DUNG BEETLES (COLEOPTERA: SCARABAEIDAE), MONKEYS, AND CONSERVATION IN AMAZONIA

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Abstract

Dung beetles are important in several ecological processes, including nutrient recycling, soil aeration, the transport of other organisms, and the burial of vertebrate dispersed and defecated seeds. Dung beetle species vary widely in their abilities as seed dispersers. The biomass of beetle species that bury no seeds, bury small seeds only, or bury small and large seeds, is significantly different among sites along the Amazon River. The abundance of monkeys that act as high quality seed dispersers also varies at different sites. Implications of these differences in seed dispersal dynamics are discussed. Recent clearing and disturbance of primary forest is having an effect on the populations of primary and secondary seed dispersers, and suggestions for conservation of these critical faunas are presented.

Key Words: dung beetles, Scarabaeidae, monkeys, primates, seed dispersal, Amazon, Brazil

Resumo

Os coleópteros coprófagos são importantes em vários processos ecológicos, incluindo reciclagem de nutrientes, aeração do solo, transporte de outros organismos e enterramento de sementes dispersadas e defecadas por vertebrados. As espécias de besouros coprófagos variam imensamente quanto a sua habilidade em dispersar sementes. A biomassa das espécies de besouros que não enterram sementes, a biomassa daqueles que enterram somente sementes pequenas, e a biomassa daqueles que enterram tanto sementes grandes como pequenas é significativamente diferente entre varios locais ao longo do Rio Amazonas. A abundância de primatas que agem como bons dispersores de sementes também varia grandemente entre diferentes locais. As implicações dessas difereças na dinâmica de dispersãa de sementes são discutidas neste trabalho. As recentes derrubadas de ávores e as perturbações de dispersores primário e secundário, e sugestões para a conservação da fauna são apresentadas.

Dung beetles, an omnipresent component of tropical biotas, perform important ecosystem functions. Several characteristics make this group of beetles ecologically significant (Hanski & Cambefort 1991; Halffter & Matthews 1966). They are particularly vulnerable to deforestation and other changes in habitat and fauna, and this sensitivity makes them useful as indicators of ecosystem health (Halffter et al. 1992; Klein 1989). As they are primarily associated with mammals, they are also indicators of mammalian abundance and possibly diversity. Nevertheless, dung beetles' functions in ecological systems go far beyond the status of an indicator. They contribute services including, recycling of nutrients, aerating the soil, serving as transport for predatory mites, and

burying of seeds in dung (Hanski & Cambefort 1991; Halffter & Matthews 1966; Estrada et al. 1991). Because of these roles, the decline in dung beetle abundance and diversity may have cascading effects on the environment. In this paper, I discuss the results of some of my studies of deforestation, rainforest disturbance, and dung beetle abundance and diversity. I also present my research on the seed burying characteristics of different species of dung beetles, and how these differences may effect seed dispersal in tropical rainforests. Finally, I will discuss rainforest survival associated with seed dispersal and some suggestions for accelerating recovery from disturbed habitat.

Dung beetles are generally grouped into dwellers, which live and nest within a dung pat, burrowers, and rollers (Hanski & Cambefort 1991; Halffter & Edmonds 1982; Halffter & Matthews 1966). Dung beetles of the burrower guild dig nests under dung pats, and those of the roller guild roll the dung away from the site of deposition to be buried later. Members of both of these guilds pack these nests with dung, usually formed into balls, and lay eggs in the balls. The larvae develop and pupate within the brood balls, and emerge as adults (Halffter & Edmonds 1982; Halffter & Matthews 1966). Additionally, most species of rollers and burrowers also make feeding balls that are buried, may be abandoned uneaten, or if eaten, contaminants (from the beetles point of view), such as seeds, are often moved underground (Vulinec, 1999). These behaviors hasten the decomposition of waste, aid in nutrient recycling, and contribute to aeration of the soil (Halffter & Matthews 1966). They also reduce pests in dung, such as dung breeding flies (Bornemissza 1970; Fincher 1981).

Additionally, dung beetles have an important role in seed dispersal. Seeds swallowed by frugivorous mammals are often defecated intact and viable (Garber 1986; de Figueiredo 1993). Nevertheless, as much as 90% of seeds defecated onto the surface of the soil may be destroyed by rodents or other seed predators unless buried; this burial is accomplished almost entirely by dung beetles (Estrada & Coates-Estrada 1991).

However, dung beetles are especially susceptible to ecosystem change (Morón 1987; Klein 1989; Halffter et al. 1992; Estrada et al. 1998). Disturbance of tropical rainforest may affect dung beetles directly by altering temperature, humidity, or soil characteristics, or indirectly by reduction in mammal faunas. Disturbance may have a number of different outcomes. Intensive land use in tropical areas, such as bulldozing, may result in degradation that will never be reversed (Buschbacher et al. 1992). On the other hand, less disturbed areas may have the potential to reforest. This rebound may be very important in developing management practices for revolving agriculture in tropical forests (Fearnside 1993). Studies done in Brazil and Costa Rica suggest that the most important factor in reforesting land is getting the seeds to the sites (Young et al. 1987; Pannell 1989; Nepstead et al. 1991; Holl 1999). Primary seed dispersers such as birds, bats, and monkeys are instrumental in this process (Chapman & Chapman 1995. As rodent density can be very high in secondary growth (Chapman & Chapman 1999), secondary dispersal and burial by dung beetles may also be an essential element in reforestation. Habitat characteristics that encourage use by these dispersers will improve an area's chance of regenerating natural rainforest.

To determine the effect of land disturbance on populations of dung beetles in rainforests, I investigated beetle abundance and diversity in three habitats at three sites in the states of Rondônia, Amazonas, and Pará, Brazil; more specifically, I censused beetle populations at the three sites, and in three habitats, primary terra firma forest, secondary growth, and clear-cuts. I also examined the most common beetles in these habitats for seed burial capabilities. I asked: What beetles are best at seed burial? Are there limits to the type of seeds that are buried by different species of beetles? What communities of beetles occur at each site? Are there differences in the communities of monkeys? What are the implications of community differences for forest regeneration? Finally, what effect will development of the Brazilian rainforest have on seed dispersal dynamics?

Sites

I examined dung beetle and monkey communities in three widely separated sites on tributaries of the Amazon River in Brazil. The land near Caucalandia in the state of Rondônia, Brazil, is mostly cattle ranches, secondary growth, and some patches of primary rainforest. Mean annual rainfall is 2300 mm, and mean annual temperature is 27°C (Landowner, pers. comm.). The state of Rondonia was undeveloped until the late 1960s, when the government brought in people from the overcrowded cities in the northeast (Page 1995). This area currently has one of the highest rates of deforestation in the world. With clearing, erosion has increased, and soil quality has decreased; laterization of the soil is common. By 1991, over 37,000 km^2 were cleared, more than 16% of the total state; a good quarter of the state is probably cleared by now (Stone et al. 1991).

My research site here was a small section, 250 ha of primary forest, bordered by overgrown banana and cacau plantations, and some areas of capoiera, natural regrowth. Hunting is discouraged on the private land; however, poachers were encountered in the primary forest area. Even so, peccaries, agoutis, jaguarundi, deer, and sloths, were often seen. Additionally, monkeys were easily observed. The work at this site was done between October 1996 and March 1997.

The city of Manaus is located in the state of Amazonas at the confluence of the Rio Negro and Rio Solimões (Amazon). Rainfall in the area averages 2200 mm per year, and average temperature is 27°C (Salati 1985). The biological station Reserva Adolfo Ducke (10,000 ha) is 25 km northeast of the city, and is surrounded by land that is rapidly being developed. Poaching is common, and most of the large mammals have been extirpated. Agoutis, which are seed predators, and coati were common, but no tapir or peccaries have been seen for possibly more than 15 years. Monkeys are the most common large mammal, but are also hunted regularly within the reserve by people in the surrounding communities. As these communities often have a higher standard of living than many parts of the Amazon, this hunting pressure is particularly unfortunate. Two dead howlers that had been shot and escaped to die later were found during my time at this site. I worked at Reserva Ducke between November 1997 and December 1998.

In Caxiuanã, Pará, is a recently created biological station (established 1990), the Ferreira Penna Scientific Research Station. It is located off the Rio Pará at the southwest side of the Ilha do Marajó. This station includes 33,000 ha, 80% of which is terra firma forest, and 20% is blackwater floodplain forest (Lisboa 1997). Annual rainfall is around 3000 mm (Lisboa 1997), however, October is the driest month, the month of my collection, and the year of my work, 1998, El Niño increased dryness and fire potential all over the Amazon. Surrounding communities of the reserve are sparsely populated, and hunting pressure is low. Monkeys, especially howlers and the silvery marmosets, have been habituated to humans by previous research. The upland area at this site is surrounded by swampy seasonally flooded habitat.

Seed Burial Experiments

The number of dung beetle species was high at some sites (> 50); I tested the most common species that are large enough to bury at least 5 cc of dung. Beetles not tested in burial experiments were assigned the same categories as similar sized congeners.

To determine what proportion of seeds imbedded in dung particular species of dung beetles bury, I used natural seeds or plastic beads that were small (<5 mm) or large (>10 mm). I placed beetles in mesh-covered buckets (40 cm diameter × 36 cm depth) filled with 150 mm sandy soil, and placed 50 cc of fresh cow dung with embed-

ded seeds in the center of each bucket. Buckets were left up for 72 hrs. The number of individuals of each species varied depending on the size of the beetles, such that biomass of beetles remained approximately equal (Vulinec 1999). Sample sizes varied depending on the number of beetles captured alive.

For smaller species (e.g., *Sybalocanthon* sp.), I placed beetles in 1-liter containers with 100 mm sandy soil, and10 cc fresh cow dung containing only small seeds. After 72 hrs., I excavated the burrows, 10 mm at a time. I recorded seeds buried and depth of burial.

Surveys

Beetles

Using baited pitfall traps set along the same route as the monkey transect, I censused beetle community composition and species abundance in three habitat types at each site: primary rain forest, secondary growth (edges of primary forest, old plantations, and previously cleared areas), and clear-cuts. Beetle traps were 1-liter plastic cups buried to the rim in soil, and topped with a 3 cm aperture funnel. A 50 ml cup baited with human dung was suspended by wire above the trap (Howden & Nealis 1975; Gill 1991). The volume of dung in the traps attracted even the largest beetles (Peck & Howden 1984). I set a total of 27 traps each census, which were left up for 24 hrs, then collected. Three traps were set at 20 m intervals at 9 different trapping stations (3 sites in primary forest, 3 in secondary growth, and 3 in clear-cut). This trapping regime yielded 1242 trap-days (sensu Klein 1989) for the three locations. Each site was surveyed for nearly the same number of trap-days.

Beetle biomass was measured as dry weight; the beetles were dried at room temperature for 1 week prior to weighing. Ten individuals of selected species, those most common, were weighed on an Ohaus balance at the USDA-ARS laboratory in Gainesville, Florida to determine mean biomass. For beetle species that were not weighed, biomass was assumed to be similar to beetles of the same size. Extrapolation was necessary only with small, less common beetles.

Beetle biomass at all sites was summed over time, and the differences between primary, secondary, and clear-cut habitats were tested with a one-way ANOVA. I used Scheffés test for multiple comparisons, and Students t-test to compare primary and secondary growth at Caxiuanã (beetle biomass in the clear-cut at this site totaled only 0.006 grams, and was excluded from the analysis).

Beetles were categorized as those that buried almost no seeds, those that buried at least 20% of small seeds, and those that buried at least 20% of both large and small seeds. These groups were then compared for their proportion of total dung beetle biomass at each site using one-way ANOVA.

Monkeys

To categorize primate primary seed dispersers, I censused monkey populations at the three sites: 36 times in Rondônia and Ducke, and 27 times in Caxiuanã. Monkey transects were stratified by the proportion of secondary and primary growth at each site. Transects were walked by 2 people, and transect pace was about 1 km/hr. Monkey species and number of individuals were recorded.

I used methods described in Chapman et al. (2000) to calculate monkey density, using a 50% cut-off rule to select the sighting distance. Observer to animal distance, as opposed to perpendicular distance was used, as quantitative comparisons suggest

perpendicular distance underestimates transect width for forest primates (Chapman et al. 1988). Densities of groups were then calculated as the number of groups sighted within the truncated sighting distance divided by the area sampled, that is, the length of the transect times the truncated distance (Chapman et al. 2000). Densities were calculated for groups per square kilometer and number of individuals per square kilometer.

The proportion of monkeys that are seed predators as opposed to seed dispersers was evaluated using a Chi-square contingency table test for differences among the three sites.

<div align="center">RESULTS</div>

Seed Burial

Some beetles, for example all species of *Euysternus*, bury almost no seeds. The quality of other species as seed buriers depends on several factors, including seed burier size. Larger beetles bury more seeds than smaller beetles simply because they bury more dung. Additionally, large species are capable of burying larger seeds (Table 1). Burrower guild beetles bury small seeds fairly well, while rollers are less capable. Seeds over 10 mm are only buried by the largest burrowers (Figs. 1 and 2).

Biomass of Seed-Burying Beetles In Different Sites

Beetle biomass differed among sites (ANOVA, F = 7.58, P < 0.03); Rondônia had nearly four times higher biomass than Reserva Ducke. The mean biomass in primary forest was significantly higher than secondary forest at Rondônia and Caxiuanã, but not at Reserva Ducke (Table 2). Biomass at all sites was highly significant between both primary and secondary forest and clear-cuts (only two beetles were collected in the clear-cut at Caxiuanã).

Biomass was significantly different among the three seed burial categories at Reserva Ducke (ANOVA, F = 4.97, P < 0.02), and Rondônia (ANOVA, F = 5.79, P < 0.005), but was not significant at Caxiuanã. Biomass of small seed buriers was low at Reserva Ducke, while beetles that buried large and small seeds dominated the biomass (Fig. 3). At Caxiuana, beetles of all size categories were somewhat equal in biomass, and at Rondônia, beetles that buried large and small seeds comprised the largest amount of biomass, but other categories were also abundant.

Proportion of Seed Predating Monkeys at Each Site

Monkey densities varied significantly among the three sites (ANOVA, F = 4.5, P < 0.01). Total densities for all species at each site were 38.55 individuals per square kilometer for Caxiuanã, 8.94 for Reserva Ducke, and 28.42 for Rondônia. Differences in the proportions of seed predators versus seed dispersers in monkey abundance were significant among the sites (χ^2: Caxiuanã vs. Ducke = 44.7, p < 0.001; Caxiuanã vs. Rondônia = 10.4, P < 0.005; Ducke vs. Rondônia = 101.0, P < 0.001; Fig. 4).

<div align="center">DISCUSSION</div>

In rainforests, seedlings have a higher survival rate when not directly under the parent tree (Howe et al. 1985; DeSteven and Putz 1984; Augspurger 1983). This survival is thought to occur because the seedling escapes from predators and pathogens

TABLE 1. SOME OF THE BEETLE SPECIES TESTED FOR SEED BURIAL CATEGORY, THE ABBREVIATIONS USED IN THE FIGURES, SOME BEHAVIORAL CHARACTERISTICS, AND MEAN BIOMASS. ABB = ABBREVIATION; GMS = GRAMS.

Species	Abb.	Type of dung manipulation	Activity period	Mean biomass gms (SE)
Canthon aequinoctialis Har.	Ca	Roller	Nocturnal	0.130 (0.045)
Canthon triangularis (Drury)	Ct	Roller	Diurnal	0.038 (0.010)
Coprophanaeus lancifer (L.)	Cl	Burrower	Crepuscular	3.260 (1.021)
Dichotomius nr. *batesi*	Dbat	Burrower	Diurnal	0.073 (0.007)
Dichotomius boreus (Oliv.)	Dbor	Burrower	Nocturnal	0.452 (0.161)
Dichotomius lucasi (Har.)	Dluc	Burrower	Nocturnal	0.099 (0.020)
Dichotomius podalirius (Fels.)	Dpod	Burrower	Nocturnal	0.452 (0.161)
Eurysternus caribaeus Herbst	Ec	Neither	Nocturnal	0.102 (0.028)
Oxysternon conspicillatum (Web.)	Oc	Burrower	Diurnal	0.798 (0.244)
Phanaeus cambeforti Arnaud	Pcam	Burrower	Diurnal	0.136 (0.042)
Phanaeus chalcomelas (Perty)	Pch	Burrower	Diurnal	0.146 (0.042)
Scybalocanthon nr. *pygidialis*	Sp	Roller	Diurnal	0.027 (0.005)

of the parent (Howe & Smallwood 1982; Connell 1971; Janzen 1970), and because dispersal reduces competition for resources (Stiles 1989).

Trees have evolved strategies to disperse their offspring to other locations. Fruit and the seeds within generally travel away from their parent inside animal guts. Monkeys are considered by many authors to be high quality seed dispersers (Castro 1991; Estrada et al. 1991; Rowell & Mitchell 1991; Chapman 1989; Howe 1989; Garber 1986). However, some monkeys are better seed dispersers than others, for example, some eat leaves or nectar in addition to fruit, some travel more, some defecate seeds out singly, or may defecate them in a mass (Veracini 1996; Zhang & Wang 1995; Castro 1991; Chapman 1989; Garber 1986). Most importantly, some monkeys, primarily the sakis, are generally seed predators (Norconk 1998; Peres 1993; Van Roosemalen et al. 1988). The proportion of seed predators in monkey communities varies greatly at each locality. These findings may reflect a very different potential in different areas for forest regeneration.

Secondary seed dispersal and burial by dung beetles may also have an impact on rainforest regeneration (Feer 1999; Andresen 1998; Estrada et al. 1991). The highly significant difference between beetle biomass at Rondônia and the other two sites might have a number of causes. It could reflect the shorter history of disturbance, the abundance of mammals, climatic factors, or vicariance. Nevertheless, the overall bio-
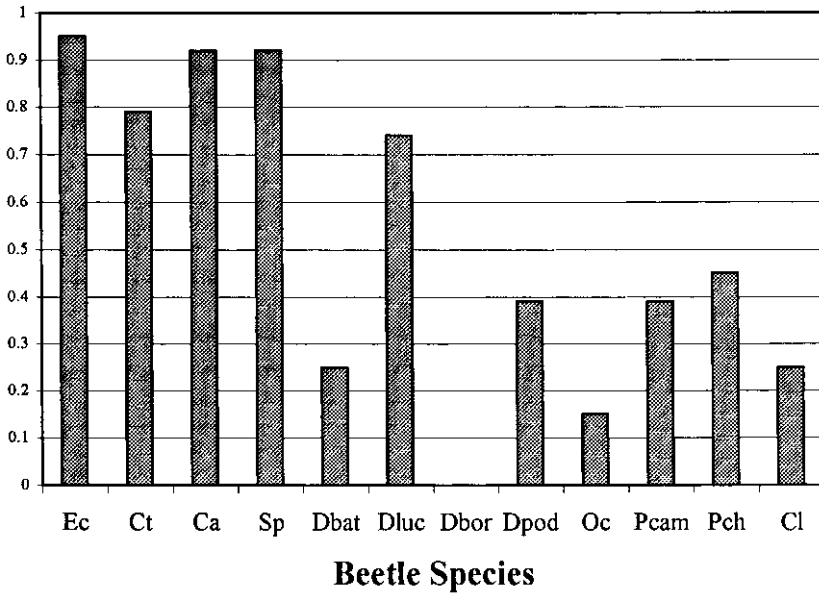
Fig. 1. The total proportion of small seeds (< 5 mm) left on the soil surface by some beetle species. See Table 1 for species abbreviations and characteristics.
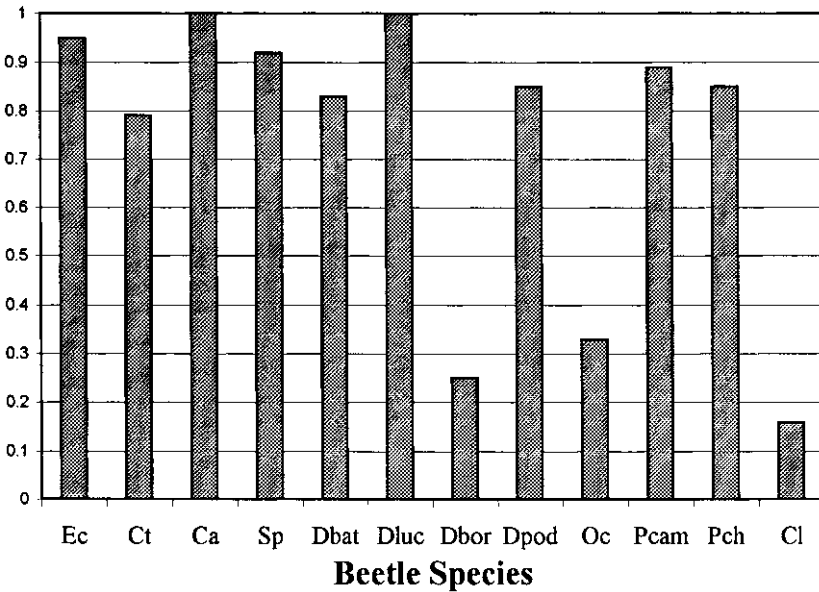

Fig. 2. The total proportion of large seeds (> 10 mm) left on the soil surface by some beetle species. See Table 1 for species abbreviations and characteristics.

TABLE 2. MEAN BEETLE BIOMASS (SE) IN EACH OF THREE HABITAT TYPES AT EACH SITE. MEANS SHARING LETTER IN EACH ROW ARE NOT SIGNIFICANTLY DIFFERENT. CAXIUANĀ (STUDENT'S T-TEST, P < 0.001), * = ONLY THREE BEETLES CAUGHT; DUCKE (SCHEFFES' MULTIPLE COMPARISONS, P ≤ 0.003) AND RONDÔNIA (SCHEFFES' MULTIPLE COMPARISONS, P ≤ 0.002).

Site	Primary forest	Secondary growth	Clear-cut
Caxiuanā	5.07 (2.65)[a]	2.49 (1.66)[b]	*
Ducke	9.85 (1.71)[a]	7.03 (1.15)[a]	0.41 (0.11)[b]
Rondônia	36.55 (4.16)[a]	19.78 (3.10)[b]	0.58 (1.10)[c]

mass of beetles and the proportion of those that bury seeds may be highly important to the local ecology. Reserva Ducke is dominated by beetles that bury both large and small seeds. The proportion of the biomass that buries only small seeds is very low. Because beetles that bury large seeds are mostly nocturnal (Vulinec 1999), the partitioning of beetle biomass may have an effect on seeds that are deposited during the day. Seeds deposited by monkeys in transit may not be buried immediately, and could be left on the ground until discovered by rodents, ants, or weevils. It would be expected that at this site, seeds may suffer higher mortality from seed predation, first by saki monkeys, and then by seed predators on the forest floor.

In regeneration of secondary growth areas, dung beetles may prove even more important than in primary forest. Primary seed dispersers, such as birds and monkeys will enter secondary growth, especially if there are trees such as bananas and *Cecropia* spp. (Holl 1999). Therefore, seeds from primary forest can get to these areas (Duncan & Chapman 1999). However, rodents are often more prevelant in secondary
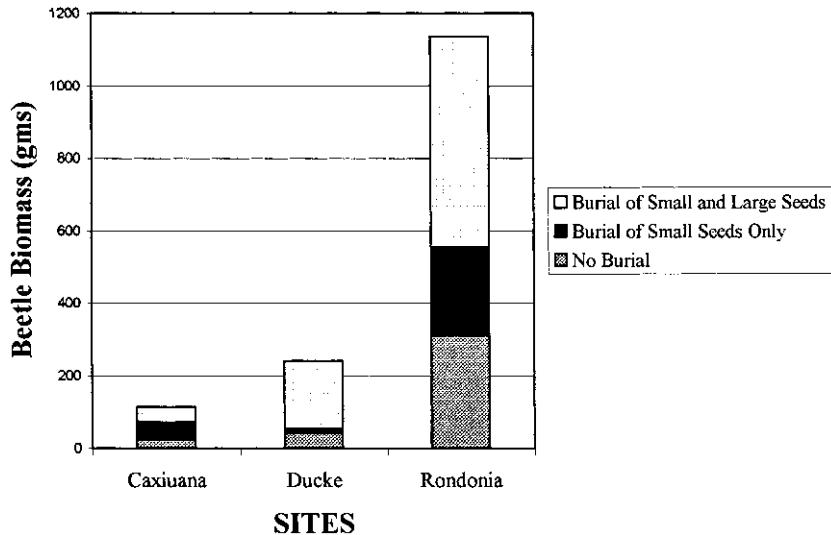

Fig. 3. Total beetle biomass at each site stratified by three categories of seed burial behavior.
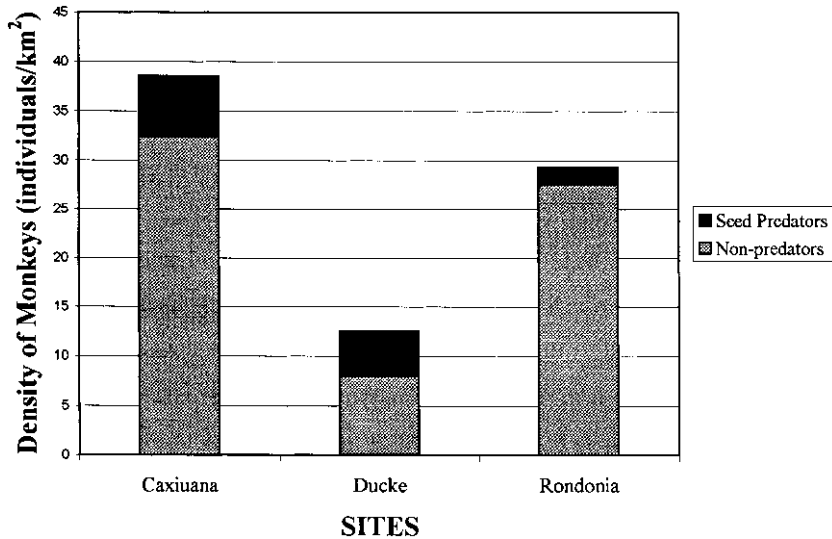
Fig. 4. Density of monkeys at each site and proportion of seed predators versus seed dispersers.

growth, so predation may also be greater (Asquith 1997). It would be advantageous to a seed to be buried quickly in these areas. Dung beetles are far more abundant in secondary growth than clear-cuts (Vulinec 1999; Estrada et al. 1998). Additionally, secondary growth has more similar microclimates and soil characteristics to primary forest than pastureland, where soil compaction and low humidity may keep many dung beetles out. Secondary growth has the potential to reforest relatively quickly given the primary and secondary dispersers that enter it. Clear-cuts have much less chance of rapid reforestation, and in some cases, no chance.

Beetles that roll dung, rather than burying it directly under the dung pat, dominate clear-cuts (Vulinec 1999; Halffter et al. 1992). Rollers, despite relocating seeds from the source, often do not bury brood balls deeply enough to protect the seeds within from rodent predation. Additionally, the generally smaller size of these beetles would make them less effective as processors of larger seeds, or a quantity of seeds. This factor suggests that savanna adapted species would probably not contribute significantly to forest regeneration in secondary growth (Vulinec 1999).

Beetles that frequent secondary forest are, like those in primary forest, more likely to be good seed "planters", due to beetle size, depth of burrowing activity, and abundance (Vulinec 1999). Nevertheless, in two of the three sites, beetle biomass was significantly greater in primary growth than secondary growth. Many beetle species are very sensitive to changes in habitat, while other species, such as *Dichotomius*, are more flexible in habitat preferences (Vulinec 1999). The factors that encourage high-quality seed buriers to enter secondary forest should be investigated. Manipulation of these factors could increase regeneration of primary forest from secondary growth areas. For example, beetles may respond to humidity when foraging or mate seeking. Planting broad leafed trees (such as *Cercropia*) in abandoned cut areas may increase ground level humidity and recruit more large dung beetles (and monkeys) from primary forest to these areas, resulting in quicker primary forest regeneration.

Amazon rainforest is disappearing at a distressing rate; in the Brazilian Amazon 2,554,000 ha of forest are cleared yearly, a number that does not include clearing due to selective logging or destruction by fires (FAO 1999). Deforestation in the Neotropics has profound effects on carbon cycling, the hydrological cycle, and soil and water quality (Salati 1985). For example, 50-75% of precipitation in the Amazon is returned to the atmosphere in the form of water vapor through evaporation of the water retained by leaves, and through transpiration of the plants (Salati 1985). Cutting the forest can radically change the water cycle.

The majority of the clear-cutting in the Amazon is for cattle ranching, and the greatest clearing is by large agribusiness corporations. According to Fearnside (1993), beef productivity on Amazon soils is low, and is unsustainable. Available phosphorous limits grass yields on oxisols and ultisols. Inedible weeds that are more adapted to the poor soils quickly invade pastureland. Massive government programs that subsidize pasture have claimed that pasture improves the soil, and is indefinitely sustainable. However, further studies have shown that maintained pasture productivity is not possible without the addition of phosphorous fertilizer. But adding fertilizer will still not solve the problem of pasture degradation. Soils become compacted through the exposure to sun and the trampling of cattle. My own measurements of soil density in forest and clear-cuts showed a 2 to 4 fold increase in relative density in clear-cuts, even without cattle (Vulinec, unpub.).

In a recent study, Holl (1999) suggests that although regeneration of forest in pastures is limited by colonization, establishment, growth, and survival, the major limiting factor in seedling establishment is lack of seed availability. She suggests pasture restoration to forest by planting native tree seedlings to increase canopy architecture, installing bird perching structures, and planting rapidly growing shrubs that quickly produce fruit and attract seed dispersers. I also suggest that there must be a nearby refuge of protected species to provide the necessary colonizers, including plants, pollinators, and dispersers, and secondary dispersers such as dung beetles.

Logging is another large-scale use of tropical forests. Currently, decisions about logging in the Amazon have no central planning or coordination. Without this planning, logging industries could easily log all of the forest in the state of Pará (Veríssimo et al. 1998). Veríssimo et al. (1998) conclude that logging could be a sustainable industry that would preserve diversity and indigenous rights and suggest several ways to do this. Logging would have to be highly monitored, however. Nepsted et al. (1998b) maintain that even selective logging diminishes forest cover, allows the drying of understory vegetation, and sets the stage for devastating fires as were seen in 1998. Even one fire in an area significantly increases the chances of future fires. The more fires in an area, the more brushy secondary growth and open canopies invite more fires in a positive feedback loop (Nepstad et al. 1998a).

Perhaps most importantly, loss of tropical rainforest leads to loss of biodiversity. There may be as many as 5-30 million species of plants and animals still undescribed, and unknown, the vast majority in tropical forests (Erwin 1982). We have yet to understand the interrelationships among the flora and fauna living in these critical areas. What we don't understand may do more than just prevent us from finding a cure for cancer. The loss of pollinators and dispersers will affect uncounted species of plants, many of potential economic and ecological importance. My research shows how even seemingly insignificant organisms may have important roles in ecosystem function. If dung beetles were gone, the buildup of feces, the increase in dung breeding pathogens, the loss of some soil turnover, would become rapidly apparent (Vulinec 1999; Klein 1989). Predatory mites that hitch rides on dung beetles would disappear. Potential antifungal and antibacterial chemicals may never be discovered. And very importantly, seeds deposited in dung would remain on the surface vulnerable to ro-

dents, fungi, and granivorous insects. Conversely, if vertebrate seed dispersers disappeared, the 60% of tree species, and almost 100% of understory plants that depend on vertebrate seed dispersal would also decline. Dung beetles would vanish with them.

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