

Impacts of Mating Behavior on Plant–Animal Seed Dispersal Mutualisms: A Case Study from a Neotropical Lek-Breeding Bird

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INTRODUCTION

Sexual selection is a profound evolutionary force that impacts animal phenotype in myriad ways. A core question in the field of sexual selection is how intraspecific variation in phenotypic traits associated with mate choice (i.e., secondary sexual characteristics) affects access to mates and, ultimately, fitness. Examples of secondary sexual characteristics may include visual, acoustic, and olfactory signals, as well as behaviors, body size, and weapons (Andersson, 1994). A rich body of literature on these and other traits robustly supports Darwin's (1871) contention that, within a species, more extreme values for secondary sexual characteristics should be associated with increased attractiveness to mates and enhanced reproductive success (Andersson, 1994). This focus on mate choice has shaped our basic understanding of how sexual selection operates, and is a cornerstone of behavioral ecology and evolutionary biology.

Lek mating systems have proved particularly useful in furthering our understanding of mate choice processes (Wiley, 1991; Andersson, 1994). Lekking is characterized by spatially and temporally clustered aggregations of males in sites where display, mate choice, and copulation take place (i.e., leks). Lekking males invest heavily in attracting mates and provide no parental care; females are exclusively responsible for provisioning young. Reproductive skew is typically pronounced among males of lek-breeding species, such that a small number of males monopolizes the vast majority of matings, and most males have low levels of reproductive success (Payne, 1984; Mackenzie *et al.*, 1995). These conditions are thought to promote heavy investment in mate attraction by males,

and to underlie the extreme levels of secondary sexual characteristics for which lekking species are known (Andersson, 1994).

Darwin (1871) also recognized that sexual selection does not operate in a vacuum, and that there may be complex, and sometimes counteracting, relationships between sexual and natural selection. Because most animals routinely interact directly or indirectly with other species, natural selection pressures often take the form of interspecific, ecological interactions. The relationship between sexual selection and ecological interactions is likely to work in both directions: ecological interactions may determine the intensity of sexual selection in a given species or population, but at the same time sexual selection may shape the nature and outcome of ecological interactions. For example, natural selection pressure from parasites and/or predators may restrict the intensity of sexual selection and limit expression of secondary sexual characteristics at the individual, population, or species level (Zuk, 1992), while degree of investment in secondary sexual characteristics is also likely to affect parasite or predator populations and evolutionary trajectories (Kirkpatrick, 1986; Knell, 1999). As such, sexually selected traits are frequently thought to represent an optimum balance between mate choice (which may select for exaggerated values), and predation risk and parasite infection, which limit trait expression.

Along with predation and parasitism, sexually selected traits are also likely to be shaped by, and to shape, mutualistic ecological interactions. Consider, for example, frugivorous animals that serve as dispersal vectors for the seeds of plants. In such plant–animal mutualisms, plants provide resources (fruits) for the animals, which in turn disperse seeds, which assist with recruitment and gene movement in plants. In such cases, the spatial distribution of resources will affect the ability to monopolize mates, and hence the opportunity for sexual selection and mating system (the “polygyny threshold”; Emlen and Oring, 1977). The strength of sexual selection and the mating system exhibited by a species are, in turn, likely to affect secondary sexual characters, movement biology, and foraging ecology. When the animal involved is a dispersal vector, these factors may influence its dispersal services, which in turn will contribute to plant distributions and resource availability. Thus, in plant–animal mutualisms, factors such as distribution of resources, mating system, sexual selection, and foraging ecology are likely to interact to affect seed dispersal outcomes in an iterative, and potentially quite complex, manner.

Terborgh (1990) estimated that 85% of all tree species in one study area in the Peruvian Amazon were animal-dispersed, and similar values have been reported for other tropical forest sites across the globe (Foster, 1982; Howe and Smallwood, 1982; Ganesh and Davidar, 2001). Though the intensity and importance of plant–animal seed dispersal mutualisms reaches its acme in tropical rainforests, animal-mediated seed dispersal is a critical ecological and genetic process for plant species across most terrestrial habitats. When viewed through this lens, sexual selection among frugivores may be considered a potentially significant, albeit indirect, factor in determining demographic and genetic

characteristics of rainforest plant species. At the same time, natural selection forces associated with frugivory may shape signaling systems and other traits associated with mate choice (see, for example, [Schaefer *et al.*, 2004](#)). For instance, sexual selection may drive changes in morphology (e.g., mouthparts or body size), sensory systems (e.g., vision or olfaction), social organization (e.g., degree of territoriality and sociality), display behavior (e.g., use of traditional display areas), diet (e.g., preferential consumption of certain fruits for compounds used in secondary sexual signals), and use of space (e.g., movement patterns and foraging ecology), all of which in turn may impact what a frugivorous animal eats and where it disperses seeds. As such, a better understanding of how sexual selection interfaces with mutualistic ecological interactions in tropical rainforest would expand our appreciation for the forces that shape and are shaped by sexual selection in the tropics and beyond.

In this chapter, we address how sexual selection among frugivorous animals may affect the seed dispersal services that associated plants receive. Our particular focus is on how mating system and associated display behaviors impact foraging ecology and seed dispersal by frugivorous, lek-breeding birds. We first provide an overview of key concepts and predictions, and then go on to illustrate these concepts with our own work on the long-wattled umbrellabird (Cotingidae: *Cephalopterus penduliger*), a lek-breeding bird from the Chocó rainforests of northwest South America. We then compare long-wattled umbrellabirds with other lekking and non-lekking tropical and temperate species whose seed dispersal services may be impacted by sexual selection and/or mating system to varying degrees. Our broad objective in this chapter is to demonstrate the indirect, but biologically significant, effect that sexual selection in general, and mating behavior in particular, may have for the demographic and genetic structure of animal-dispersed plants in tropical rainforest and other habitats.

OVERVIEW AND PREDICTIONS

Lekking in birds is broadly distributed both taxonomically and geographically; this behavior has been recorded for approximately 100 species representing 15 avian families distributed across temperate and tropical regions of the globe ([Höglund and Alatalo, 1995](#)). This broad taxonomic range makes it difficult to make broad generalizations about the behavioral ecology of temperate versus tropical lek breeders. However, there does exist one striking difference among tropical versus temperate lekking bird species: diet. Whereas nearly all tropical lek-breeding species of bird are primarily frugivorous or nectarivorous, these food types do not constitute an important part of the diet for lek-breeding species from the temperate zone ([Höglund and Alatalo, 1995](#)). Lek-breeding birds from the temperate zone eat primarily grains and seeds (e.g., Ploecidae wydahs and widowbirds, $n=6$ species classified as lek breeders in [Höglund and Alatalo, 1995](#)), invertebrates (e.g., Scolopacidae ruff and sandpipers, $n=3$ species), or

some combination thereof (e.g., Tetraoninae grouse, $n=9$ species; Phasianinae pheasant and peafowl, $n=2$ species; Meleagrinae turkey, $n=1$ species; and Otidae bustard, $n=1$ species). In contrast, tropical lek breeders are dominated by frugivorous families such as Cotingidae (cotingas, $n=18$ species), Pipridae (manakins, $n=18$ species), and Paradisaeidae (birds of paradise, $n=13$ species), as well as the nectarivorous family Trochilidae (hummingbirds, $n=14$ species).

What factor or factors can explain this marked difference in diet between temperate versus tropical lek breeders? Male emancipation from parental care, and the associated ability for females alone to provide adequate parental care for successful reproduction, is a first requisite for lekking to evolve and be maintained. Clutch sizes typically drop with decreasing latitude, perhaps because of more intense predation pressure (Skutch, 1949) or increased adult survival near the tropics (Martin *et al.*, 2000), but this is unlikely to be related to differences in diet between temperate and tropical lekking species. Although there is strong evidence for the role of phylogenetic inertia in determining the occurrence of lekking, as seen by the fact that this phenomenon is concentrated in just a few families, this also cannot fully explain the high incidence of frugivory among tropical species because of the independent origin of lekking behavior among many of the major families.

We consider it likely that differences in the temporal and spatial distribution of fruit may play a fundamental role in determining why most lekking species are frugivores in the tropics, but not the temperate zone. First and foremost, because fruit is abundant in tropical rainforest relative to most other habitat types, and is available year-round, males from species relying on this resource may be emancipated from parental care and thus able to engage in lekking behavior. Second, as pointed out by Emlen and Oring's (1977) aforementioned paper on the environmental potential for polygyny, the distribution of resources in time and space will likely determine a species' mating system. When resources essential for females are clumped and easily defended, we might expect resource defense polygyny to evolve. When resources are dispersed but female groups can be easily followed, we might expect female defense polygyny to evolve. It is only when resources or females are not defensible that "male dominance" polygyny (e.g., lekking) may evolve (Oring, 1982). In the tropics, fruit may be distributed in such a way that it is sufficiently abundant to emancipate males from parental care, yet diffuse enough that neither fruit nor groups of females may be economically defended by males. In these circumstances, we might expect lekking to evolve. In the temperate zone, invertebrates and grains may exhibit attributes similar to those of fruit in tropical rainforest that promote lekking behavior. As such, on an evolutionary timescale, the underlying distribution of resources can shape the mating system of a given species, which in turn shapes the intensity of sexual selection on that species.

The distribution of resources is also likely to impact animal-mediated seed dispersal services on an ecological timescale. Frugivorous vertebrates vary widely in their seed dispersal services (Dennis and Westcott, 2006; Jordano

et al., 2007), both quantitatively (e.g., the number of fruits removed) and qualitatively (e.g., what and where they forage, how seeds are treated during ingestion and digestion, and how they are moved around and finally deposited; Schupp, 1993; Schupp *et al.*, 2010). This variation in dispersal services is directly related to foraging ecology (Murray, 1988; Westcott *et al.*, 2005; Jordano *et al.*, 2007), which on an ecological timescale is driven by the location of fruits in combination with constraints placed on movement by social organization, mating system, or other factors (Karubian and Durães, 2009). Foraging ecology in turn underlies observed patterns of seed movement and deposition (e.g., Karubian *et al.*, 2012a).

The variation in seed dispersal outcomes driven by these forces is likely to have significant demographic and genetic consequences for plant species and communities. Seed dispersal is a fundamental demographic process in plants, in that it determines seedling establishment and the distribution of species within and between populations (Howe and Smallwood, 1982; Levey *et al.*, 2002; Wang and Smith, 2002; Dennis *et al.*, 2007). Dispersal patterns shape the spatial distribution of dispersed seeds, including distance seeds are moved (Clark *et al.*, 2005; Jordano *et al.*, 2007), probability of deposition into microsites that may be particularly advantageous for germination or recruitment (Davidson and Morton, 1981; Reid, 1989; Wenny, 2001), and aggregation patterns (clustered vs scattered) of deposited seeds (Howe, 1989; Vander Wall and Beck, 2012).

The degree to which seeds are dispersed in a clumped manner is of particular interest because clustering can reduce survival of seeds and seedlings due to density-dependent effects (Janzen, 1970; Connell, 1979; Kwit *et al.*, 2004; Jansen *et al.*, 2008). Clustering of non-dispersed seeds falling directly underneath the parent tree is ubiquitous in nature and often leads to near-complete mortality, but frugivores often yield clumped distributions of seeds both underneath fruiting trees and away from them (Jordano and Godoy, 2002). This “spatially contagious” (Schupp *et al.*, 2002) or “destination-based” (Karubian *et al.*, 2010) pattern of seed dispersal can result in few sites receiving many seeds and most sites receiving few to none – a pattern that can have profound demographic consequences for plant populations due to the limited dissemination of propagules (Jordano and Godoy, 2002; Schupp *et al.*, 2002). Based on the microsite characteristics, it may also enhance or diminish probability of seed survival and recruitment (Davidson and Morton, 1981; Reid, 1989; Wenny, 2001; Holland *et al.*, 2009). Long-distance dispersal is thought to be particularly advantageous for plants because it reduces density-dependent mechanisms of competition, predation and disease, and increases arrival into favorable new sites (Nathan and Muller-Landau, 2000; Nathan *et al.*, 2008). Scaling up, these demographic processes also have important consequences for community structure of plant populations, metapopulation dynamics, long-term species persistence, and range expansion (Cain *et al.*, 2000; Pakeman, 2001; Laurance *et al.*, 2006).

Seed dispersal is also a fundamental genetic process in plants, in that it shapes the distribution of genotypes within a population, and gene movement within and among populations (Nathan and Muller-Landau, 2000; Sork and Smouse, 2006; Dennis *et al.*, 2007). While pollen represents the first phase of gametic dispersal, dispersal of seeds may have a larger impact on genetic processes because it determines the location of an individual with all its inherent risks of mortality, and it moves both maternal and paternal gametic genomes (Crawford, 1984; Hamilton, 1999; Grivet *et al.*, 2009). In this sense, the movement of seeds provided by frugivores directly shapes the fine-scale genetic structure of plant populations, as well as connectivity between populations and colonization of new patches (Sork and Smouse, 2006).

The use of genotypes from maternally inherited tissue in seed or fruit (Godoy and Jordano, 2001) provides a powerful tool to assess the genetic consequences of animal-mediated dispersal. Genetic methods have provided novel insights into the distances that seeds are moved by frugivores, and the genetic homogeneity of the seed pools that frugivores generate. Applying recently developed analytical methods to genotypic data derived from natural systems, researchers have found that animal-mediated seed dispersal often appears to result in a non-random and highly structured distribution of maternal genotypes (i.e., seeds) away from the maternal seed source (Grivet *et al.*, 2005; García *et al.*, 2009). However, although many studies consistently point to structured seed populations among vertebrate-dispersed plants, it would be premature to conclude that animal-mediated seed dispersal universally results in genetic bottlenecks because a relatively narrow range of (mostly temperate zone) species has been studied to date.

At present, three factors would significantly aid efforts to understand the demographic and genetic consequences of animal-mediated seed dispersal in general, as well as the effects of sexual selection and mating system on dispersal outcomes in particular. First, it would be useful to establish a direct linkage between a single dispersal agent or behavior and subsequent dispersal outcomes. This is because studies often lack a detailed knowledge of the frugivore species responsible for observed patterns of dispersal, meaning that genetic patterns observed among dispersed seeds could be due to a variety of dispersal agents exhibiting a potentially wide range of behaviors and activities. There has been a recent focus on this linkage (e.g., Grivet *et al.*, 2005; Jordano *et al.*, 2007; García *et al.*, 2009), but data are still scarce.

Second, the vast majority of relevant genetic studies focus on temperate systems in which dispersal agents exhibit similar forms of social organization consisting of social pairs or cooperative family groups that defend and forage within a fixed territory. As such, characterizing dispersal processes for a broader diversity of species, with a range of mating systems including lek breeding, would move us closer to a more robust understanding of the relationship between behavior and seed dispersal outcomes.

Third, a better integration of traditional ecological and more recent molecular methods is needed. Currently, molecular and observational estimates of seed dispersal are rarely combined in a single study system, despite the fact that both

approaches have potentially significant limitations when employed in isolation. Direct observational studies of dispersal are likely to miss rare but important longer-distance dispersal events, and can pose significant challenges for tracking movement of individual seeds (Koenig *et al.*, 1996; Nathan, 2006; Scofield *et al.*, 2011). Molecular studies, in turn, may fail to capture the proximate factors driving observed genetic patterns because they rarely identify the seed dispersal vector and/or behavior responsible for the seed arriving at its final location (but see Jordano *et al.*, 2007; Scofield *et al.*, 2010). For these reasons, integrating molecular results with a mechanistic understanding of underlying seed dispersal and deposition processes (e.g., frugivore behavior and movement) is desirable when possible.

The remainder of this chapter focuses on how lek-breeding may influence seed dispersal outcomes. As we have seen, among lek-breeding birds, frugivorous species are clustered in tropical, and especially neotropical, rainforests, and are largely absent from other habitat types. For this reason, the impacts of lek breeding on seed dispersal will be most pronounced in the tropics. Also, the relatively long duration of fruit availability in tropical rainforests allows extended, and in some cases year-round, activity at leks, thereby amplifying the effect of this mating system on seed dispersal outcomes in these habitats. This focus on lek mating systems in the tropics is meant to be illustrative of a broader point: the mating system and mating behavior exhibited by frugivorous animals will shape seed dispersal outcomes, regardless of what form that mating system takes.

In the following sections, we will use the long-wattled umbrellabird as a case study to illustrate how lekking behavior impacts foraging ecology, seed movement and deposition, and, ultimately, patterns of recruitment and genetic structure among plant populations. In doing so, we will test the following expectations: (1) males and females in lek-breeding species will exhibit marked differences in their movement patterns and foraging ecology that are directly attributable to their distinctive mating and reproductive strategies; (2) these differences in movement and foraging ecology will lead to differences in seed movement and deposition, which in the case of long-wattled umbrellabirds will lead to males yielding longer dispersal distances and a higher density of dispersed seeds at leks relative to areas outside the lek; (3) the high density of seeds at leks will be associated with reduced survival relative to areas outside leks unless some other factor, such as leks being particularly favorable microsites for seed recruitment, is relevant; and (4) dispersed seeds in leks will exhibit high degrees of genetic heterogeneity relative to areas outside leks because, over time, displaying males will bring seeds from a variety of seed sources surrounding leks.

FOCAL STUDY SPECIES

Long-wattled umbrellabirds (hereafter “umbrellabirds”) are large frugivorous birds endemic to the humid Chocó rain forests of northwestern Ecuador and western Colombia (Snow, 1982, 2004; Fig. 14.1). The species is considered



FIGURE 14.1 A male long-wattled umbrellabird in northwest Ecuador. This male is perched on his display territory on a lek, and is in the act of regurgitating a palm seed. *Photograph courtesy of Murray Cooper.*

“Vulnerable” to extinction, due primarily to widespread deforestation in this area (BirdLife International, 2000; IUCN, 2011). Umbrellabirds belong to the neotropical family Cotingidae, a group known for lekking behavior and exuberant secondary sexual characteristics (Snow, 1982). As is typical for lek-breeding species, males and females exhibit morphological and behavioral attributes that are likely related to their distinctive mating and reproductive strategies. Males are approximately 1.5 times larger than females and have large crests and long wattles, both of which are present but much reduced in females (Tori *et al.*, 2008). Groups of 5–15 males congregate in leks of ~1 ha in area, with a peak in sexual display activity in early mornings and late afternoons from August to February, and lower levels of activity at other times of the year (Tori *et al.*, 2008). Most males, which we refer to as “territorial” males, hold small (*ca.* 25 m²), long-term display territories on a single lek, which in turn allows us to link seeds dispersed into these display territories to male umbrellabird mating behavior (see below). Unusually for a lek-breeding bird, males from the same lek often forage together away from the lek in a relatively large, cohesive group (Tori *et al.*, 2008).

A subset of males, referred to as “floater” males, exhibits a qualitatively different strategy. Instead of holding a territory at a single lek, these males move between multiple leks without holding a fixed display territory. This behavior may be relatively common among lek-breeding species (Théry, 1992; Westcott and Smith, 1994; Tello, 2001), especially among younger males, but is poorly understood – in part because of challenges involved with tracking these individuals over large spatial areas. We have confirmed floating behavior in three of the 30 total umbrellabird males (10%) we have tracked with telemetry (below) for at least two radio-tracking sessions. One floater was not fully grown in either body size or sexual ornamentation, but the other two floater males were morphologically indistinguishable from territorial males. As such, we are uncertain

at present what the true incidence of this behavior is, and whether this represents a fixed alternative mating strategy or a flexible strategy that may only be employed for a portion of a male's life.

Female umbrellabirds are largely solitary. They appear to visit the lek only for purposes of mate choice and copulation (or occasionally to forage if there happens to be a fruiting tree in the lek), but spend the majority of the time alone. Females provide all parental care (Karubian *et al.*, 2003), and nesting is concentrated from January to May, which, curiously, only overlaps partially with peak male display activity at the leks (Tori *et al.*, 2008). They typically lay a single egg, and our observations suggest that post-fledging parental care lasts for several months (J. Karubian, unpublished data). Most females appear to visit only a single lek each mating season, though in rare instances we have recorded a female visiting two leks in a single season (J. Karubian, unpublished data). Although both sexes are highly frugivorous, females appear to consume a higher proportion of insects and small vertebrates than do males, especially when nesting (Karubian *et al.*, 2003; J. Karubian, unpublished data).

As one of the few large avian frugivores in the Chocó, umbrellabirds are important dispersers of large-seeded fruits typical of mature rainforest. The species consumes fruits of at least 35 plant species in our study area in north-west Ecuador, but exhibits a preference for species of the palm, avocado, and nutmeg families (Arecaceae, Lauraceae, and Myristicaceae, respectively). Fruits of these species present a single, large seed surrounded by a thin, lipid-rich aril, and umbrellabirds ingest fruit at the source tree before regurgitating the seed at some later point, usually away from the source tree. In contrast, umbrellabirds defecate smaller seeds associated with smaller fruits, such as the strangler fig *Ficus crassiuscula* (Moraceae).

In our study area in northwest Ecuador, umbrellabirds have a particularly tight ecological relationship with the canopy palm species *Oenocarpus bataua* (hereafter *Oenocarpus*; see Karubian *et al.*, 2010). *Oenocarpus* produces large-seeded (35 × 22 mm; Karubian *et al.*, 2012b), lipid-rich fruits in single infructescences of up to 2000 fruits (Goulding and Smith, 2007). Individual trees have ripe fruits for 3–4 weeks, and fruits are an important food source for both humans and large frugivores across the species' range, which extends from Panama to Bolivia on both sides of the Andes (Henderson *et al.*, 1995; Goulding and Smith, 2007). In our study area, umbrellabirds are the primary seed dispersal agents for *Oenocarpus*, with a lesser contribution by toucans (Ramphastidae); primate seed dispersal agents for *Oenocarpus* are absent from the site. We focus specifically on the mutualism between *Oenocarpus* and umbrellabirds for many of the analyses presented below.

GENERAL METHODS

We have been studying umbrellabird lekking behavior and seed dispersal since October 2002 in the Bilsa Biological Station (hereafter BBS; 79°45' W, 0°22' N,

330–730 m asl), a 3500-ha reserve of humid pre-montane Chocó rainforest in northwest Ecuador (see [Karubian et al., 2007](#) for more information on BBS). We have located a total of nine lek sites in BBS, and we monitor four of them for activity year round. Leks are typically located on forested ridges, and are separated by 1.7 ± 0.2 km (J. Karubian, unpublished data).

One important advantage of the umbrellabird system is that it allows us to link individual seeds dispersed into display territories on leks to male umbrellabird mating behavior. This is because males spend large amounts of time on these traditional display areas within the lek from which they effectively exclude other large avian frugivores, thereby dominating seed dispersal into these areas (see [Karubian et al., 2010, 2012b](#)). It is more challenging to link specific seeds encountered in other areas in the forest to a specific dispersal agent. For example, for the majority of seeds encountered outside the lek we are unable to determine which of the several potential vectors is responsible for the arrival of the seed at that point. This list of potential dispersal agents of *Oenocarpus* outside umbrellabird leks includes female umbrellabirds, male umbrellabirds in transit between foraging sites and the lek, toucans, terrestrial rodents, water, and gravity.

To test our first prediction regarding movement patterns of males vs females (Prediction One), we used two complementary tracking approaches. Umbrellabirds we captured at leks in mist nets placed in the canopy, measured, color-banded, and equipped with either tail-mounted radio-transmitters (Holohil Systems Ltd, Ontario, Canada) or backpack-style GPS tracking devices (e-obs, Hamburg Germany; see [Holland et al., 2009](#)). Radio-tracking was conducted on foot using hand-held GPS devices (Garmin LTD) to record locations at 30-minute intervals; GPS tracking devices record locations at 15-minute intervals and download data to a handheld base station. Movement data was visualized in ArcView GIS 3.2 (ESRI™, Redlands, California) and home ranges estimated using the Animal Movement ArcView Extension v. 2.04 ([Hooge and Eichenlaub, 2001](#)).

To estimate patterns of seed movement and deposition by umbrellabirds (Prediction Two), we integrated information on movement from radio-tracking with gut retention time, i.e., the time from ingestion to regurgitation (for four large-seeded species: two *Arecaceae*, *Oenocarpus* and *Bactris setulosa*; and two *Myristicaceae*, *Virola dixonii* and *Otoba gordonifolia*) or defecation (*F. crassiuscula*) to calculate seed dispersal distributions, following [Murray \(1988\)](#). As described in [Karubian et al. \(2012b\)](#), we also extended this method to produce “spatially explicit” seed dispersal distributions which calculate deposition patterns relative to a fixed location, such as the lek. We used these empirically based distributional models to generate predictions about the density of dispersed seeds in lek sites versus “control” sites outside the lek. To test these predictions, on a monthly basis we quantified seed rain into 1-m² seed traps placed in leks. These seed traps consisted of a square of PVC tubing around canvas material supported by strings approximately 1 m above the ground ([Karubian et al., 2012b](#)).

We used two approaches to assess demographic consequences of umbrellabird dispersal for the five focal plant species (Prediction Three). First, we compared initial seed rain to density of established seedlings and adults in both leks and control sites to assess the degree to which seed rain density was associated with the probability of transition from one age class to the next (Karubian *et al.*, 2012b). Second, we experimentally planted germinated seedlings (which were raised from seed in common nursery conditions as part of a pollen flow study; see Ottewell *et al.*, 2012) in leks and control sites to assess survival at this life stage. We have also tested possible effects of habitat structure among leks vs control sites in this experiment, as well as degree of relatedness (i.e., siblings or not) among experimental seedlings.

To quantify the genetic consequences of umbrellabird dispersal (Prediction Four), we focused exclusively on the palm *Oenocarpus* and made use of the fact that the pericarp tissue of dispersed seeds is of maternal origin, meaning that the genetic profile of the pericarp of a dispersed seed exactly matches that of the source tree from which it came (Godoy and Jordano, 2001). We used a direct genotype matching procedure based on results from microsatellite markers to link dispersed seeds to their maternal (source) tree (Karubian *et al.*, 2010). Samples were gathered from 10-m diameter patches, which we refer to as “seed pools”. Seed pools were randomly situated in a single lek or in control areas within a 30-ha study parcel surrounding the lek in which all adult *Oenocarpus* individuals were mapped and genotyped (Karubian *et al.*, 2010). Each seed pool in the lek is likely to represent seed dispersal by a single male, because males hold and defend stable territories within the lek. Outside the lek, “control” seed pools are likely to be generated by seeds dispersed by a broad range of vectors.

Because we can link dispersed seeds arriving in lek sites to umbrellabird display behavior, we can use Godoy and Jordano’s (2001) genetic approach to work backward from the dispersed seed to the source tree to gain insights into umbrellabird foraging ecology and dispersal patterns. We used a seed pool structure approach to assess the degree of overlap among seed sources (i.e., maternal trees) contributing to a single patch of dispersed seeds, as well as the overlap between different seed patches. The probability of maternal identity (PMI) approach (Grivet *et al.*, 2005) estimates the number of seed sources per seed pool, which can tell us, for example, whether clumped distributions represent genetic bottlenecks or areas of unusually high genetic mixing (Scofield *et al.*, 2010, 2011). PMI can also utilize the degree of genetic overlap in seed sources between different seed pools to provide insights into the distance seeds are being moved. An advantage of PMI is that one can test the genetic consequences of seed dispersal without locating and mapping the genotypes of all adults. At the same time, if one has a site where all adult trees are mapped and genotyped, traditional maternity analysis can be used to document exact dispersal distances (e.g., García *et al.*, 2007, 2009) as well as the frequency of immigrant seeds, which do not match any maternal genotype in the study area and are therefore likely to represent long-distance dispersal events (e.g., Jordano *et al.*, 2007).

HOW DOES LEKKING BEHAVIOR AFFECT SEED DISPERSAL OUTCOMES IN LONG-WATTLED UMBRELLABIRDS?

Prediction One: Umbrellabird Movement

In umbrellabirds, as in other lek-breeding species, the vast majority of male display behavior, female inspection and mate choice, and actual matings all take place at the lek. As such, males are predicted to spend as much time as possible at the lek in order to maximize their fitness (Fiske *et al.*, 1998). One might therefore expect that “territorial” male umbrellabirds would forage in close proximity to leks when possible in order to minimize reproductive “opportunity costs” associated with foraging away from the lek. However, the relatively high density of males present at a given lek may exhaust nearby resources, requiring these individuals to travel relatively long distances to find sufficient fruit when local supplies dwindle. Thus, uncertainty exists concerning the degree to which males from a single lek will exhibit highly overlapping, relatively small home ranges around the lek (indicative of foraging at nearby trees, presumably leading to low seed dispersal distances and high overlap in the seed pools generated by different males at the lek) versus larger home ranges with less overlap (indicative of foraging at more distant trees, presumably leading to longer seed dispersal distances, and less overlap between seed pools generated by different males at the lek). Females, in contrast, have no focal location equivalent to the lek except when they are nesting, and we have had no direct evidence that any of the females we studied were nesting during relevant data collection periods. As such, we expected females to maintain largely non-overlapping home ranges and to move evenly across these home ranges. “Floater” males were expected to exhibit a third distinctive pattern of movement, characterized by traveling relatively long distances between multiple leks.

We tested these predictions by tracking the movement of radio-equipped umbrellabirds in 2003–2004, as described in Karubian *et al.* (2012b). As expected, radio-tracking demonstrated that territorial males do indeed spend the vast majority of their time at the lek: these individuals spent 95% of their time in an area of only 7.3 ± 2.4 ha centered on the lek, and 50% in a 1.0 ± 0.2 ha area that corresponds to the lek itself (as demonstrated by 95% and 50% kernels, respectively). However, males also made occasional relatively long foraging trips, such that the overall foraging range (as measured by minimum convex polygons, or MCPs; Mohr, 1947) for radio-tracked territorial males was 37.8 ± 7.4 ha. Within the course of a day, males were present at the lek during peak display periods in the early morning and late afternoon, but traveled between the lek and fruiting trees on foraging trips of varying length and duration during the rest of the day (Fig. 14.2).

A single floater male that we radio-tracked exhibited a movement pattern distinctive from those of territorial males. The floater home range included

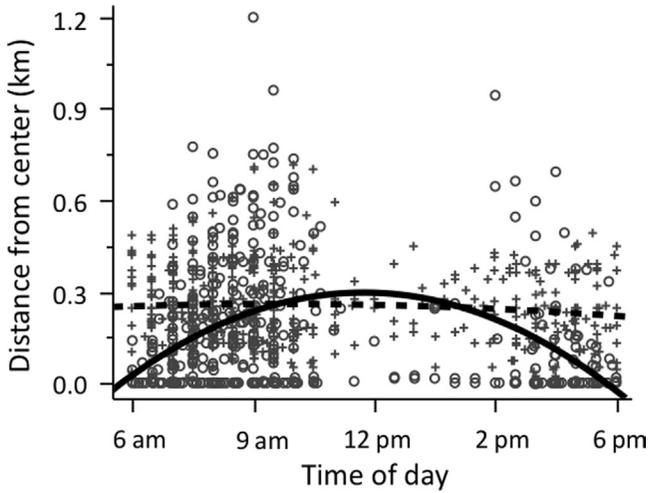


FIGURE 14.2 Distance moved from home range center for male (open circles) and female (crosses) long-wattled umbrellabirds as a function of time of day. For males, home range center corresponds to the lek. Lines represent the fit of separate quadratic functions to the distribution of points for males (solid line) and females (dashed line). Males exhibit a strong tendency to be present at the lek during early morning and late afternoon hours, but depart during the middle of the day to forage away from the lek ($R^2=0.13$, $F_{2,535}=39.61$, $P<0.0001$) whereas females exhibit no discernible movement pattern in relation to time of day ($R^2=0.01$, $F_{2,465}=1.57$, $P=0.21$).

three leks, and this male remained in the vicinity of a single lek for periods of 3–10 days before moving to another lek. The floater male overall (MCP) home range (596.3 ha), 95% kernel (250.1 ha), and 50% kernel (24.9 ha) were approximately an order of magnitude larger than corresponding values for territorial males (Karubian *et al.*, 2012b).

Females maintained an overall (MCP) home range of 49.2 ± 8.5 ha, which was slightly larger, but not significantly different, than that of territorial males. However, females used their home ranges much more evenly than did males. They spent 95% of their time in an area of 37.3 ± 6.2 ha, and 50% of their time in a core area of 4.7 ± 0.6 ha. These values are approximately five times greater than equivalent measures for territorial males. Unlike territorial males, females showed no discernible daily pattern of movement relative to the center of their home ranges (Fig. 14.2). These findings reflect the fact that females did not focus their movements on a specific location such as the lek, but instead moved across their home-range area without a strong bias towards any particular point. In this sense, the movement patterns of female umbrellabirds may be qualitatively similar to those of many non-lekking species of tropical frugivorous bird (e.g., toucans, Ramphastidae) that maintain regular home ranges and do not have the need to return regularly to a central display site (i.e., the lek). As such, female umbrellabird dispersal patterns may be useful to gain a qualitative sense for dispersal patterns generated by non-lekking species.

Umbrellabirds are capable of moving large distances rapidly, and males in particular often fly above the canopy to traverse watersheds and ridges. As a consequence, birds sometimes flew out of range during our radio-tracking sessions and our efforts to track radio-equipped birds on foot may have failed to capture the full range of movement. To assess the degree to which our radio telemetry data may underestimate the extent of movements and size of home ranges for this species, we have begun preliminary data collection placing GPS tags on birds captured at leks. These units log location data at 15-minute intervals every third day, which can then be remotely downloaded to a hand-held base station. We tracked one territorial male and one floater male captured at a single lek from December 2011 through April 2012 (a similar duration and time period as that of radio-tracked individuals in previous years) using this technology.

The GPS-equipped territorial male had an overall (MCP) home range of 97.4 ha; 95% and 50% kernels were 6.9 ha and 1.7 ha, respectively (Fig. 14.3).



FIGURE 14.3 Home range usage patterns by two male long-wattled umbrellabirds in north-west Ecuador. Data were obtained with GPS tracking devices during a three month period in a single breeding season (2011–2012). Unweighted minimum convex polygon (MCP) estimates and 95% and 50% kernels are shown for a “floater” male (dashed borders) and a territorial male.

Thus, although the overall home range for this individual was two- to three-fold larger than that recorded for other territorial males via conventional radio-tracking, its core usage areas (i.e., 95% and 50% kernels) were virtually identical. The GPS-equipped floater male's overall home range was 871 ha; 95% and 50% kernels were 118 ha and 17 ha, respectively. This GPS-equipped floater male visited two areas, at least one of which is likely to represent a new lek that we were previously unaware of. In this case, the GPS-equipped individual had an overall home range 1.5 times larger than that of the radio-tracked floater (above), and its core usage areas were smaller.

We consider it notable that the core usage areas remained relatively concentrated around leks regardless of the method used, suggesting that the longer foraging trips that underlie the relatively large MCP home ranges for both territorial and floater males may contribute relatively little to overall seed movement in terms of numbers of seeds moved. Instead, the majority of seed movement is likely to occur within the core usage areas, around the leks. On the other hand, these foraging trips away from the lek may be critical to the occurrence of rare but biologically important long-distance seed dispersal events (Nathan *et al.*, 2008).

In sum, animal tracking demonstrates that territorial males, floater males, and females each exhibit dramatically different movement patterns: territorial males concentrate their time in and around their home lek but occasionally forage further afield, females move evenly over moderate-sized home ranges, and floater males travel at a landscape scale that greatly exceeds that of territorial males and females. These differences in foraging ecology can be directly related to the respective mating and reproductive strategies of these three classes of bird. In the following section, we explore how foraging ecology of territorial lek-breeding males impacts seed movement and deposition.

Prediction Two: Seed Movement and Deposition

When, where, and how often a frugivore engages in display behavior should impact the source trees it visits, and the locations where it deposits seeds from those source trees (Wenny and Levey, 1998). We calculated seed dispersal distributions to assess the extent to which distinctive reproductive strategies of territorial male, floater male, and female umbrellabirds would drive biologically meaningful differences in seed transport and deposition (Karubian *et al.*, 2012b). These analyses are restricted to radio-tracked individuals (i.e., they do not include GPS-equipped individuals). Territorial males and females produced similarly shaped distributions of seed dispersal distances from the source tree for both large-seeded and small-seeded tree species, with probability of deposition decreasing sharply as distance from the source tree increased. However, mean dispersal distance from the source tree to deposition site by territorial males was longer than that of females for both large-seeded fruits (257 vs 218 m, respectively) and the small-seeded *F. crassiuscula* (326 vs 244 m). For

both fruit types, maximum dispersal distance was also greater for territorial males than for females (1338 vs 1108 m). The single floater male tracked for this study, in contrast, yielded a “flatter” seed dispersal distribution and much longer mean and maximum seed movement distances, reflecting the relatively high frequency with which it undertook long flights, such as those between leks. Mean dispersal distance from the source tree was 542 m for large-seeded fruit and 723 m for *Ficus*, approximately twice the corresponding values for territorial males and females; maximum dispersal distance was 2650 m (Karubian *et al.*, 2012b).

We also predicted that, as a consequence of male display behavior, seed deposition should be spatially aggregated at lek sites relative to areas outside the lek. In keeping with this prediction, “spatially explicit” seed dispersal distributions indicated that territorial males deposit a high proportion of the ingested seeds (>50%) into lek sites. This finding was consistent for both large, regurgitated seeds and smaller, defecated seeds favored by umbrellabirds. Floater males were estimated to deposit 20% of the large seeds they ingest into lek sites. Females, in contrast, were estimated to deposit most seeds >200 m from the center of their home ranges. We confirmed the results of the seed dispersal distribution model empirically in the field; relative to control seed traps located outside the lek, seed traps in leks received more than four times as many dispersed seeds from our five focal tree species (Karubian *et al.*, 2012b). Thus, both the seed movement and deposition patterns we recorded appear to follow directly from the mating behavior and foraging ecology differences our movement analyses uncovered. In the following section, we explore the demographic consequences of clumped seed deposition patterns in leks.

Prediction Three: Demographic Consequences

The high density of seeds deposited beneath display perches by umbrellabirds might be expected to reduce seed and seedling survival via density-dependent mortality and competition processes (Janzen, 1970; Connell, 1971; Kwit *et al.*, 2004; Jansen *et al.*, 2008). Interestingly, we found no evidence for the expected decrease in germination rates among seeds in leks vs outside leks (Karubian *et al.*, 2012b). To further explore this issue, we have implemented a field-based experiment in which seedlings of known provenance that were raised in a common nursery were planted in a standardized design in either leks or control areas outside leks. This experiment, currently in its third year, is still in progress, but preliminary results strongly indicate that seedling survival is significantly higher in leks relative to control areas outside leks (J. Karubian, unpublished data).

These departures from predicted density-dependent mortality suggest that some other factor, such as the lek being a particularly favorable microsite for seed recruitment, may be relevant in this system. However, our measures at leks versus non-leks have uncovered no obvious differences in basic forest

structure parameters such as ambient light or canopy height (J. Karubian, unpublished data). We are currently testing the potential impact of soil quality, and in particular the idea that displaying male umbrellabirds may effectively fertilize seeds in leks via repeated defecation from display perches – a pattern reported beneath roosts of other frugivorous birds (T. Carlo, personal communication).

Another possible explanation is that, despite the constraints imposed by lek attendance on foraging behavior, territorial males still forage from multiple trees and move seeds relatively long distances. A relatively high incidence of long-distance dispersal and foraging from multiple trees are both expected to contribute to higher genetic diversity among seed pools at leks, and this genetic variety might in turn enhance survival at leks via a “rare allele” effect (Levin, 1975). “Spatially explicit” seed dispersal distributions used in Karubian *et al.* (2012b) reveal that the average distance territorial males move seeds from source trees to their home range center (i.e., the lek) is shorter than equivalent measures for females (259 vs 325 m for large-seeded fruits and 330 vs 286 m for *Ficus*, respectively). However, maximum dispersal distance from source tree to territory center is greater for territorial males than females (1129 vs 853 m). Also, both ecological observation and genetic analyses (see below) suggest males may bring seeds from a large number of source trees back with them to the lek. However, in the seedling survival experiment described above, we have not been able to detect an effect of relatedness on survival probability.

Regardless of the mechanisms driving this pattern of higher than expected survival in leks versus outside leks, these findings suggest that umbrellabird dispersal may provide an important survival advantage to dispersed seeds. Interestingly, however, this effect appeared not to carry through to adults of the five focal tree species, in that there was no difference in density of adults in leks vs outside leks. This is not necessarily surprising, given the highly stochastic nature of the transition from seedling to adult. Also, leks move over time; we have recorded one lek abandonment and one lek formation over 71 lek-years of monitoring. This uncertainty over how long a lek has been located in a particular location complicates tests of the long-term demographic or genetic consequences of umbrellabird lekking behavior.

Prediction Four: Genetic Consequences

Radio-tracking and opportunistic observations in the field led us to believe that umbrellabird males forage from multiple trees within a day. Over time, we expected that this foraging behavior would lead to accumulation of seeds from multiple source trees beneath each male’s perch. We therefore predicted that lekking behavior would lead to high levels of seed-source diversity at fine spatial scales relative to control plots situated outside leks. This in turn may have important consequences for the distribution of genotypes and fine-scale genetic structure exhibited by plant species dispersed by umbrellabirds.

Genetic analyses on *Oenocarpus* seeds collected in the field reveal that the genetic composition of seed pools in a single umbrellabird lek is far more heterogeneous than in areas outside the lek (Karubian *et al.*, 2010). Using the PMI approach to estimate N_{em} , the effective number of seed sources per seed pool (Grivet *et al.*, 2005), we found that seed pools within the focal lek represented over five times more source trees than equivalent seed pools outside the focal lek ($N_{em} = 27$ in leks vs 5.2 outside leks). This value fits well with the prediction that males are bringing seeds from multiple source trees back to their territories on the lek. Thus, it does appear that the display behavior of individual umbrellabirds contributes to significant mixing of propagules from different seed sources beneath display perches at the lek, although corroboration from multiple leks is desirable.

Because males often forage in flocks (J. Karubian, unpublished data) and have highly overlapping home ranges that include the same sets of source trees surrounding the lek, one might predict relatively high overlap among the source trees of seeds encountered beneath display perches of different males in the same lek. When conducting between-plot comparisons of overlap, we found that, relative to control plots, lek plots exhibited a more gradual decline in inter-plot maternal overlap (r_{ij}) as inter-plot distance increased (Karubian *et al.*, 2010). This indicates that males from the same lek may be foraging at overlapping but diverse sets of trees, concordant with the ecological observations of overlap in foraging range. This finding is also consistent with the idea that the spatial scale of seed dispersal outside the lek is limited, leading to high levels of overlap among seed plots separated by short distances, a rapid decline of overlap as pairwise distance between seed plots increases, and very low levels of overlap at longer distances between seed plots (see Figure 2 in Karubian *et al.*, 2010).

We also used genetic analyses to directly estimate the spatial scale of seed movement. In keeping with the predictions of our seed dispersal distributions, males are expected to move seeds longer distances than those frugivores contributing to control plots. The proportion of “immigrant seeds” from outside the boundary of our study parcel was higher in the lek than in control plots, suggesting a higher rate of long-distance dispersal from outside the parcel’s boundaries into the lek than into the control plots, despite the fact that, on average, control plots were located closer to the parcel’s boundaries (Karubian *et al.*, 2010). Genetic analyses of seed movement, using direct matching of genotypes between dispersed seeds and maternal source trees, are currently in progress.

These dispersal differences led to significantly lower spatial genetic autocorrelation at all distance classes analyzed in the lek than outside the lek (Karubian *et al.*, 2010). Thus, destination-based dispersal driven by male umbrellabird display behavior promotes gene movement and homogenizes local genetic structure of *Oenocarpus* seedlings.

COMPARISONS WITH OTHER LEKING AND NON-LEKING SPECIES

To what extent can the relationships and patterns we have documented for umbrellabirds be extended to other species of lek-breeding frugivores? We consider it likely that, like umbrellabirds, most if not all lek-breeding species exhibit qualitative differences between the sexes in foraging ecology and movement patterns. This is because sex-specific movement patterns arise directly from the distinctive male and female mating strategies which define the lek mating system. That is, females of lek-breeding species will typically move more evenly across the landscape (when not nesting) relative to males (Westcott and Graham, 2000), which will in turn have smaller core usage areas centered on the lek (Théry, 1992). High attendance at the lek by males should lead to high clustering of seeds at these display sites for all lek-breeding species. Available empirical evidence, though sparse, corroborates this expectation. Lek sites of both manakins and cotingas have higher densities of favored food plants than do control areas outside the leks (Théry and Larpin, 1993; Ryder *et al.*, 2006). There is also a higher density of seeds in the seed bank of manakin leks relative to control areas (Krijger *et al.*, 1997). The degree to which seeds are clustered at leks of different species (or even between different leks of the same species) will depend on the intensity of display behavior, the number of males at a given lek, and the spatial aggregation of displaying males (i.e., classical vs “exploded” leks).

Floater males also appear to be a common element of lek mating systems in many tropical lek-breeding frugivores (e.g., Théry, 1992; Westcott and Smith, 1994; Tello, 2001). However, because this behavior is still so poorly understood, few generalizations can be made for how it should affect seed movement and deposition patterns across species. It does seem likely that floating behavior will lead to longer dispersal distances (e.g., Théry, 1992) and flatter dispersal distributions as birds move between leks, but this issue requires more data. More broadly, the existence of two or even three distinctive reproductive strategies within a single lek-breeding species provides a convenient venue in which to examine the effects of social behavior on seed dispersal outcomes.

The distances that seeds are moved between maternal source tree and lek are likely to vary across, and even within, lek-breeding species. This is because the spatial and temporal distribution of fruiting trees will interact with mating system to shape foraging patterns and space use, which will in turn determine the distances that seeds are moved. Species of bird with a high concentration of fruiting trees in or near the lek (e.g., Ryder *et al.*, 2006) will be expected to transport seeds shorter distances than species forced to forage further afield. Unfortunately, very few data are currently available on seed movement distances attributable to lek-breeding species.

Demographic and genetic consequences of lek breeding are also likely to be system-dependent. Survival probability for seeds dispersed into lek sites is likely to be a function of the microhabitat associated with the lek or display site, though few case studies beyond [Wenny and Levey's \(1998\)](#) aforementioned bellbird study exist. Data are even more sparse for the genetic consequences of dispersal by lek-breeding tropical birds. In the case of umbrellabirds, high levels of genetic mixing among seed pools in the lek can be traced to a relatively high density of maternal source trees around the lek from which males forage. Over time, males bring the seeds from multiple trees back with them to the lek and thereby generate diverse seed pools representing multiple source trees. There are currently few other data available with which to compare these results. In theory, the degree to which this scenario applies to other lekking (or non-lekking) species will depend upon the spatial and temporal distribution of fruiting trees. In contrast to our results from umbrellabirds, for example, if favored food sources are abundant on or adjacent to a male's display territory, as appears to be the case for some manakin species ([Ryder et al., 2006](#)), we might expect extremely low dispersal distances and seed source diversity among seed pools generated by these species of bird.

In summary, there currently exist very few data from tropical birds, be they lek-breeding or not, with which to compare umbrellabirds. A priority for future research is to assess animal movement, seed movement, and genetic and demographic consequences in the context of mating system for a broader range of lek-breeding species (as well as other species). A related goal is to account for the distribution of fruiting trees in shaping foraging ecology and dispersal outcomes (e.g., [Carlo and Morales, 2008](#)). These are challenging tasks, but are necessary to fully understand the complex dynamics described here.

Comparisons between umbrellabirds and temperate zone species benefit from the fact that much more work has been done in the temperate zone than in the tropics. However, because lek-breeding among frugivorous bird species is essentially absent from the temperate zone, we must limit our comparisons to species that exhibit other mating systems. One particularly well-studied system is that of acorn dispersal of the oak *Quercus lobata* by acorn woodpeckers *Melanerpes formicivorus*. Unlike umbrellabirds, acorn woodpeckers live in highly territorial social groups and tend to forage in the trees proximal to their storage sites, with each territorial group gathering acorns from non-overlapping territories and hence from different trees ([Grivet et al., 2005](#); [Scofield et al., 2010, 2011](#)). This mating system and social organization results in pronounced structuring of seed pools in granaries where the acorns are stored ([Grivet et al., 2005](#); [Scofield et al., 2010, 2011](#)). In a separate study of dispersed *Q. lobata* seedlings ([Grivet et al., 2009](#)), the combined effect of several vertebrate dispersal agents also produced pronounced structuring of seedling populations. Relative to umbrellabird dispersal, then, acorn woodpeckers generate seed patches (i.e., granaries) characterized by very low maternal seed-source diversity and very limited overlap between seed patches on different territories. These differences

can be directly attributed to the mating systems of the two species, with the strong territoriality of acorn woodpeckers essentially constraining potential source trees to those located within the territorial boundary.

Similarly, a community of frugivorous birds in Spain (García *et al.*, 2009) dispersed *Prunus mahaleb* seeds long distances from source trees but still yielded strong clustering of maternal genotypes in seed traps. This pattern, which is likely explained by preferences for certain microhabitat types as foraging, resting or roosting sites, and/or by the fact that several fruits may be consumed in a single foraging bout and deposited together, shows that genetic bottlenecks can arise despite long-distance movement of seeds. Although the majority of avian species in this study form socially monogamous pair bonds, it is not clear to what extent the breeding system *per se* contributes to observed seed dispersal outcomes.

CONCLUSIONS

In sum, variation in seed dispersal associated with sexual selection and mating system is likely to be an indirect but nonetheless important factor in determining demography, gene flow, and genetic structure for animal-dispersed plant species. Among umbrellabirds, we observe patterns of seed movement and deposition that can be directly traced back to mating system, and which favorably impact seed survival and fine-scale genetic structure for the plants these birds disperse. This phenomenon is likely to apply across lek-breeding birds, which constitute an important part of the tropical avifauna, but data are lacking and the scale and even the direction of the impacts will vary across lekking species. We expect reduced distances of seed movement, less clustering of seeds, and less genotypic heterogeneity within seed pools for territorial species in both tropical and temperate regions, but again data are sparse. In all cases, the distribution of resources will be an important factor that interacts with mating system to shape foraging ecology and determine seed dispersal outcomes. Also in all cases, but particularly in the tropics, more data are needed to advance our understanding of the relationship between mating system and seed dispersal outcomes.

Our understanding of the relationships between mating system and seed dispersal outcomes is still in its nascent stages. A better understanding of these relationships would illuminate the interaction between sexual selection and mutualistic ecological interactions, which have been relatively neglected in this context relative to antagonistic ecological interactions such as predation and parasitism. A more refined understanding of this phenomenon would also enhance conservation efforts. The breakdown of dispersal syndromes is expected to alter forest dynamics (Terborgh *et al.*, 2008), and a better understanding of how the mating system shapes dispersal services would improve the ability to assess and predict consequences of perturbation to these systems, such as extirpation of dispersal agents or fragmentation of habitats (Karubian and Durães, 2009).

Clearly, animal behaviors directly impacting seed dispersal outcomes can vary dramatically between species and even within a species (e.g., between the sexes or across a geographic range), with potentially important ecological and evolutionary implications for plant species and communities. As such, we hope this chapter highlights the need to expand the breadth and depth of studies that explicitly consider the social behavior of animals when investigating seed dispersal dynamics, and motivates additional research in the field, particularly in the tropics.

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