERACEAE										
<i>Dacryodes normandii</i>	MC	1.8	*	0.4	DR	M	PURPLE	L	1	1
<i>Santiria trimera</i>	MC	0.2	21.6	0.6	DR	M	PURPLE	M	1	1
CALOPHYLLACEAE										
<i>Mammea africana</i>	UC	*	*	1.0	DR	L	BROWN	VL	4	3
CANNABACEAE										
<i>Celtis tessmannii</i>	UC	*	2.0	1.0	DR	M	PURPLE	M		
CLUSIACEAE										
<i>Pentadesma butyracea</i>	MC	0.6	*	0.8	BE	VL	BROWN	VL	4/3	1
EBENACEAE										
<i>Diospyros dendo</i>	LC	11.4	2.4		BE	M	RED	M	2	1
<i>D. mannii</i>	MC	1.8	*	0.4	BE	VL	YELLOW	VL		
<i>D. polystemon</i>	UC	12.8	1.2	0.7	BE	M	RED	M	2	1
<i>D. zenkeri</i>	MC	0.8	0.4	0.2	BE	L	YELLOW	L		

Appendix B (continued).

Species ¹	life-form ²	Density ³		max dbh ⁴	fruit type ⁵	fruit size ⁶	color	seed size ⁷	seed fate ⁸	import in diet ⁹
		MF	CCF							
FABACEAE										
<i>Dialium lopesense</i>	MC	2.8	1.6		PI		BROWN			
<i>Parkia bicolor</i>	UC	0.2	0.8	1.0	PI	VL	PURPLE	M	1	2
<i>P. filicoidea</i>	UC	0.2	*	1.0	PI	VL	GREEN	M	1	2
HUMIRIACEAE										
<i>Sacoglottis gabonensis</i>	UC	0.4		2.0	DR	L	GREEN	L	4	3
IRVINGIACEAE										
<i>Irvingia gabonensis</i>	MC	2.2	2.4	1.5	DR	L	GREEN	VL	4/1	1
<i>I. grandifolia</i>	UC	0.6	0.4	1.5	DR	L	GREEN	VL	4/1	4
<i>Klainedoxa gabonensis</i>	UC	5.8	0.8	1.5	DR	L	GREEN	VL	4/1	2
<i>K. trillesii</i>		1.6	1.2		DR					
LAMIACEAE										
<i>Vitex doniana</i>	LC	*		0.5?	DR	M	BLACK	M	1	5
LECYTHIDACEAE										
<i>Scytopetalum</i> sp. LJTW 0017	LC	1.2	2.4	0.4	DR	M	PURPLE	M	1	3
MALVACEAE										
<i>Cola lizae</i>	MC	74.6		0.7	CA	L	RED	L	1	1
<i>Duboscia macrocarpa</i>	MC	0.4	1.2		DR	L	BROWN	S	1	5
MORACEAE										
<i>Ficus bubu</i>	EP				SY		GREEN			
<i>F. mucuso</i>	MC			0.6	SY	M	GREEN	S	1	5
<i>F. recurvata</i>	EP	*			SY	M	GREEN	S	1	5
<i>F. thonningii</i>	EP				SY	S	GREEN	S	1	5
MYRTACEAE										
<i>Psidium guineensis</i>	SH				BE	M	YELLOW	S	1	1
OLACACEAE										
<i>Heisteria parvifolia</i>	MC	1.2	2.4	0.5	DR	M	WHITE	M	1	2

Appendix B (continued).

Species ¹	life-form ²	Density ³		max dbh ⁴	fruit type ⁵	fruit size ⁶	color	seed size ⁷	seed fate ⁸	import in diet ⁹
		MF	CCF							
PHYLLANTHACEAE										
<i>Antidesma vogelianum</i>	SH	*	0.4		DR	S	PURPLE	S	1	2
<i>Uapaca guineensis</i>	MC	0.2		1.2	DR	M	GREEN	M	2	1
<i>Uapaca</i> spp.										
RUBIACEAE										
<i>Nauclea didderrichi</i>	UC	0.2	6.0	1.5	SY	L	BROWN	S	1	2
<i>N. vanderghuchtii</i>	MC	0.6	*	0.8	SY	L	GREEN	S	1	3
<i>Porterandia cladantha</i>	MC	1.2	*	0.4	BE?	M	ORANGE	S	1	2
<i>Psychotria peduncularis</i>	SH				BE	S	BLUE	S	1	3
<i>P. vogeliana</i>	LC				BE	S	WHITE	S	1	2
SAPINDACEAE										
<i>Ganophyllum giganteum</i>	UC	0.8		1.0	DR	M	YW-OR			
<i>Lecaniodiscus cupanoides</i>	MC	1.0		0.6	CA	M	BROWN	M	1	1
SAPOTACEAE										
<i>Baillonella toxisperma</i>	UC	*	0.4	3.0	BE	L	GREEN	VL		
<i>Gambeya africana</i>	MC	*	0.4	0.8	BE	L	YW-OR	L	1	1
<i>G. subnuda</i>	MC	*	0.4	0.5	BE	L	YW-GR			
<i>Pachystella brevipes</i>	UC	*	*		BE	M	YELLOW			
URTICACEAE										
<i>Myrianthus arboreus</i>	LC	*		1.0	SY	VL	YELLOW	M	1	4
VITACEAE										
<i>Cissus dinklagei</i>	L	*	*		DR	M	ORANGE	M	1	2
<i>C. leonardi</i>	L				BE	M	YELLOW			

Notes:

¹ Nomenclature follows the Tropicos® botanical electronic database, Tropicos.org. Missouri Botanical Garden. 16 Oct 2011
<http://www.tropicos.org>, and The Angiosperm Phylogeny Group (2003).

- ² UC = upper canopy species (adult heights >30m), MC = mid-canopy species (adult heights 15-30m), LC = lower canopy species (adult height 7-15m), SH = shrub (adult height <7m), CS = climbing shrub, L = liana, and EP = epiphytic species.
- ³ units on densities are stems · ha⁻¹ (≥ 10 cm dbh); MF = Marantaceae forest, and CCF = closed canopy forest; * is present but not recorded; data are from Williamson (1988), White (1992), and Tutin et al. (1994a).
- ⁴ Max dbh in meters. Diameter of bole 1.3 m above ground.
- ⁵ Fruit types follow Gautier-Hion et al. (1985), CA = capsule (dry dehiscent fruit consisting of more than one carpel, follicle is one carpel), BE = berry (or berry-like, apocarpic by definition, coming from one pistil, many seeded, ie. tomato), APO (coming from one pistil/carpel; ex. the mericarpous fruits of Annonaceae); DR = drupe, PI = pod (husk) indehiscent, and SY = all syncarpic forms (multi carpellate origin and aggregates). I and D = indehiscent and dehiscent respectively.
- ⁶ Fruit size classes are measured by largest diameter of whole fruit: S = small, <0.5 cm; M = medium, 0.5-3 cm; L = large, 3-10 cm; VL = very large, >10 cm.
- ⁷ Seed size classes are measured by largest diameter of whole seed: S = small, <0.5 cm; M = medium, 0.5-1.5 cm; L = large, 1.5-4 cm; VL = very large, >4 cm.
- ⁸ Fate of seeds: (following Tutin et al., 1991a)
- 1: passed intact in feces
 - 2: majority of seeds passed intact, minority destroyed by chewing
 - 3: all seeds destroyed in feeding
 - 4: seeds not swallowed
- ⁹ Importance in diet: (following Tutin et al., 1991a)
- 1: eaten whenever available
 - 2: frequency / quantity of consumption less than would be expected from availability
 - 3: uncommon species, thus availability always limited
 - 4: consumed infrequently and / or in small amounts
 - 5: large differences in patterns of consumption