EFFECTS OF SEED DISPERSER SOCIAL BEHAVIOR ON PATTERNS OF SEED MOVEMENT AND DEPOSITION

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ABSTRACT

Seed dispersal is critical to the maintenance of healthy terrestrial habitats and to the regeneration of degraded habitats. As anthropogenic deforestation, fragmentation, and defaunation continue, animal-mediated seed dispersal mutualisms are likely to be disrupted, with potentially serious consequences for forest dynamics. In this review, we examine the degree to which disperser sociality may influence seed dispersal outcomes. Available data are sparse and suggest that the relationship is complex, but some basic trends do emerge from the work to date. Degree of sociality, or group size, may increase the distance seeds are dispersed but also can lead to increased clumped distributions. Territoriality and the resulting defense of resources are likely to reduce the scale of dispersal and lead to clumped seed distributions. Nesting and mating behaviors such as male display are also likely to lead to more clumped distributions. Clumped deposition can have either positive or negative impacts on seed fate, depending on microsite quality, which can vary greatly. In all cases, however, there are exceptions and caveats and the one clear finding from this review is that more work is needed on this subject. We suggest that comparative studies which assess seed dispersal services offered by closely related, syntopic species that vary in key behavioral parameters will be most enlightening. We also highlight the recent use of molecular markers as a particularly effective tool to infer the dispersal services of given species, and to assess the consequences for genetic structure of the plants they disperse.

Keywords: Seed dispersal, frugivorous birds, social behavior, mating system, territoriality, Janzen-Connell effects.

RESUMO

EFEITOS DO COMPORTAMENTO SOCIAL DE AGENTES DISPERSORES NOS PADRÕES DE MOVIMENTO E DEPOSIÇÃO DE SEMENTES. A dispersão de sementes é crucial para a manutenção dos ecossistemas terrestres e regeneração de áreas degradadas. Com a continuidade de atividades antropogênicas que levem ao desmatamento e consequente fragmentação e defaunamento de florestas tropicais, mutualismos entre plantas e animais dispersores podem ser interrompidos, com sérias consequências para as dinâmicas florestais. Nós examinamos como o comportamento social de agentes dispersores pode influenciar padrões de dispersão de sementes. Dados disponíveis na literatura são esparsos e sugerem que esta é uma relação complexa, porém algumas tendências podem ser identificadas. Sugerimos que o grau de socialidade, ou tamanho de grupo, deve aumentar a distância de dispersão mas também a agregação espacial das sementes dispersadas. Territorialidade e defesa de recursos podem limitar a escala espacial da dispersão, e também causar agregação das sementes. Nidificação e outros comportamentos reprodutivos tais como apresentações sexuais de machos podem, igualmente, causar distribuição agregada de sementes. Essa distribuição agregada pode ter efeitos positivos ou negativos sobre a sobrevivência das sementes, dependendo da qualidade do micro-habitat onde são depositadas. Para todas as tendências apresentadas existem muitas exceções e problemas, e uma das poucas conclusões claras extraídas desta revisão é de que muito mais estudos são necessários sobre este tema. Em particular, marcadores moleculares têm sido particularmente úteis neste campo, tanto para inferir como animais dispersam sementes, como para entender as consequências genéticas para as plantas dispersadas. Sugerimos que estudos comparativos sobre os serviços de dispersão prestados por espécies proximamente relacionadas e sintópicas mas divergentes em comportamentos chave serão especialmente esclarecedores.

Palavras-Chave: dispersão de sementes, aves frugívoras, comportamento social, sistema de acasalamento, territorialidade, efeitos de Janzen-Connell.

RESUMEN

EFECTOS DEL COMPORTAMIENTO SOCIAL DE LA FAUNA DISPERSORA DE SEMILLAS SOBRE LOS PATRONES DE DEPOSICIÓN Y MOVIMIENTO DE SEMILLAS. La dispersión de semillas es un evento importante para el mantenimiento de ecosistemas terrestres saludables y para la regeneración de hábitats degradados. Debido a la continua deforestación, fragmentación y pérdida de fauna silvestre, los mutualismos entre plantas y animales dispersores pueden ser interrumpidos, lo que tendría serias consecuencias para la dinámica del bosque. En esta revisión examinamos el nivel en el que la conducta social de los dispersores puede influenciar los patrones de dispersión de semillas. La información disponible es escasa y sugiere que la relación entre estos es compleja, pero algunos patrones pueden ser identificados. El grado de "sociabilidad" o tamaño de grupo puede aumentar la distancia de dispersión de las semillas pero también la agregación espacial de las semillas dispersadas. Se espera también que la territorialidad y la defensa por los recursos reduzcan la distribución espacial de la dispersión y causen una agregación de las semillas. La anidación y otros comportamientos reproductivos como los despliegues sexuales de los machos, también pueden dar lugar a una dispersión agregada de semillas. La agregación de semillas puede tener efectos positivos o negativos en la sobrevivencia de estas dependiendo de la calidad del micro-hábitat, la cual puede variar en gran manera. No obstante, para todos los casos hay excepciones y problemas y una de las conclusiones de esta revisión es que se necesita trabajar mas sobre este tema. En especial los estudios con marcadores moleculares han sido particularmente útiles en este campo, para inferir como los animales dispersan las semillas y para entender las consecuencias genéticas para las plantas dispersadas. Sugerimos que los estudios comparativos sobre los servicios de dispersión prestados por especies relacionadas y sintópicas que varían en su comportamiento serán particularmente esclarecedores.

Palabras clave: Dispersión de semillas, aves frugívoras, comportamiento social, territorialidad, efecto Janzen-Connell.

INTRODUCTION

Seed dispersal is a fundamental ecological and genetic process that establishes the template upon which demographic and evolutionary processes act for plant populations (Nathan & Muller-Landau 2000, Levey *et al.* 2002, Wang & Smith 2002, Dennis *et al.* 2007). Seed dispersal is also critical in maintaining forest dynamics (Terborgh *et al.* 2002). In tropical forests, anthropogenic activities such as fragmentation, defaunation, and land transformation are likely to continue or increase in the coming decades (FAO 2005). Considering that as much as 85% of the tropical tree species are dispersed by vertebrates (Terborgh 1990) and that animals can be especially important for long-distance seed dispersal (Hamrick *et al.* 1993, Holbrook & Smith 2000, Clark *et al.* 2005), disruption in animal dispersal syndromes are likely to cause further perturbation (Wright 2003). To predict how anthropogenic activities will affect dispersal outcomes, we must understand the underlying mechanisms that produce the deposition patterns we observe in nature. In this review article, we explore the role of one possible mechanism – disperser social behavior – on patterns of seed movement and deposition.

A major paradigm in seed dispersal is that dispersal away from the parent plant is critical to seedling survival. This idea, commonly referred to as the Janzen-Connell Hypothesis, proposes that clumped distributions of seeds (or 'spatially contagious' seed dispersal) commonly found under parent trees reduces seed and seedling survival via increased competition and/or risk of attack by seed predators, herbivores, or pathogens (Janzen 1970, Connell 1971). Following this same assumption, dispersal away from the source trees that eventually results in highly clumped distributions of seeds in other areas, such as beneath other fruiting trees or under roosting or sleeping sites, may offer little advantage from the seed's point of view (Jordano & Godoy 2002, Schupp *et al.* 2002). On the other hand, the negative effects of clumping

may be somewhat ameliorated, e.g., by deposition in microsites favorable for seedling recruitment (i.e., directed dispersal, Wenny 2001) or by production of clumped distributions that contain a genetically diverse group of seeds (i.e., from a number of source trees, Hardesty *et al.* 2006). Thus, the outcome of seed dispersal depends on a complex set of factors including distance from the source tree, degree of clumping, and deposition microsite characteristics.

The breakdown of dispersal syndromes is expected to alter forest dynamics. Change in disperser composition or behavior can alter the distribution and density of seedling populations (Dirzo *et al.* 2007, Stoner *et al.* 2007, Wang *et al.* 2007, Terborgh *et al.* 2008), which in turn affect the probability of density or distance-dependent mortality (Janzen 1970, Connell 1971, Kwit *et al.* 2004, Jansen *et al.* 2008). They can also affect the probability that seeds will reach suitable microsites for establishment (Jordano & Godoy 2002, Schupp *et al.* 2002). These effects can spill over and affect both the demography (Loiselle & Blake 2002) and genetic structure (Hamrick *et al.* 1993, Loiselle *et al.* 1995) of plant populations. At the community-level, limitation in seed dissemination can result in reduction in plant diversity due to competitive exclusion and recruitment failure (Laurance *et al.* 2006). Moving up in scale, seed dispersal is an important mechanism for gene-flow and its disruption can affect evolutionary processes such as range expansion (Iverson *et al.* 2004), diversification (Restrepo *et al.* 2002) and adaptability in the face of environmental stressors such as climate change (Ledig *et al.* 2002, Iverson *et al.* 2004, Fischlin *et al.* 2007).

The importance of animal-mediated seed-dispersal is now widely recognized, yet the processes that lead to the distributions we observe in nature are still not well understood. We know that seed and fruit-eating vertebrates vary widely in their seed dispersal services (Dennis & Westcott 2006, Jordano *et al.* 2007), both quantitatively (e.g., in relation to the number of fruits removed) and qualitatively (e.g., in relation to how seeds are treated during ingestion and digestion, and to how they are moved around and finally deposited). Yet, we still lack a general framework for predicting how different disperser agents will contribute to seed movement and subsequent spatial and genetic patterns of seedling recruitment. This gap in our knowledge has important conservation consequences because it limits our ability to predict how anthropogenic disturbance will affect connectivity through animal-mediated seed transport to new sites (e.g., Galetti *et al.* 2006, Montoya *et al.* 2008) and the probability of genetic bottlenecks in plant populations (Aldrich & Hamrick 1998, Sezen *et al.* 2005, Hardesty *et al.* 2006, Sezen *et al.* 2007). A more nuanced understanding of the processes driving seed dispersal outcomes is needed in order to fully characterize contemporary patterns of animal-mediated seed movement and predict the consequences of future perturbations for tropical forest tree species.

This review article explores how linkages among the sociality of dispersal agents, foraging behavior, and effective seed movement may affect outcomes of animal-mediated seed dispersal we observe in nature. After a brief overview of methodological approaches that have been employed to study this question, we review what is currently known about how disperser sociality affects seed movement. We focus primarily, but not completely, on examples of tropical birds. We conclude by briefly discussing advances in the field provided by the use of molecular markers and by pointing out key directions for future studies. Although some basic patterns are emerging, we conclude that additional studies are needed for a better understanding of the relationships between disperser sociality and seed movement, and that this represents a promising line of research in behavioral ecology.

METHODOLOGICAL APPROACHES

The study of seed dispersal presents many challenges (e.g., Wang & Smith 2002), but the combination of traditional methods with more recent techniques is introducing exciting new possibilities to the field. Traditionally, studies on seed dispersal have relied upon field observations of disperser behavior or patterns of seed rain or seedling recruitment. These include making direct observations at fruiting trees (Howe *et al.* 1985, Wheelwright 1991); tracking the movement of dispersed seeds in the field (Wenny & Levey 1998, Levey & Sargent 2000); quantifying the distribution and germination success of dispersed seeds in the field (Russo & Augspurger 2004); and synthesizing information on disperser movement patterns with seed retention time to estimate seed

dispersal distributions (Murray 1988, Holbrook & Smith 2000, Westcott & Graham 2000). Estimation of seed dispersal distributions can provide important information unlikely to be yielded by empirical measurement alone, in particular the capture of long-distance dispersal events which are rare but may be disproportionately important for plant fitness (Nathan & Mueller-Landau 2000). More recently, seed dispersal research has made major strides with the use of genetic markers. Although a more detailed synopsis is beyond the scope of this review, we note that molecular analyses not only allow us to track seed movement, but also to demonstrate the genetic consequences of such movements (Godoy & Jordano 2001, Sork & Smouse 2006).

None of these approaches in isolation provides complete information on the process of seed dispersal but their combination has proven to be powerful (Wang & Smith 2002). Recently, these approaches have yielded valuable information about the role of vertebrates in seed movement (Murray 1988, Wenny & Levey 1998, Holbrook & Smith 2000, Westcott & Graham 2000, Westcott *et al.* 2005, Jordano *et al.* 2007). Below, we review this body of work to address the specific question of how the social behavior of dispersers may affect seed dispersal outcomes.

HOW DOES DISPERSER SOCIALITY AFFECT SEED DISPERSAL?

The quality of animal-mediated dispersal varies widely, and is directly related to spatial and temporal patterns of disperser movement (Murray 1988, Westcott *et al.* 2005, Jordano *et al.* 2007). Disperser movement patterns effectively determine the spatial distribution of dispersed seeds, including probability of deposition into microsites that may be particularly advantageous or disadvantageous for germination or recruitment, and aggregation patterns (clustered vs. scattered) of deposited seeds. Clustering of non-dispersed seeds falling directly underneath the parent tree is ubiquitous in nature, but animal-mediated seed deposition is also often clumped, occurring both underneath and away from fruiting trees (Jordano & Godoy 2002). The degree to which seeds are dispersed in a clumped, or "spatially contagious", manner is of interest because clustering can reduce survival of seeds and seedlings due to density-dependent effects (Janzen 1979, Connell 1971, Jansen *et al.* 2008). In addition, spatially contagious seed dispersal can result in few sites receiving many seeds and most sites receiving few to none, a pattern that can have demographic consequences for plant populations due to the limited dissemination of propagules (Jordano & Godoy 2002, Schupp *et al*. 2002).

Because animal social behavior plays a large role in determining movement patterns, it is logical to expect that it would therefore also play an important role in determining dispersal outcomes. Yet surprisingly little formal attention has been paid to this relationship. Schupp *et al.* (2002) provide a partial list of processes which can lead to clumped distributions of seeds by animal dispersal agents, several of which are related to social behavior. For example, these authors point out that the use of foraging or sleeping roosts, latrines, display sites, and visiting other fruiting trees should lead to clumped distributions of seeds. Similarly, Dennis & Westcott (2006) propose a classification of vertebrate seed dispersers according to their functional similarity that identifies several social traits as important variables influencing the performance of the dispersers, such as group size and home range size. Here, we expand upon these relationships between disperser sociality and seed deposition patterns by explicitly considering the importance of animal social behavior per se. We focus on three related aspects of disperser social behavior: social organization, territoriality, and mating system. These three components are often confounded in the life history spectrum of organisms, but we focus on the potential effects of each one for the performance of animals as seed dispersers, particularly for the distances seeds may be moved from the source tree and the resulting spatial distribution of the seeds. This review is therefore not intended to be exhaustive, but rather illustrates key patterns between sociality and dispersal outcomes.

SOCIAL ORGANIZATION AND GROUP SIZE

Social organization of seed dispersal agents ranges from species in which individuals are largely solitary (e.g., females of many lek-breeding birds) to species in which individuals forage in flocks of dozens (e.g., many social mammals) or even hundreds of individuals (e.g., socially gregarious

bats and birds). This variation in group size is likely to influence dispersal outcomes in a variety of ways. Below, we review studies that are relevant to two working hypotheses: (1) that dispersal distance will increase as a function of group size; and (2) that degree of clumping will also increase as a function of group size.

The relative costs and benefits of group foraging, and thus the relationship between group size and foraging performance, involve trade-offs that are likely to have important consequences for seed dispersal. On the one hand, group foraging may increase mean food intake rates of individuals via a reduction in the time spent watching for predators and/or an increase in resource detectability (Beauchamp 1998). On the other hand, competition is stronger in large groups, since food needs to be shared among more individuals and/or due to increased aggression and foraging interference (Ranta *et al.* 1993, Beauchamp 1998, McConkey & Drake 2006). Therefore, all other things being equal, we might expect that larger groups may require more food sources, yielding larger home ranges and longer foraging trips (e.g., Sherman & Eason 1998).

For example, animals living in large groups may deplete available fruit on individual trees more quickly and therefore need to visit more trees in a larger area to satiate all members of the group. This relationship was experimentally demonstrated by Avgar *et al.* (2008) in two species of ants that serve as seed predators rather than seed dispersers. *Messor arenarius*, which forages solitarily, was better at detecting new food patches and more efficient in foraging on sparse and low-density seed patches. In contrast, *Messor ebeninus*, which forages in large groups, was slower in finding new seed patches but faster in depleting them after detection. Seed predators can also serve as important secondary dispersal agents for seeds (Vander Wall *et al.* 2005) and these two ant species produced different post-dispersal seed shadows, suggesting a direct link between the sociality of these seed-foragers and plant demography. A further example of this relationship comes from a field study in the Ecuadorian Amazon in which home range size and distances traveled by araçari birds (*Pteroglossus pluricinctus*), which are cooperative breeders and forage in groups, were twice as large as those of toucans (*Ramphastos* spp.), which are 2-3 times heavier than araçaris but forage solitarily or in pairs (Holbrook 2006).

Group foraging can also increase seed dispersal distances by mechanisms other than food depletion. For example, dispersal distances can be increased due to foraging interference among group members, as demonstrated for flying foxes (*Pteropus tonganus*, McConkey & Drake 2006). These mammals, which are key dispersers of large seeds on tropical Pacific islands, cease to function as effective seed dispersers at low population densities because aggressive interactions are more frequent in high-density groups and force foraging individuals away from the fruiting tree. At lower densities, individuals spend more time on fruiting trees, depositing a large proportion of the seeds underneath them. Alternatively, as discussed in the following section, larger group sizes may allow animals to defend fruiting trees as resources, potentially reducing the quality of dispersal.

At a finer scale, however, group foraging may increase clumping of seeds because individuals will tend to disperse seeds together in time and space. For example, socially gregarious frugivores like bats and primates often produce clumped distributions of dispersed seeds beneath roosting, resting, latrine, or foraging areas (Schupp *et al.* 2002, Fragoso *et al.* 2003, Chapman & Russo 2006, Russo *et al.* 2006). In this case, the larger the group becomes, the more clumping of seeds can be expected as a result of the overlapping in seed shadows produced by individual group members. Of course, the degree to which these deposition sites are traditional or vary over time will play an important role in determining the magnitude of this effect for forest dynamics in the long run. In contrast, species in which individuals live in smaller groups, pairs, or are solitary might be expected to produce less clumped distributions of seeds simply because there are fewer individuals depositing seeds at the same place. All else being equal, we could thus expect that the spatial distribution of seeds may be more heterogeneous and aggregated for social than for solitary species.

More empirical studies are needed that focus on the relationship between group size and spatial distribution of seeds dispersed by frugivores before any firm conclusions can be reached about these questions. Available results are consistent with the idea that group size may lead to longer dispersal distances and to more clumping, but a broader range of studies are needed, particularly in a comparative framework

using closely related species. Another important area of inquiry concerns the relative importance of these two putative effects of group size (i.e., dispersal distances vs. degree of aggregation in seed deposition), and in particular whether the increased genetic structure that presumably arises from local clumping is balanced or overridden by movement of seeds across the home range of the foraging group.

TERRITORIALITY AND RESOURCE DEFENSE

Territoriality and/or resource defense is likely to be important for seed dispersal because they constrain the space used by an individual and may limit the number of potential dispersal agents visiting a given source tree. In this review, we follow Wilson (1975) in adopting a broad definition of territory as "an area occupied more or less exclusively by an animal or group of animals by means of repulsion through overt defense or advertisement", encompassing a broad range of territory types, from those with sharp limits maintained by aggression against conspecifics to home ranges that overlap extensively but that are defended to some extent against conspecifics, especially within core areas (Adams 2001). Territoriality may influence the shape and distribution of the seed dispersal shadow by affecting (1) the number of fruiting plants (i.e., seed sources) visited by an individual; (2) the proportion of fruits removed; (3) the time spent per tree; (4) the number of other potential dispersal agents that visit the tree; and (5) the spatial extent of dispersal and degree of clumping in seed deposition patterns. The working hypothesis we explore below is that degree of territoriality, and especially resource defense, will limit the quality of seed dispersal offered by a given dispersal agent.

From the plant perspective, territorial species may be more reliable visitors to fruiting trees within their home range than wide-ranging species (Sun *et al.* 1997). We might therefore expect species that maintain a relatively small, traditional home range to visit fewer plants but remove a higher proportion of fruit per plant within their territory relative to nomadic or wide-ranging species. These high removal rates may increase the proportion of seeds dispersed away from the tree, but the reverse could be true when territoriality grades into resource defense. If species are able to monopolize a single fruiting tree, the time they spend in the tree is likely to increase and thus the proportion of seeds that are actually carried away from the tree may drop, leading to a high number of seeds that are deposited directly beneath the adult tree despite being consumed.

If territories are largely non-overlapping or if individuals are successful in defending territories or fruiting resources against conspecifics, then the quality of seed dispersal services may be reduced. One of the most compelling examples of this matter comes from a recent study using molecular markers to establish the source of acorns cashed into granaries by the acorn woodpecker (*Melanerpes formicivorous*) (Grivet *et al.* 2005). The social organization of these birds allows them to defend a small number of oak trees that produce huge numbers of acorns during masting years. A small number of these trees is sufficient to maintain a group, and for this reason a typical granary contains seeds from an average of only two source trees. This surprisingly restricted seed dispersal pattern, especially given the fact that acorn woodpeckers can fly more than 10 km in a single day (Koenig *et al.* 1996), in addition to the little overlap among woodpecker group territories, is likely to lead to strong genetic structuring among granaries (Grivet *et al.* 2005).

As seen in the previous example, degree of clumping during seed dispersal is also likely to be affected by territoriality. Within a given territory, constraints in movement do not necessarily need to lead to clumping of seeds if animals use territories in a more or less regular fashion. It is more likely, however, that movement patterns vary both in time and space, and as some areas within the territory are used more often than others, seed deposition is also expected to be spatially heterogeneous (e.g., Westcott *et al.* 2005). Female ochre-bellied flycatchers (*Mionectes oleagineous*), for example, tend to use regular pathways to move between areas within their home ranges (Westcott 1997, Westcott & Graham 2000). Completely homogeneous deposition of seeds within a territory is biologically unlikely in any species, and the degree of aggregation in the seed shadow should be influenced by the spatial distribution of food resources and the patterns of spatial use intrinsic to each species.

It is important to note that degree of territoriality

and resource defense rely in large part on the underlying distribution of resources (e.g., Emlen & Oring 1977). Fruit is a highly patchy resource, in both time and space, and fluctuations in fruit availability can therefore affect patterns of territoriality and ranging behavior. Some species of hornbills and monkeys, for example, can exhibit facultative territoriality, in which individuals live as resident, territorial pairs when fruit is abundant and can be defended within territories, but travel larger distances and join wide-ranging foraging flocks in times or areas characterized by fruit scarcity (Anggraini *et al.* 2000). Temporal variation in food availability may also lead frugivorous birds to undergo seasonal movements in order to track fruiting resources (Loiselle & Blake 1991, Whitney & Smith 1998) or to engage in movement between fruiting patches, which has been suggested as a key mechanism for habitat connectivity and forest regeneration (Wunderle 1997, Levey *et al.* 2005).

Mixed foraging flocks are a common fixture of rain forests that provide interesting contrasts to territoriality. Flocks formed by several frugivorous species move through relatively large areas consuming and dispersing seeds. Many primarily territorial species join mixed-species flocks as they move through their territory, but tend not to cross the territory's boundaries (e.g., Valburg 1992), while other species move more freely while in the flock. Foraging flocks are thus likely to increase the spatial scale of seed dispersal and reduce clumping because birds are moving larger distances and also because flocks can overcome efforts at resource defense by a resident individual or pair.

In sum, both territoriality and degree of resource defense are shaped by the underlying distribution of resources and, to a lesser degree, by group size. Territoriality, especially when it is associated with competitive exclusion and monopolization of resources, is likely to reduce the effectiveness of seed dispersal. Temporally or spatially patchy distributions of fruit resources may increase the cost to benefit ratio of territoriality or resource defense and may cause dispersers to travel larger distances, thereby yielding larger dispersal distances and less clumped distributions. More extensive seed movement might also be expected in times of food scarcity in comparison to times of fruit abundance for the same reasons.

MATING SYSTEM AND BREEDING

The distribution of resources critical to reproduction – such as food – may influence a species' mating system, and vice-versa. For example, aggregated resources that can be monopolized by a single male should increase the environmental potential for polygyny, while more dispersed resources should promote monogamy (Emlen & Oring 1977). On the other hand, the mating system of a species may also have an effect on the spatial distribution of food resources used by that species. For example, breeding activities such as nesting and display behavior are likely to affect seed dispersal services, to the extent that they affect patterns of movement and space use by both males and females. In this review, we focus on this second idea, i.e., how mating system and breeding behavior may affect seed dispersal outcomes.

Nesting is likely to lead to clumped distributions of seeds near or beneath nest sites, and this effect is likely magnified when there is bi-parental care or cooperative care. Hornbills have very large home ranges during the non-breeding season, but during nesting females and chicks are concealed inside their tree cavity nests and are fed by the male (Whitney *et al.* 1998). Large amounts of seeds accumulate and germinate underneath the nest as a result of fruit dropping during delivery and seed passage by the male and by the nest occupants. As such, hornbills are scatter-dispersers during the non-breeding season but are likely to be clumped-dispersers during the breeding season (Holbrook & Smith 2000). This same pattern seems likely to apply to most frugivorous birds.

Nest site location can also have critical importance for seed fate. On one end of the spectrum, oilbirds (*Steatornis caripensis*) nest inside caves, where a large number of palm seeds are deposited, only to die in the absence of light (pers. obs.). Female green manakins (*Chloropipo holochlora*), on the other hand, nest along creeks and rivers (P. Mena & J. Karubian, unpublished data), which could potentially lead to long distance dispersal of seeds as they are swept downstream by the current. Nest height and architecture may also have important consequences for degree of clumping and, in the case of cavity nesters, whether the seeds make it to the ground at all.

Male display behavior may also be important if males display in traditional sites because this will lead

to clumped distributions of seeds (Schupp *et al.* 2002). A classic example is the display behavior of the bellbird (*Procnias tricarunculata*). Males of this cotinga prefer to sing from snags in forest gaps, a display behavior that leads to directed dispersal of seeds into forest gaps (Wenny & Levey 1998). Because gaps are favorable microhabitats for seedling recruitment in many species due to the light and space availability, this type of directed dispersal may have a significant impact on plant demography (Wenny 2001).

In many rain forest bird species, males display in leks, large aggregations sometimes numbering dozens of males. Lekking is exhibited by several well known groups of frugivorous Neotropical rain forests birds such as manakins and cotingas (Höglund & Alatalo 1995). Leks are likely to be traditional in both time and space (e.g., Durães *et al.* 2008), and because males spend most of their time during the breeding season on the lek, this mating system is likely to lead to clumped distributions of seeds. Empirical evidence suggests that lekking behavior does indeed lead to a higher density of seeds in leks relative to non-leks. Leks in French Guiana and Ecuador had a higher density of favored food plants than control areas, likely because manakins and cotingas are bringing seeds back into the leks (Théry & Larpin 1993, Ryder *et al.* 2006). There was also a higher density of seeds in the seed bank at manakin lek sites relative to control areas (Krijger *et al.* 1997). Our own work on Long-wattled Umbrellabirds (*Cephalopterus penduliger*) in Ecuador also suggests that males of this lekking cotinga bring > 50% of the seeds they ingest back into their territories on the lek, and that this behavior yields a higher density of seeds and seedlings in leks relative to control areas (Karubian *et al.*, unpublished data). The type of lek can also make a difference: species with 'exploded' or dispersed leks, in which males hold contiguous but independent territories e.g., umbrellabird cotingas and several species of manakins (Castro-Astor *et al.* 2004, 2007, Durães *et al.* 2008, Tori *et al.* 2008), should lead to less clumped seed deposition patterns than species with the 'classical' or concentrated leks found in cock-of-the-rocks (*Rupicula* spp., Théry & Larpin 1993) and some *Pipra* manakins (e.g., Prum 1994). Finally, the quality of lek areas as microsites for germination will have an important impact on seed fate. For example, while some lekking birds such as the bellbirds can direct dispersal into gaps and have a positive impact on seed germination (Wenny & Levey 1998), other species, such as some manakins, display and deposit seeds on the shady forest understory floor, where they remain dormant unless light conditions change (Krijger *et al.* 1997).

Territorial males only contribute part of the seed dispersal services given by lekking species, yet little attention has been played to seed dispersal by females in lek-breeding species. In contrast to males, females of most lek breeding species are largely solitary, have larger home ranges and visit the lek only for the purposes of reproduction (e.g., Théry 1992, Westcott & Graham 2000). Because the reproductive behavior of males and females of lek breeding species differ so strongly, these species provide a convenient system in which to examine the effects of social behavior on seed dispersal outcomes. In the long-wattled umbrellabird, this leads to females yielding much more even distributions of dispersed seeds throughout their territories. Whereas males bring most seeds to a central point (i.e. the lek), females distribute seeds more broadly with a peak of ~300 m from the territory center (Karubian *et al.*, unpublished data).

In sum, mating system may have potentially important consequences for seed movement and deposition. Both nesting and male display behaviors are likely to lead to some degree of clumping, though the quality of the microsites in which seeds are distributed may vary from advantageous to very poor. When parental care is conducted by two or more individuals, or display sites are congregated, as in lekking species, the degree of clumping is likely to be compounded by the cumulative effect of many individuals depositing seeds in the same general area.

FUTURE DIRECTIONS

There is a clear need for more studies that assess the role of sociality per se on seed dispersal outcomes. This could be most effectively carried out by comparative studies assessing seed dispersal services by closely related species which live syntopically but vary in important aspects of their sociality. As one example, on our own study site in northwestern Ecuador the long-wattled umbrellabird lives syntopically with the purple-throated fruit-crow (*Querula querula*), the most closely related species within its range. Whereas

the long-wattled umbrellabird is a lek breeder, the purple-throated fruit-crow is a cooperative breeder which maintains year-round territories. Based on the studies above, several hypotheses could be generated for how these differences in social organization might affect seed dispersal outcomes. Another potentially useful group to examine is the manakins, in which at least one species (the green manakin; J. Karubian & P. Mena, unpublished data) does not form leks whereas most other species do. Within-species comparisons are also likely to be useful in discerning the effects of disperser sociality when the sexes differ strongly in their behaviors. Lek-breeding species are a good example because males and females exhibit such distinctive behavioral repertoires. Other examples are species where females travel in groups with other females and young, while males are largely solitary (e.g., peccaries, some primates).

Another promising approach for future work on seed dispersal is the use of molecular markers, which recently have become an important tool in the study of seed dispersal. Molecular techniques rely upon the fact that in many flowering plants the seed coat, or pericarp, is a maternally inherited tissue. By using hypervariable molecular markers such as microsatellites, the genotype of the source tree can be determined for an already-dispersed seed. Assuming the genotypes of all or most adult trees in the area are known, one can therefore work backward from the dispersed seed to identify the source tree via direct parentage assignment. In the first application of this genetic innovation, Godoy & Jordano (2001) documented seed dispersal distances in the animal-dispersed *Prunus mahaleb* (Rosaceae) by assigning seed genotypes to the seed source in a study site where all adults were genotyped and mapped. Later studies of other animal-mediated systems have provided elegant models of seed dispersal curves showing a high frequency of restricted seed dispersal with occasional long-distance events (Robledo-Arnuncio & Garcia 2007, Garcia *et al.* 2007), and have also quantified the relative importance of different dispersal agents for short or long distance dispersal events (Jordano *et al.* 2007).

However, for those cases where potential seed parents for a species occur in low abundances and are spread over a very large area, or, alternatively, occur in very high densities, it may be difficult to genotype all relevant adults. Moreover, it may not always be possible to identify all potential seed sources when animal seed dispersers are hard to track or travel very long distances while foraging. Also, it is often technically difficult to obtain adequate genetic resolution of (sometimes highly) degraded seed coats that allows for precise maternal assignment. To overcome these challenges associated with the direct parentage assignment used by Godoy & Jordano (2001), Grivet *et al.* (2005) introduced an alternative approach using the maternal genotypes from seed coat tissue to study movement of valley oak acorns (*Quercus lobata*) by acorn woodpeckers. Without mapping the genotypes of all adults, this new approach instead uses the probability of maternal identity (PMI) to estimate the number of seed sources (i.e., maternal trees) contributing to a given seed pool and the degree of overlap in seed sources among seed pools. As discussed above, the authors were able to show that families of woodpeckers forage very close to their seed storage sites, and that different families visit different trees, with important consequences for genetic structure of the plants they disperse.

These molecular approaches have ushered in a new era in the study of seed dispersal in which we are able to gather previously unobtainable data on the spatial and temporal scale of seed movement, and to make inferences on the genetic consequences for the plants. Future work on the effects of disperser sociality will be able to use these tools both to better understand implications for seed movement and, importantly, to understand how this in turn may affect the local genetic structure of the plant species they disperse.

CONCLUSIONS

Seed dispersal is a key ecological process which is likely to be influenced by current and future human activities such as deforestation and hunting. To effectively conserve the process of seed dispersal in heavily impacted areas, it would be useful to be able to predict how these forces may affect dispersal syndromes. This in turn requires an understanding of the mechanisms that result in the dispersal patterns we observe in nature. In the current review, we explore the effectiveness of disperser sociality as a tool for predicting seed dispersal services provided by a given species. In particular, we assess the possible effects

of degree of sociality (or group size), territoriality or resource defense, and mating behavior on dispersal outcomes. Our review suggests that sociality may play an important role, but that the relationship is likely to be complex and is influenced by a number of factors. Currently, there is a lack of data on the subject and more studies are needed to adequately address this question. The use of molecular markers for these future studies seems to be a particularly promising approach.

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REFERENCES

ADAMS, E.S. 2001. Approaches to the study of territory size and shape. *Annual Review of Ecology and Systematics*, 32: 277-303.

ALDRICH, P.R. & HAMRICK, J.L. 1998. Reproductive dominance of pasture trees in fragmented tropical forest mosaic. *Science*, 281: 103-105.

ANGGRAINI, K.; KINNAIRD, M. & O'BRIEN, T. 2000. The effects of fruit availability and habitat disturbance on an assemblage of Sumatran hornbills. *Bird Conservation International*, 10: 189-202.

AVGAR, T.; GILADI, I. & NATHAN, R. 2008. Linking traits of foraging animals to spatial patterns of plants: social and solitary ants generate opposing patterns of surviving seeds. *Ecology Letters*, 11: 224-234.

BEAUCHAMP, G. 1998. The effect of group size on mean food intake rate in birds. *Biological Reviews*, 73: 449-472.

CASTRO-ASTOR, I.N.; ALVES, M.A.S. & CAVALCANTI, R.B. 2004. Display behavior and spatial distribution of the Red-headed Manakin in the Atlantic Forest of Brazil. *Condor*, 106: 320-335.

CASTRO-ASTOR, I.N.; ALVES, M.A.S. & CAVALCANTI, R.B. 2007. Display behavior and spatial distribution of the White-crowned manakin in the Atlantic Forest of Brazil. *Condor*, 109: 155-166.

CHAPMAN, C.A. & RUSSO, S.E. 2006. Primate seed dispersal: linking behavioral ecology with forest community structure. Pp 510-525. *In*: C.J. Campbell, A.F. Fuentes, K.C. MacKinnon, M. Panger & S. Bearder (eds.). Primates in perspective. Oxford University Press, New York, NY. 720p.

CLARK, C.J.; POULSEN, J.R.; BOLKER, B.M.; CONNOR, E.F. & PARKER, V.T. 2005. Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. *Ecology*, 86: 2684-2694.

CONNELL, J.H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pp. 298-313. *In*: P.J. den Boer & G.R Gradwell (eds.). Dynamics of populations: Proceedings of the Advanced Study Institute on Dynamics of Numbers in Populations, Oosterbeek, 1970. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands. 611p.

DENNIS, A.J. & WESTCOTT, D.A. 2006. Reducing complexity when studying seed dispersal at community scales: a functional classification of vertebrate seed dispersers in tropical forests. *Oecologia*, 149: 620-634.

DENNIS, A.J.; GREEN, R.J.; SCHUPP, E.W. & WESTCOTT, D.A. (eds.) 2007. *Seed dispersal: theory and its application in a changing world*. CABI Publishing, New York, NY. 720p.

DIRZO, R.; MENDOZA, E. & ORTIZ, P. 2007. Size-related differential seed predation in a heavily defaunated neotropical rain forest. *Biotropica*, 39: 355-362.

DURÃES, R.; LOISELLE, B.A. & BLAKE, J.G. 2008. Spatial and temporal dynamics at manakin leks: reconciling lek traditionality with male turnover. *Behavioral Ecology and Sociobiology*, 62: 1947-1957.

EMLEN, S.T., & ORING, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, 197: 215-223.

FAO. 2005. *Global Forest Resources Assessment 2005: Progress towards sustainable forest management.* FAO, Rome. 320p.

FISCHLIN, A.; Midgley, G.F.; Price, J.T.; Leemans, R.; Gopal, B.; Turley, C.; Rounsevell, M.D.A.; Dube, O.P.; Tarazona, J. & Velichko, A.A. 2007. Ecosystems, their properties, goods and services. Pp. 211-272. *In*: M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden & C.E. Hanson (eds.). Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernamental Panel on Climate Change. Cambridge University Press. Cambridge, UK. 976p.

FRAGOSO, J.M.V.; SILVIUS, K.M. & CORREA, J.A. 2003. Long-distance seed dispersal by tapirs increases seed survival and aggregates tropical trees. *Ecology*, 84: 1998-2006.

GALETTI, M.; DONATTI, C.I.; PIRES, A.S.; GUIMARÃES,

P.R. & JORDANO, P. 2006. Seed survival and dispersal of an endemic Atlantic forest palm: the combined effects of defaunation and forest fragmentation. *Botanical Journal of the Linnean Society*, 151: 141-149.

GARCIA, C.; JORDANO, P. & GODOY, J.A. 2007. Contemporary pollen and seed dispersal in a *Prunus mahaleb* population: patterns in distance and direction. *Molecular Ecology*, 16: 1947-1955.

GODOY, J.A. & JORDANO, P. 2001. Seed dispersal by animals: exact identification of source trees with endocarp DNA microsatellites. *Molecular Ecology*, 10: 2275-2283.

GRIVET, D.; SMOUSE, P.E. & SORK, V.L. 2005. A new approach to the study of seed dispersal: a novel approach to an old problem. *Molecular Ecology*, 14: 3585-3595.

HAMRICK, J.L.; MURAWSKI, D.A. & NASON, J.D. 1993. The influence of seed dispersal mechanisms on the genetic structure of tropical tree populations. *Vegetatio*, 107-108: 281-297.

HARDESTY, B.D.; HUBBELL, S.P. & BERMINGHAM, E. 2006. Genetic evidence of frequent long-distance recruitment in a vertebrate-dispersed tree. *Ecology Letters*, 9: 516-525.

HOLBROOK, K.M. 2006. *Seed dispersal limitation in a neotropical nutmeg, Virola flexuosa (Myristicaceae): an ecological and genetic approach*. PhD dissertation, University of Missouri-St. Louis, Saint Louis, MO. 173p.

HOLBROOK, K.M. & SMITH, T.B. 2000. Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest. *Oecologia*, 125: 249-257.

HÖGLUND, J. & ALATALO, R.V. 1995. Leks. Princeton University Press, Princeton, NJ. 248p.

HOWE, H.F.; SCHUPP, E.W. & WESTLEY, L.C. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology*, 66: 781-791.

IVERSON, L.R.; SCHWARTZ, M.W. & PRASAD, A.M. 2004. Potential colonization of newly available tree-species habitat under climate change: an analysis for five eastern US species. *Landscape Ecology*, 19: 787-799

JANSEN, P.A.; BONGERS, F. & VAN DER MEER, P.J. 2008. Is farther seed dispersal better? Spatial patterns of offspring mortality in three rainforest tree species with different dispersal abilities. *Ecography*, 31: 43-52.

JANZEN, D.H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist*, 104: 501-528.

JORDANO, P. & GODOY, J.A. 2002. Frugivore-generated seed shadows: a landscape view of demographic and genetic effects. Pp. 305-321. *In*: D.J. Levey, W.R. Silva & M. Galetti (eds.). Seed dispersal and frugivory: ecology, evolution and conservation. CABI Publishing, New York, NY. 536p.

JORDANO, P.; GARCÍA, C.; GODOY, J.A. & GARCÍA-CASTAÑO, J.L. 2007. Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences of the United States of America*, 104: 3278-3282.

KOENIG, W.D.; VAN VUREN, D. & HOOGE, P.N. 1996. Detectability, philopatry and the distribution of dispersal distances in vertebrates. *Trends in Ecology and Evolution*, 11: 514-517.

KRIJGER, C.L.; OPDAM, M.; THÉRY, M. & BONGERS, F. 1997. Courtship behavior of manakins and seed bank composition in a French Guianan rain forest. *Journal of Tropical Ecology*, 13: 631-636.

KWIT, C.; LEVEY, D.J. & GREENBERG, C.H. 2004. Contagious seed dispersal beneath heterospecific fruiting trees and its consequences. *Oikos*, 107: 303-308.

LAURANCE, W.F.; NASCIMENTO, H.E.M.; LAURANCE, S.G.; ANDRADE, A.; RIBEIRO, J.E.L.S.; GIRALDO, J.P.; LOVEJOY, T.E.; CONDIT, R.; CHAVE, J.; HARMS, K.E. & D'ANGELO, S. 2006. Rapid decay of tree-community composition in Amazonian forest fragments. *Proceedings of the National Academy of Sciences of the United States of America*, 103: 19010-19014.

LEDIG, F.T.; HODGSKISS, P.D. & JACOB-CERVANTES, V. 2002. Genetic diversity, mating system, and conservation of a Mexican subalpine relict, *Picea mexicana* Martinez. *Conservation Genetics*, 3: 113-122.

LEVEY, D.J., BOLKER, B.M.; TEWKSBURY, J.J.; SARGENT, S. & HADDAD, N.M. 2005. Effects of landscape corridors on seed dispersal by birds. *Science*, 309: 146-148.

LEVEY, D.J.; SILVA, W.R. & GALETTI, M. (eds.). 2002. *Seed dispersal and frugivory: ecology, evolution, and conservation*. CABI Publishing, New York, NY. 511p.

LEVEY, D.J. & SARGENT, S. 2000. A simple method for tracking vertebrate-dispersed seeds. *Ecology*, 81: 267-274.

LOISELLE, B.A. & BLAKE, J.G. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology*, 72: 180-193.

LOISELLE, B.A. & BLAKE, J.G. 2002. Potential consequences of extinction of frugivorous birds for shrubs of a tropical wet forest. Pp 397-405. *In*: D.J. Levey, W.R. Silva & M. Galetti

(eds.), Seed dispersal and frugivory: ecology, evolution and conservation. CABI Publishing, New York, NY. 536p.

LOISELLE, B.A.; SORK, V.L.; NASON, J. & GRAHAM, C. 1995. Spatial genetic structure of a tropical understory shrub, *Psychotria officinalis* (Rubiaceae). *American Journal of Botany*, 82: 1420-1425.

MCCONKEY, K.R. & DRAKE, D.R. 2006. Flying foxes cease to function as seed dispersers long before they become rare. *Ecology*, 87: 271-276.

MONTOYA, D.; ZAVALA, M.A.; RODRÍGUEZ, M.A. & PURVES, D.W. 2008. Animal versus wind dispersal and the robustness of tree species to deforestation. *Science*, 320: 1502-1504.

MURRAY, K.G. 1988. Avian seed dispersal of three neotropical gap-dependent plants. *Ecological Monographs*, 58: 271-298.

NATHAN, R. & MULLER-LANDAU, H.C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution*, 15: 278-285.

PRUM, R.O. 1994. Phylogenetic analysis of the evolution of alternative social behavior in the manakins (Aves: Pipridae). *Evolution*, 48: 1657-1675.

RANTA, E.; RITA, H. & LINDSTROM, K. 1993. Competition versus cooperation – success of individuals foraging alone and in groups. *American Naturalist*, 142: 42-58.

RESTREPO, C.; SARGENT, C.; LEVEY, D.J. & WATSON, D.M. 2002. The role of vertebrates in the diversification of New World mistletoes. Pp. 83-98. *In*: D.J. Levey, W.R. Silva & M. Galetti (eds.). Seed dispersal and frugivory: ecology, evolution and conservation. CABI Publishing, New York, NY. 536p.

ROBLEDO-ARNUNCIO, J.J. & GARCIA, C. 2007. Estimation of the seed dispersal kernel from exact identification of source plants. *Molecular Ecology*, 16: 5098-5109.

RUSSO, S.E., & AUGSPURGER, C.K. 2004. Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. *Ecology Letters*, 7: 1058-1067.

RUSSO, S.E.; PORTNOY, S. & AUGSPURGER, C.K. 2006. Incorporating animal behavior into seed dispersal models: implications for seed shadows. *Ecology*, 87: 3160-3174.

RYDER, T.B.; BLAKE, J.G. & LOISELLE, B.A. 2006. A test of the environmental hotspot hypothesis for lek placement in three species of manakins (Pipridae) in Ecuador. *Auk*, 123: 247-258.

SCHUPP, E.W.; MILLERON, T. & RUSSO, S.E. 2002. Dissemination limitation and the origin and maintenance of species-rich tropical forests. Pp. 19-33. *In*: D.J. Levey, W.R. Silva & M. Galetti (eds.). Seed dispersal and frugivory: ecology, evolution and conservation. CABI Publishing, New York. 536p

SEZEN, U.U.; CHAZDON, R.L. & HOLSINGER, K.E. 2005. Genetic consequences of tropical second-growth forest regeneration. *Science*, 307: 891-891.

SEZEN, U.U.; CHAZDON, R.L. & HOLSINGER, K.E. 2007. Multigenerational genetic analysis of tropical secondary regeneration in a canopy palm. *Ecology*, 88: 3065-3075.

SHERMAN, P.T. & EASON, P.K. 1998. Size determinants in territory with inflexible boundaries: manipulation experiments on White-winged Trumpeters' territories. *Ecology*, 79: 1147-1159.

SORK, V.L. & SMOUSE, P.E. 2006. Genetic analysis of landscape connectivity in tree populations. *Landscape Ecology*, 21: 821-836.

STONER, K.E.; RIBA-HERNANDEZ, P.; VULINEC, K. & LAMBERT, J.E. 2007. The role of mammals in creating and modifying seed shadows in tropical forests and some possible consequences of their elimination. *Biotropica*, 39: 316-327.

SUN, C., IVES, A.R.; KRAEUTER, H.J. & MOERMOND, T.C. 1997. Effectiveness of three turacos as seed dispersers in a tropical montane forest. *Oecologia*, 112: 94-103.

TERBORGH, J. 1990. Seed and fruit dispersal – commentary. Pp. 181-190. *In*: K.S. Bawa & M. Handley (eds.), Reproductive ecology of tropical forest plants. The Parthenon Publishing Group, Paris, France. 422p.

TERBORGH, J.; NUNEZ-ITURRI, G.; PITMAN, N.C.A.; VALVERDE, F.H.C.; ALVAREZ, P.; SWAMY, V.; PRINGLE, E.G. & PAINE, C.E.T. 2008. Tree recruitment in an empty forest. *Ecology*, 89: 1757-1768.

TERBORGH, J.; PITMAN, N.; SILMAN, M.; SCHICHTER, H. & NUNEZ, V.P. 2002. Maintenance of tree diversity in tropical forests. Pp. 1-17. *In*: D.J. Levey, W.R. Silva & M. Galetti (eds.), Seed dispersal and frugivory: ecology, evolution and conservation. CABI Publishing, New York. 536p.

THÉRY, M. 1992. The evolution of leks through female choice: differential clustering and space utilization in six sympatric manakins. *Behavioral Ecology and Sociobiology*, 30: 227-237.

THÉRY, M. & LARPIN, D. 1993. Seed dispersal and vegetation dynamics at a cock-of-the-rock's lek in the tropical forest of French Guiana. *Journal of Tropical Ecology*, 91: 109-116.

TORI, W.P.; DURÃES, R.; RYDER, T.B.; ANCIÃES, M.; KARUBIAN, J.; MACEDO, R.H.; UY, J.A.C.; PARKER,

P.G.; SMITH, T.B.; STEIN, A.C.; WEBSTER, M.S.; BLAKE, J.G. & LOISELLE, B.A. 2008. Advances in sexual selection theory: insights from tropical avifauna. *Ornitologia Neotropical*, 19(Suppl.): 151-163.

VALBURG, L.K. 1992. Flocking and frugivory - the effect of social groupings on resource use in the common bush-tanager. *Condor*, 94: 358-363.

VANDER WALL, S.B.; KUHN, K.M. & BECK, M.J. 2005. Seed removal, seed predation, and secondary dispersal. *Ecology*, 86: 801-806.

WANG, B.C. & SMITH, T.B. 2002. Closing the seed dispersal loop. *Trends in Ecology and Evolution*, 17: 379-385.

WANG, B.C.; SORK, V.L.; LEONG, M.T. & SMITH, T.B. 2007. Hunting of mammals reduces seed removal and dispersal of the afrotropical tree *Antrocaryon klaineanum* (Anacardiaceae). *Biotropica*, 39: 340-347.

WENNY, D.G. 2001. Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evolutionary Ecology Research*, 3: 51-74.

WENNY, D.G. & LEVEY, D.J. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences of the United States of America*, 95: 6204-6207.

WESTCOTT, D.A. 1997. Lek locations and patterns of female movement and distribution in a Neotropical frugivorous bird. *Animal Behaviour*, 53: 235-247.

WESTCOTT, D.A. & GRAHAM, D.L. 2000. Patterns of movement and seed dispersal of a tropical frugivore. *Oecologia*, 122: 249-257.

WESTCOTT, D.A.; BENTRUPPERBAUMER, J.; BRADFORD, M.G. & MCKEOWN, A. 2005. Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. *Oecologia*, 146: 57-67.

WHEELWRIGHT, N. T. 1991. How long do fruit-eating birds stay in the plants where they feed? *Biotropica*, 23: 29-40.

WHITNEY, K.D. & SMITH, T.B. 1998. Habitat use and resource tracking by African *Ceratogymna* hornbills: implications for seed dispersal and forest conservations. *Animal Conservation*, 1: 107-117.

WHITNEY, K. D.; FOGIEL, M.K.; LAMPERTI, A.M.; HOLBROOK, K.M.; STAUFFER, D.J.; HARDESTY, B.D.; PARKER, V.T. & SMITH, T.B. 1998. Seed dispersal by *Ceratogymna* hornbills in the Dja Reserve, Cameroon. *Journal of Tropical Ecology*, 14: 351-371.

WILSON, E.O. 1975. *Sociobiology: The new synthesis*. Harvard University Press, Cambridge, MA. 697p.

WRIGHT, S.J. 2003. The myriad consequences of hunting for vertebrates and plants in tropical forests. *Perspectives in Plant Ecology Evolution and Systematics*, 6: 73-86.

WUNDERLE, J.M. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest Ecology and Management*, 99: 223-235.

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