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Mating Behavior Drives Seed Dispersal by the Long-wattled Umbrellabird *Cephalopterus penduliger*

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ABSTRACT

Frugivores exhibit considerable variation in the seed dispersal services they provide. Understanding what drives these differences is a key goal for ecologists because of the central role seed dispersal plays in shaping ecological and genetic diversity in plant populations. The lek-mating system of the Long-wattled Umbrellabird (*Cephalopterus penduliger*) provides a powerful lens to examine how mating behavior may impact seed dispersal outcomes. As in all lek-breeding species, male Umbrellabirds congregate in traditional sites (leks) to display, whereas females are solitary and visit leks only rarely. This study demonstrates how differences in mating behavior between the sexes drive distinctive seed movement and deposition patterns by male vs. female Umbrellabirds. Using radio tracking and gut retention trials, we documented divergent movement patterns between the sexes that are directly attributable to mating behavior differences. These movement differences led males to disperse seeds long distances from source trees and to deposit the majority of seeds they ingested within the lek; females dispersed seeds shorter distances and more evenly across the landscape. We empirically confirmed that the density of dispersed seeds was higher in leks than in control areas outside the lek, yet found no evidence that this higher density of seeds in leks reduced probability of seedling establishment. This research not only provides a mechanistic explanation for long dispersal distances and high levels of genetic diversity previously reported for seeds in Umbrellabird leks, but also highlights the importance of explicitly considering behavior in studies of animal-mediated seed dispersal.

Abstract in Spanish is available in the online version of this article.

Key words: Ecuador; *Ficus crassiuscula*; Janzen-Connell; lek; Neotropical Chocó rain forest; *Oenocarpus bataua*; radio telemetry; *Virola dixonii*.

ANIMAL-MEDIATED SEED DISPERSAL IS IMPORTANT IN MANY TERRESTRIAL ECOSYSTEMS (Howe & Smallwood 1982), and reaches its apex in tropical rain forests, where over 85 percent of trees may produce fleshy fruits adapted for animal consumption (Terborgh 1990). Animal vectors differ in dispersal characteristics such as the number of seeds dispersed, the distances seeds are moved, the degree of aggregation of deposited seeds, and the microhabitat characteristics of deposition sites (*e.g.*, Holbrook & Smith 2000, Fragoso *et al.* 2003, Dennis & Westcott 2006, Jordano *et al.* 2007, Muscarella & Fleming 2007, Galetti *et al.* 2008). These dispersal characteristics, in turn, impact seed survival (*e.g.*, Nathan & Muller-Landau 2000, Wenny 2001, Jansen *et al.* 2008) and patterns of genetic and ecological diversity within and between plant populations (*e.g.*, Grivet *et al.* 2005, Vellend 2005, Garcia *et al.* 2009). Consequently, characterizing and comparing dispersal services provided by frugivores continues to be a topic of ecological interest, but difficulties of tracking animals in the field, and connecting individual dispersed seeds to the particular animal that dispersed them, make this a challenging subject to address. For this reason, improving our mechanistic understanding of what drives variation in animal-mediated seed movement and deposition patterns remains a priority in the field of ecology (Schupp *et al.* 2010).

Animal foraging and social behavior may shape seed dispersal (Westcott *et al.* 2005, Russo *et al.* 2006, Karubian & Durães 2009). Field-based studies of communal roosting by primates (Russo & Augspurger 2004, Chapman & Russo 2006) and avian display behavior (Théry & Larpin 1993, Krijger *et al.* 1997, Wenny & Levey 1998) report clumped distributions of seeds at these sites. This may increase seed survival when deposition occurs in favorable sites for germination (*i.e.*, 'directed dispersal'; Wenny & Levey 1998) or decrease survival via density-dependent susceptibility to predation or disease (Russo & Augspurger 2004). Similarly, studies using molecular markers have demonstrated that scale of seed movement and genetic heterogeneity of dispersed seeds may vary in relation to a disperser's social biology and/or foraging ecology (Jordano *et al.* 2007, Garcia *et al.* 2009).

The Long-wattled Umbrellabird *Cephalopterus penduliger* (Snow 1982) exhibits a lek-breeding system that can potentially be used to refine our mechanistic understanding of how mating behavior may impact seed dispersal. As one of the few large avian

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frugivores in the Chocó rain forests of northwestern Ecuador and western Colombia, Long-wattled Umbrellabirds are important dispersers of large-seeded fruits typical of mature rain forest. As in all lek-breeding species, male and female Long-wattled Umbrellabirds exhibit pronounced differences in mating behavior. Most males congregate in traditional display areas (leks) and defend a fixed territory at a single lek during the extended breeding season. Display territories typically contain no resources, so males make foraging trips between the lek and fruiting trees. Females are largely solitary and visit the lek only rarely for purposes of copulation.

Our objective in the present study was to assess the degree to which differences in mating behavior between male vs. female Umbrellabirds can be mechanistically linked to distinctive seed movement and deposition patterns by the sexes. We reasoned that male and female movement should differ in a manner directly attributable to their respective reproductive strategies (*i.e.*, that movement should be focused around leks for males, but not females). Based on these expected movement differences, we predicted that males should bring a high proportion of the seeds they ingest while foraging away from the lek back to their display areas, yielding a high density of dispersed seeds in lek sites. In contrast, we predicted that females should deposit seeds more evenly across their home ranges. We also reasoned that increased densities of seeds in leks might lead to reduced germination success in these sites. In testing these predictions, our broader goal was to demonstrate the importance of explicitly incorporating animal behavior when studying animal-mediated seed dispersal.

METHODS

Study area and species.—Field data were gathered from October 2002 to May 2005 in Bilsa Biological Station (79°45′ W, 0° 22′ N, 330; 730 m asl), a 3500 ha reserve of humid pre-montane Chocó rain forest in northwest Ecuador (Karubian *et al.* 2007). Long-wattled Umbrellabirds (hereafter 'Umbrellabirds') are endemic to Chocó habitat and 'vulnerable to extinction' due to widespread deforestation in this area (BirdLife International 2000). Groups of 5–15 males congregate in leks of ~1 ha, with a peak in activity in early mornings and late afternoons from August to February, and low levels of activity year-round (Tori *et al.* 2008). Most males, which we refer to as 'territorial' males, defend small (*ca* 25 m^2) display territories on the lek. A small proportion of males, which we refer to as 'floater' males, move between leks without holding a fixed display territory. Females are largely solitary and visit the lek only to copulate, after which they care for the young alone (Karubian *et al.* 2003). Both sexes are highly frugivorous, although females may consume a higher proportion of insects and small vertebrates, especially when nesting (Karubian *et al.* 2003).

We studied Umbrellabird dispersal of three focal tree species: *Oenocarpus bataua* Mart (Arecaceae; hereafter *Oenocarpus*), *Virola dixonii* Little (Myristicaceae; hereafter *Virola*), and *Ficus crassiuscula* Warb. ex Standl. (Moraceae, hereafter *Ficus*) (Jørgensen & León-Yánez 1999, Clark *et al.* 2006). All three species are common on our study site and constitute an important part of the diet of both male and female Umbrellabirds. All fruit types are ingested whole, and seeds are viable following Umbrellabird gut passage. *Oenocarpus* and *Virola* fruit contain a large seed surrounded by a thin, lipid-rich aril. *Ficus*, a strangler fig, has berry-like fruits containing hundreds of small seeds. Umbrellabirds regurgitate the seeds of *Virola* and *Oenocarpus* fruits but defecate the seeds of *Ficus* fruits.

Capture and radio telemetry.—Birds were captured at leks in aerial mist nets and equipped with tail-mounted RI-2C radiotransmitters (Holohil Systems, Ltd., Carp, Ontario, Canada) weighing <1.7 percent of average weight, following Holbrook and Smith (2000). Radio tracking was conducted for 10 mo in each year (August–May) on foot using TR4 receivers with a RA-2AK 'H' antennae (Telonics Inc., Mesa, Arizona, U.S.A.). Researchers recorded fixes of a radio-equipped bird's location as UTM coordinates using handheld Garmin GPS 76-S units with extended antennae (Garmin, Ltd., Olathe, Kansas, U.S.A) at 30 min intervals using visual observation and/or triangulation with a maximum error of ±30 m based on field tests of triangulation accuracy (White & Garrott 1990). Fixes were visualized in ArcView GIS 3.2 (ESRI™, Redlands, California, U.S.A.) and home ranges estimated using the Animal Movement ArcView Extension v.2.04 (Hooge & Eichenlaub 2001) as 100 percent minimum convex polygons (MCP, Mohr 1947) and 95 and 50 percent fixed kernel isopleths using least-squares cross validation with a 1 m^2 cell size and *ad hoc* smoothing factors (Worton 1989, Seamann & Powell 1996). MCP provides an un-weighted boundary of overall home range whereas kernel analyses weight areas within the home range in relation to the proportion of time the focal animal spends on them (Powell 2000).

All statistical comparisons are limited to females vs. territorial males (*i.e.*, the single floater male was not included in any statistical comparisons). Analyses were limited to individuals with >40 fixes (Powell 2000) and there were no differences between the sexes in days tracked ($t_{15} = 0.07$, $P = 0.94$) or number of fixes recorded ($t_{15} = 0.17$, $P = 0.87$). Differences in home range size between the sexes were tested while controlling for any effects of year by using nested ANOVA (sex nested within year) on log-transformed data.

Gut retention time and seed dispersal distributions.—Seed dispersal distributions were estimated by combining distributions of gut retention time (GRT, time from ingestion to regurgitation of the seed) and movement patterns (Murray 1988). To establish GRT, each of five male and four female Umbrellabirds were held without food for 180 min and then placed in a 1.5 × 1 × 1 m cylindrical cage for 4–24 h with *ad libitum* access to water and banana. Captive birds were fed two marked ripe fruits at a time (for *Virola* and *Oenocarpus*) or 5–8 ripe fruits (for *Ficus*) and GRT was recorded. For *Virola* and *Oenocarpus*, GRT distributions were calculated by summing the number of seeds regurgitated during each 30 min interval following ingestion (*e.g.*, 0–30, 30–60 min, etc.); all seeds were regurgitated and recovered, and birds never regurgitated more seeds than they we fed them. The sample sizes we collected for these large-seeded species allowed us to calculate separate but directly comparable GRT distributions for each of the sexes. Because *Oenocarpus* and *Virola* were of similar size and had similar GRT, the two tree species were combined within each sex to calculate GRT distributions (there was no qualitative change in results when each of these tree species was analyzed separately). For *Ficus*, we recorded time elapsed between first and last defecations that had *Ficus* seeds present, but we did not count the number of seeds passed during each 30 min time interval. For this reason, we used the mean amount of time elapsed between ingestion and first and last passage per individual to calculate a probability distribution of GRT for *Ficus*. We also report GRT for *Bactris setulosa* Karst (Arecaceae) and *Otoba gordonifolia* Gentry (Myristicaceae) (Jørgensen & León-Yánez 1999, Clark *et al.* 2006) because of the relative paucity of this type of information, but these tree species were not used to calculate seed dispersal distributions.

To estimate seed dispersal distributions, we calculated separate distributions of distances moved at 30 min intervals for each individual bird and combined these distributions with the corresponding GRT distribution for that sex. This allowed us to estimate the proportion of ingested seeds each individual bird was expected to disperse at 100 m intervals. Dispersal distributions were then averaged across all individuals of a given sex to provide the summary distributions we present below. We calculated two different types of dispersal distributions for each seed type. The first, which we term 'standard distributions', estimates the probability of seeds being dispersed at given 100 m intervals relative to a fruiting tree where the seed was ingested (*e.g.*, Murray 1988). The second, which we term 'spatially explicit distributions' estimates the probability of seeds being dispersed at 100 m intervals relative to the center of an individual's home range, which in the case of males is the center of the lek. We calculated both distributions using distance intervals of 100 m because this corresponds with average lek sizes of ~1 ha (or ~100 × 100 m), such that seeds deposited within 100 m of the geographic center of a male's home range would fall within the boundaries of the lek. Please refer to the Supporting Information (Appendix S1) for details on calculation of dispersal distributions.

Empirical validation and consequences for seed survival.—To empirically validate the seed dispersal distributions, density of seeds, seedlings, and adults of all five tree species were compared at leks relative to control areas outside of leks. All five species are included in this component of the study because each is a common food source for Umbrellabirds; qualitative results of analyses restricted to *Oenocarpus*, *Virola*, and *Ficus* do not differ from those presented below. There was no difference in canopy cover, number of trees with diameter at breast height (dbh) ≥ 10 cm, mean dbh of trees, canopy height, or elevation of plots at leks vs. control areas (ANOVA's $P > 0.4$ for all tests). Lek boundaries were defined via repeated observation of banded individuals. We quantified seed rain using a total of 96 1-m^2 seed traps distributed across three leks. Seed traps were suspended 1 m above the ground and consisted of fine plastic mesh framed by thin PVC tubes. For each lek, 16 traps were randomly placed within male territories and eight pairs of control seed traps were placed at 50 m intervals along each of two transects beginning 100 m from the boundary of each lek (*i.e.*, 16 control traps/lek). Seed traps were collected and emptied bi-weekly and seeds identified using voucher specimens. It was noted whether the seeds could have dropped from a nearby adult into the trap; if not, seeds were assumed dispersed.

Seedling recruitment at leks and control areas was compared using 1-m^2 grids randomly located on the forest floor in each of five leks and corresponding control areas. In each lek, a 100 m transect bisecting the lek was established. Twenty-four points were randomly selected along this transect, and from each point a distance (0–20 m) and a perpendicular direction were randomly selected for grid establishment (*i.e.*, total of 24 grids/lek). Two 100 m control transects beginning 100 m from each lek's boundary were established, and 12 grids were randomly placed along each transect (total of 24 control grids/lek). Saplings (≤ 3 m high) of the target species in each grid were counted and it was noted whether the individual was dispersed or not by looking for a potential parent tree nearby. To assess probability of survival from seed to seedling in lek vs. non-lek sites, a mixed effects model with a random intercept assuming a negative binomial distribution was used to test the effect of the interaction between stage (seed or seedling) and site (lek vs. non-lek) on density of individuals; a significant interaction term in this model would suggest that a difference in survival from one stage to the next exists between lek vs. non-lek sites. Finally, relative density of adults was determined by counting all adult individuals in six 10 m radius circular plots within each of five leks and six control plots per lek, each located 100 m from the lek boundary.

RESULTS

Umbrellabird movement.—At least 40 radio tracking fixes were obtained for each of 17 adult Umbrellabirds: eight females, eight territorial males, and one floater male. The floater male was an adult whose morphology did not differ from that of territorial males. These individuals were tracked throughout periods of 137.9 ± 15.3 d (mean ± SE, range: 36–251 d) during which 93.8 ± 8.8 fixes were obtained in 20.5 ± 2.3 tracking sessions per individual.

There was no difference in overall home ranges of territorial males vs. females (MCP areas: 37.84 ± 7.37 vs. 49.18 ± 8.47 ha, respectively; nested ANOVA with sex (year): $F_{3,10} = 0.50$, $P = 0.6940$; Figs. 1A and B). Territorial males, however, had significantly smaller core usage areas than did females, as estimated by 95 percent kernels (7.33 ± 2.41 vs. 37.30 ± 6.22 ha; $F_{3,10} = 19.37$, $P = 0.0002$) and 50 percent kernels (1.03 ± 0.17 vs. 4.74 ± 0.58 ha; $F_{3,10} = 38.58$, $P < 0.0001$) (Figs. 1C and D). In other words, despite having similar overall home ranges to females, territorial males spent more time in a smaller portion of their range. Further examination of the 95 percent and especially 50 percent kernel estimates reveals that territorial males centered

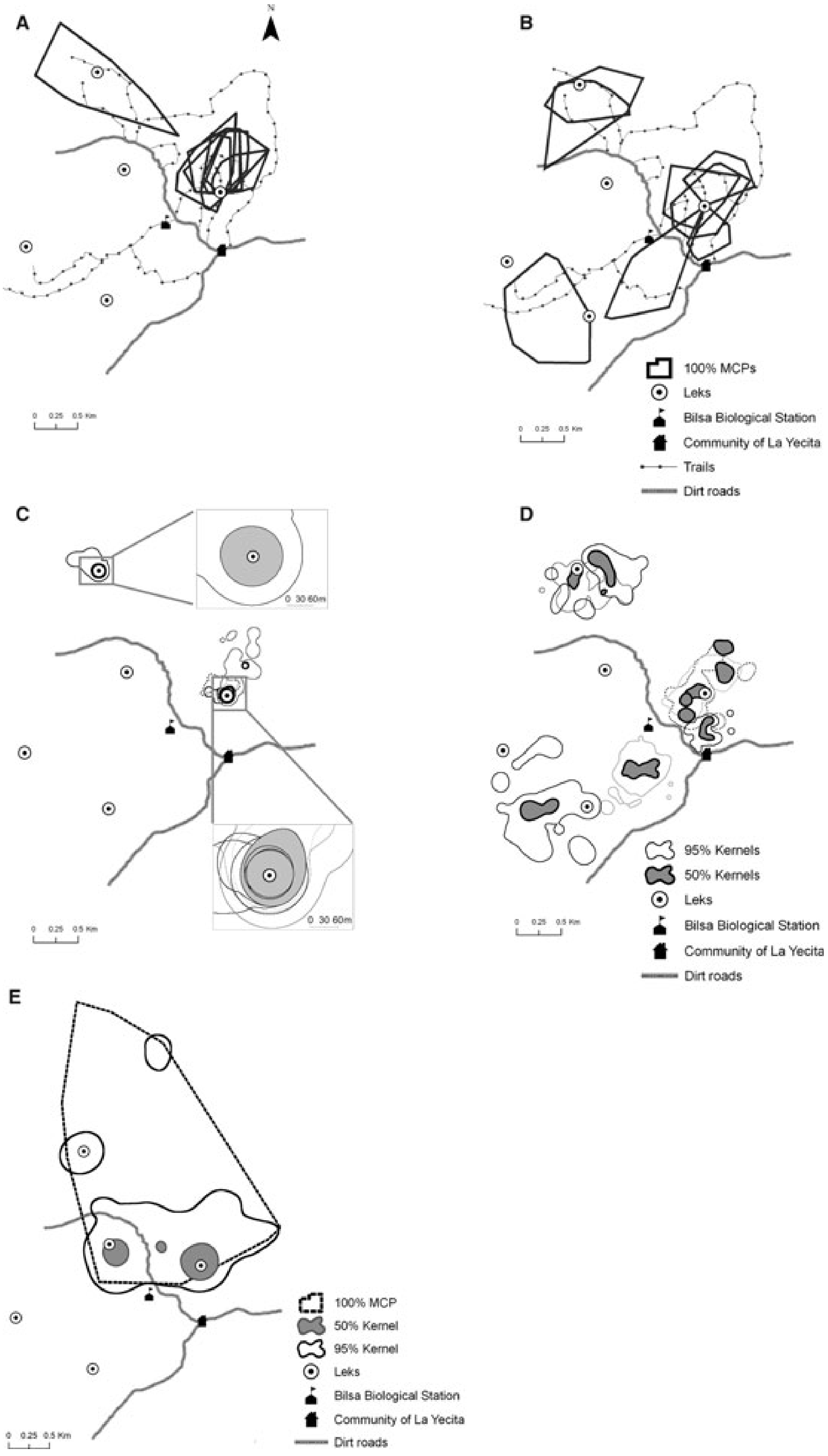

FIGURE 1. Home range usage patterns by lek-breeding Long-wattled Umbrellabirds in northwest Ecuador. Unweighted minimum convex polygon (MCP) estimates of overall home range size did not differ among males (A) or females (B). In contrast, 95 and 50 percent kernels, which weight home range estimates by usage patterns, demonstrate that male movement (C) is heavily concentrated in and around lek sites whereas female movement (D) is more evenly distributed across their home ranges; the two insets in (C) show concentration of 50 percent kernels (core usage areas) for multiple males around the center of the leks. The bottom left panel (E) presents home range estimates (100 percent MCP, 95 percent and 50 percent kernels) for a single 'floater' male.

TABLE 1. *Gut retention time (GRT, time from ingestion to passage) for seeds of five species of fruit consumed by Long-wattled Umbrellabirds in northwest Ecuador. Shown are data for males* (n = *5) and females* (n = *4). Bold font is used for those species whose GRT were subsequently used to calculate seed dispersal distributions.*

	Tree species (Family)	Seed diameter Mean ± SE (mm)	Processing method	No. fruits fed	GRT Mean ± SE (min)
Males	*Bactris setulosa* (Arecaceae)	16.97 ± 0.22	Regurgitated	3	92.33 ± 3.33
	Oenocarpus bataua (Arecaceae)	22.91 ± 0.60	Regurgitated	3	70.00 ± 7.77
	Otoba gordonifolia (Myristicaceae)	32.10 ± 0.46	Regurgitated	2	97.50 ± 1.50
	Virola dixonii (Myristicaceae)	18.90 ± 0.49	Regurgitated	11	61.00 ± 10.33
	Ficus crassiuscula (Moraceae)	1.55 ± 0.04	Defecated	11	115.17 ± 12.28
Females	***O. bataua*** (Arecaceae)	22.91 ± 0.60	Regurgitated	1	105
	V. dixonii (Myristicaceae)	18.90 ± 0.49	Regurgitated	9	77 ± 8.60
	F. crassiuscula (Moraceae)	1.55 ± 0.04	Defecated	8	165.5

their movements in and around leks, whereas female movement was more evenly distributed throughout the home range.

The floater male had much larger MCP (596.27 ha), 95 percent kernel (250.10 ha), and 50 percent kernel (24.85 ha) estimates than those of territorial males or females (Fig. 1E). The floater home range included multiple leks.

IMPLICATIONS FOR SEED MOVEMENT AND DEPOSITION.—Seed dispersal distributions for each class of Umbrellabird were estimated by integrating GRT for our three focal tree species (Table 1) with movement data. Males and females exhibited distinctive GRT distributions for fruits of large-seeded tree species (*i.e.*, *Oenocarpus* and *Virola*); a third distribution (which combines data from males and females) was observed for small-seeded *Ficus* fruits (Fig. 2).

Territorial males and females had similarly shaped distributions of seed dispersal distances from the source tree for both fruit types (Figs. 3A and C) with probability of deposition decreasing in a leptokurtic manner as distance from the source tree increased. Mean dispersal distance from the source tree by territorial males, however, was slightly longer than that of females for both large-seeded fruits (257 vs. 218 m, respectively) and *Ficus* sp. (326 vs. 244 m). For both fruit types, maximum dispersal distance was also greater for territorial males than that for females (1338 vs. 1108 m).

In contrast, territorial males and females exhibited strikingly different seed dispersal distributions relative to lek or territory centroid (*i.e.*, ‘spatially explicit’ distributions). Territorial males were estimated to deposit ~50 percent of seeds of both fruit types into the lek, whereas females were estimated to deposit most seeds >200 m from the territory center (Figs. 3B and D). This leads to a qualitative difference between the sexes in the spatially explicit dispersal distributions: probabilities of seed deposition by territorial males decline in an exponential-like fashion as distance from lek increases, while for females this distribution is bell-shaped with a mean of ~300 m from territory center. Mean dispersal distance from centroid by territorial males is shorter than that of females (259 vs. 325 m for large-seeded fruits and 330 vs. 286 m for *Ficus*, respectively), although maximum dispersal distance remains greater for territorial males (1129 vs. 853 m).

The single floater male exhibited a third type of dispersal distribution distinct from those of territorial males and females, with few seeds deposited close to the source tree and a much higher incidence of long-distance dispersal. 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 (Fig. 3E). In the spatially explicit distribution, ~20 percent of large seeds were estimated to be deposited in the lek by the floater male, whereas no *Ficus* seeds were estimated to be deposited within 200 m of the lek (Fig. 3F). Mean dispersal distance in these spatially explicit models was 877 m for large-seeded species and 942 m for *Ficus*; maximum dispersal from the lek was 2008 m.

EMPIRICAL VALIDATION AND CONSEQUENCES FOR SEED SURVIVAL.—Congruent with seed dispersal distributions, numbers of seeds and seedlings of focal tree species were higher in leks than in control sites (Wilcoxon $Z = 3.94$, df = 1, $P < 0.0001$, and $Z = 2.76$, df = 1, $P < 0.01$, respectively; Fig. 4). In addition, a higher proportion of both seeds and seedlings were dispersed into lek sites relative to control sites ($\chi^2_1 = 60.64$, $P < 0.0001$, and $\chi^2_1 = 8.87$, $P < 0.01$, respectively). There was no significant interaction effect between plant stage (seed vs. seedling) and site (lek vs. non-lek) on density of individuals ($Z = 0.80$, $P = 0.43$, $n = 336$ observations), indicating that probability of survival from seed to seedling is similar at leks and non-lek sites. Density of adult trees of focal tree species did not differ between lek and control sites ($Z = -1.23$, df = 1, $P = 0.22$).

DISCUSSION

This study refines our mechanistic understanding for how differences in frugivore behavior, even among individuals of the same species, can drive important consequences for seed movement, deposition, and survival. In the case of the Long-wattled Umbrellabird, differing reproductive strategies in the context of a

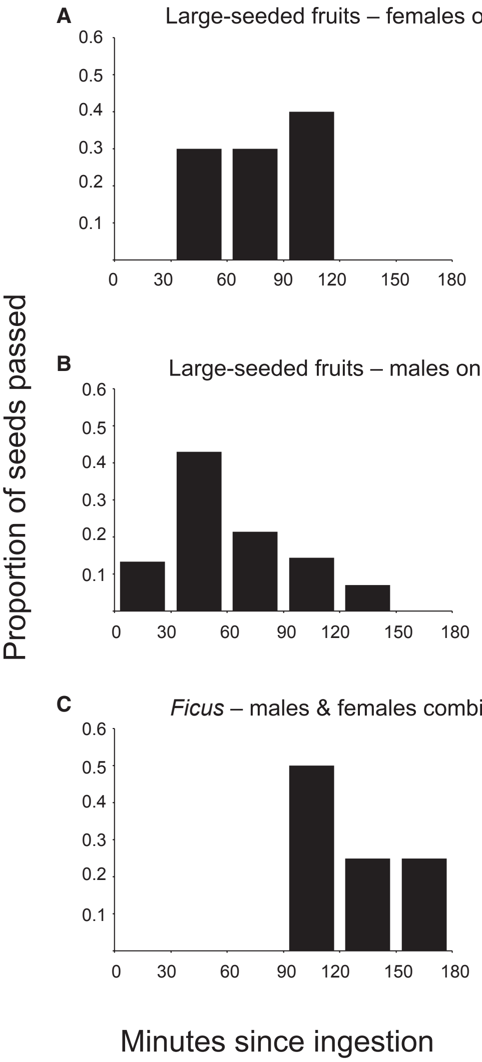

FIGURE 2. Distributions of gut retention time (GRT) by Long-wattled Umbrellabirds used to calculate seed dispersal distributions. (A) and (B) depict the distribution of GRT for large-seeded tree species (*Oenocarpus bataua* and *Virola dixonii*) by female and male Umbrellabirds, respectively. (C) depicts a single GRT distribution for *Ficus crassiuscula* that combines data from female and male Umbrellabirds.

lek-mating system yield distinctive movement patterns for males and females. Males of lek-breeding species are expected to maximize lek attendance to increase reproductive success (Fiske *et al.* 1998), but must leave their display territories to forage away from the lek. Radio tracking revealed that these 'territorial' male Umbrellabirds spent most of their time at the lek, but undertook foraging trips of varying length and direction before returning to the lek by the end of the day. As a consequence, these males maintained relatively large overall (MCP) ranges, but focused most of their time in very small core usage areas centered at the lek. In contrast, females in lek-breeding species are often solitary and visit leks only to select a mate and copulate (Westcott 1997, Durães *et al.* 2007). Female Umbrellabirds maintained home ranges with slight overlap and exhibited no discernable diurnal movement pattern across these ranges; this resulted in significantly larger core usage areas for females relative to males even though there was no difference in overall home ranges between these two classes of birds.

Frugivore movement is likely to have important implications for seed movement and deposition (Holbrook & Smith 2000, Westcott & Graham 2000). This study introduces a spatially explicit method for calculating seed dispersal distributions that uncovered biologically meaningful differences in dispersal not captured by traditional methods based on Murray (1988). The traditional method yielded similar dispersal distributions for males and females, with most seeds deposited within 200 m of the source tree. When we estimated dispersal distributions, however, in a spatially explicit context—relative to the territory center, which in the case of males was the lek—we uncovered dramatic differences between the sexes. Males were expected to deposit approximately half of ingested seeds within the lek, which is in turn magnified by the fact that 5–15 males bring seeds back to the same lek, whereas females distribute seeds more evenly throughout their territories. Corroborating the expected dispersal distributions for males, we recorded significantly higher densities of seeds and seedlings of our target tree species in leks relative to control areas located outside the leks. As such, this study provides a clear linkage between mating behavior and seed dispersal outcomes, as mediated by movement.

An alternative male reproductive strategy reported for lek-breeding species but still not well understood is that of the 'floater' male (Théry 1992, Westcott & Smith 1994, Tello 2001). These males, which are often young, move between leks within a single season without holding a fixed display territory. In our study a single adult floater male visited at least three leks and maintained a home range one order of magnitude larger than those of 'territorial' males and females. The movement pattern exhibited by the floater male yielded long seed movement distances, with a relatively low proportion of seeds deposited into leks. Although represented by only a single individual, the case of the floater male further underscores the role that reproductive behavior, as mediated by movement, may have on seed dispersal outcomes.

Field-based estimates of GRT, including those presented herein, are often based on relatively small sample sizes. As such, it would be useful to better understand how variation in GRT impacts seed dispersion estimates. Within each panel of Figure 3, identical movement data were used to calculate dispersal distributions for both large-seeded species and *Ficus*. As such, any differences between seed types within a given panel are directly attributable to variation in GRT. GRT variation did not affect the qualitative results of this study for territorial males and females. We did, however, consistently obtain longer dispersal estimates for *Ficus* within each panel, which is likely to be biologically relevant given the importance of thickness of the tail of dispersal kernels (Nathan 2006). This trend was modest within territorial males and females, but pronounced within the floater male. Within a tracking session, the floater male often moved rapidly

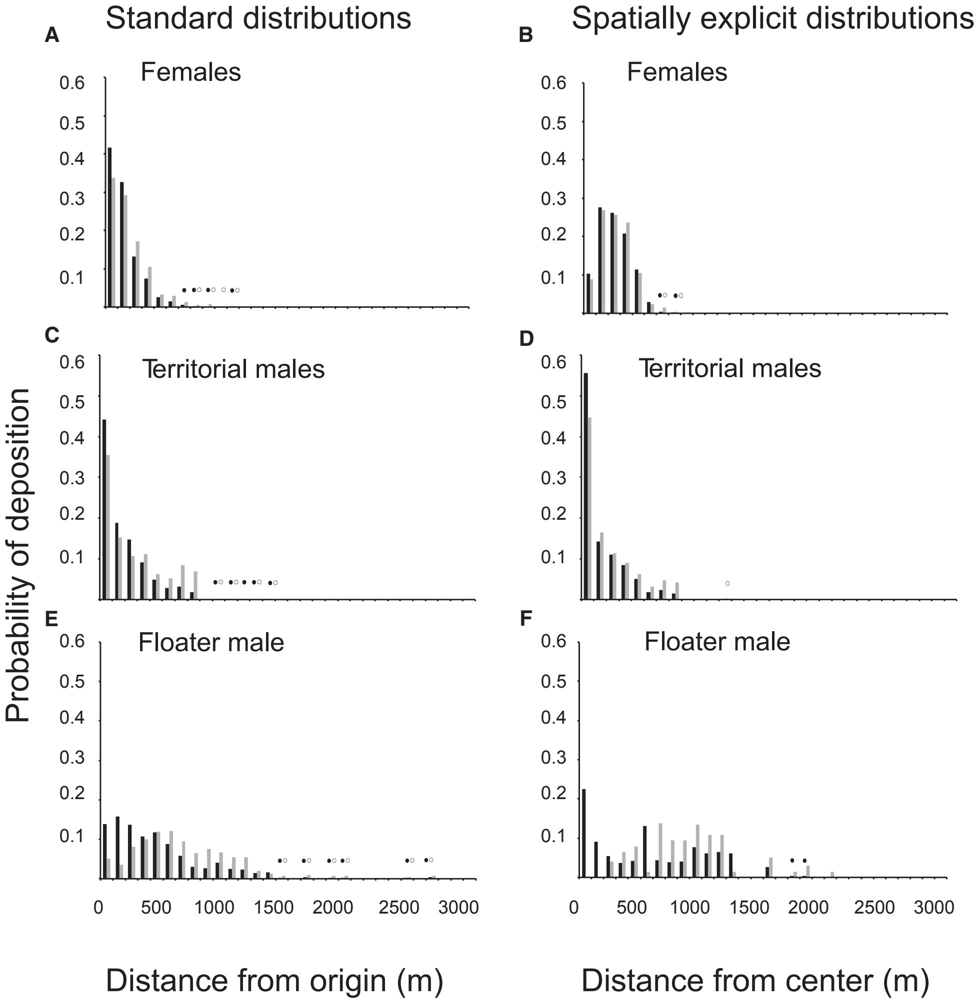

FIGURE 3. Seed dispersal distributions generated by Long-wattled Umbrellabirds for large, regurgitated seeds (*Oenocarpus bataua* and *Virola dixonii*, represented by dark bars) and small, defecated seeds (*Ficus crassiuscula*, represented by light bars). Panels on the left present the estimated distances seeds are dispersed from the parent tree (origin) by (A) females, (C) territorial males, and (E) floater male. Panels on the right present 'spatially explicit' seed dispersal distributions in relation to (B) home range center by females, (D) center of home lek by territorial males, and (F) center of most recently visited lek for floater male. For all distributions, circles (● and ○) refer to non-zero values <0.01 for large and small seeds, respectively.

over long distances in a uni-directional manner (*e.g.*, from one lek to another), while territorial males and females engaged in non-linear movements (*e.g.*, circular foraging trips that originate and terminate in the same location). We propose that these differences in directionality by the floater male vs. territorial males and females may explain why the relative impact of GRT on dispersal estimates was greater in the floater male. Future studies of seed dispersal in this system might explore this relationship using more sophisticated measures of movement, increased sample sizes to estimate GRT for a broader range of tree species, and/or simulations of how different GRT distributions impact dispersal outcomes.

Tests of the Janzen-Connell hypothesis (Janzen 1970, Connell 1971) often neglect to distinguish between density-dependent and distance-dependent mortality because they assess survival of seeds clumped beneath the parent tree. The clumped distribution of seeds at Umbrellabird leks provides an opportunity to test for density-dependent effects on seeds already dispersed away from the parent tree. The lack of any detectable effect of clumping in leks on seed recruitment contrasts with data collected on *Virola calophylla* seeds aggregated under sleeping sites of spider monkeys (*Ateles paniscus*; Russo & Augspurger 2004), and suggests that leks may be favorable microsites for seed establishment that confer benefits outweighing costs of clumping. In keeping with this idea, lek sites are situated on ridge tops that are well drained and receive relatively high levels of light. Also, leks receive seeds from a relatively large number of source trees (Karubian *et al.* 2010), hinting that genetic diversity among pools of dispersed seeds may potentially reduce costs of clumping. We are currently conducting a field-based experiment designed to

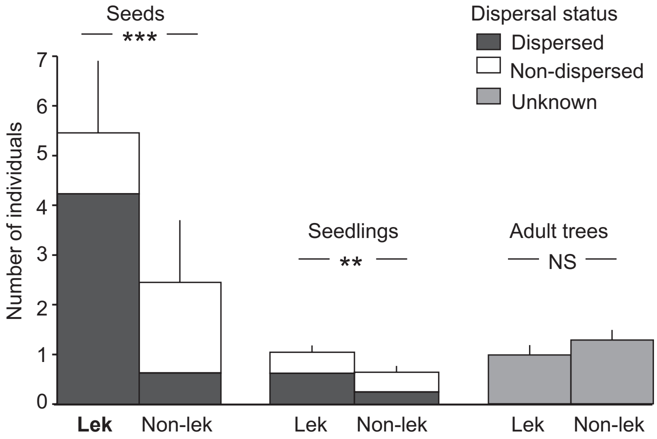

FIGURE 4. Number of seeds, seedlings, and adults of focal tree species recorded in lek sites and non-lek (control) sites. A significantly higher number of seeds and seedlings were recorded in lek sites, but there was no difference for adult trees. 'Number of individuals' on the *Y*-axis refers to the cumulative number of seeds recorded per 1-m^2 seed trap during the study period; the number of established seedlings per 1-m^2 sampling plot; and the number of adult trees per 10 m radius circular plot, as applicable. The shaded area in the bars represents the proportion of seeds and seedlings that were dispersed, and the clear portion of the bars represents proportion of non-dispersed individuals. A higher proportion of seeds and seedlings were dispersed into the lek relative to non-lek (** and *** denote statistical significance at the $P < 0.01$ and 0.001 levels, respectively).

assess the relative influence of these two parameters on seed survival.

The higher density of seeds in leks in combination with their relatively high survival suggests that male Umbrellabirds may have an ecologically meaningful effect on the spatial structure of the tree species they disperse (Russo & Augspurger 2004). We did not find more clumping of adult trees in leks relative to control sites, but this is not necessarily surprising given the highly stochastic nature of the transition from seedling to adult. These trees take many decades to mature and we know little about how long leks may persist at given locations. We have recorded two instances of leks moving >400 m in 62 lek-years of observation (5–10 yrs of monitoring each of seven leks). This uncertainty complicates tests for how Umbrellabird lekking affects spatial structure and community composition of rain forest trees because we cannot assume that an adult tree's current location reflects its proximity to a lek when it established. It is also possible that sampling at different spatial scales around lek sites and/or distinguishing between male and female individuals of dioecious species (*V. dixonii* and *O. gordonifolia*) might uncover biologically relevant patterns that we missed in the current study.

A recent molecular study (Karubian *et al.* 2010) revealed that dispersed *Oenocarpus* seed pools encountered in Umbrellabird leks exhibited higher genotypic diversity than equivalent seed pools outside the lek. This finding begs an explanation, because both field-based observation (Russo & Augspurger 2004, McConkey & Drake 2006, Koenig *et al.* 2008) and molecular analyses (Aldrich & Hamrick 1998, Grivet *et al.* 2005, Sezen *et al.* 2005, Torimaru *et al.* 2007, Garcia *et al.* 2009) suggest that vertebrate dispersal to central locations such as leks should yield genetic bottlenecks. The current study provides a solution to Karubian *et al.*'s (2010) paradoxical result. Radio tracked male Umbrellabirds made foraging trips away from the lek that potentially included multiple fruiting trees and invariably returned to their display territories on the lek after foraging. Seed dispersal distributions show that they brought most of the seeds they ingested while foraging back to the lek with them, with a relatively high frequency of long dispersal events. Female behavior, in contrast, was consistent with lower levels of genetic diversity encountered outside the lek. Females moved through their territories relatively evenly with no detectable pattern of space use throughout the day, and deposited most seeds 200–400 m from the territory center with lower densities of dispersed seeds at any one point.

Combining the dispersal services of males and females to generalize about the species, we conclude that the Long-wattled Umbrellabird is a key seed dispersal agent in the Chocó. Both female and male Umbrellabirds engaged in frequent long-distance dispersal from the source tree, with dispersal distances of at least 0.8 and 2.6 km, respectively. Umbrellabirds also provide connectivity between fragmented habitats (Sork & Smouse 2006); both males and females frequently move between primary and regenerating (secondary) forests, and we have documented males crossing secondary forest and pasture to enter isolated fragments 250 m from contiguous forest. Within continuous forest, Umbrellabird dispersal promotes gene flow and enhances genetic diversity of seed and seedling populations (Karubian *et al.* 2010). These observations suggest that the Long-wattled Umbrellabird is an ecologically important seed disperser capable of linking fragmented patches of habitat, homogenizing genetic structure in plant populations, and fostering forest regeneration in degraded areas. As with many other large-bodied vertebrates, the Long-wattled Umbrellabird is an endangered species threatened by continuing fragmentation and hunting in Chocó rain forest (BirdLife International 2000). The mechanistic understanding of the linkage between this species' mating behavior and seed dispersal presented herein can assist with conservation efforts to maintain the integrity of Long-wattled Umbrellabird seed dispersal services in the Chocó.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

APPENDIX S1. *Calculation of seed dispersal distributions.*

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