

Spatial and Temporal Patterns of Frugivorous Hornbill Movements in Central Africa and their Implications for Rain Forest Conservation

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ABSTRACT

Tropical forest conservation and restoration require an understanding of the movements and habitat preferences of important seed dispersers. With forests now being altered at an unprecedented rate, avian frugivores are becoming increasingly vital for forest regeneration. Seed movement, however, is highly dependent on the behavioral characteristics of their dispersers. Here, we examined the movements, habitat preferences, and range sizes of two African frugivores: the Black casqued (*Ceratogymna atrata*) and the White thighed (*Bycanistes albotibialis*) Hornbill, in the lowland rain forests of southern Cameroon. Using satellite transmitters, we tracked eight hornbills for 3 yr to characterize their movements and relate them to environmental landscape features. Hornbill movements differed significantly, with *B. albotibialis* ranging over larger areas (mean = 20,274 ha) than *C. atrata* (mean = 5604 ha), and females of both species covering over 15 times the area of males. Evidence suggests that movements are irruptive during particular periods, perhaps driven by low resource availability. In addition, hornbills often returned to the same localities within a year, although movements were not characterized as migratory. Both species displayed significant differences in habitat preference, with *B. albotibialis* utilizing disturbed habitat more frequently than *C. atrata* ($t = -22.04$, $P = 2.2 \times 10^{-16}$). Major roads were found to act as barriers for *C. atrata*, but not for *B. albotibialis*. The ability of both hornbill species to move large distances suggests hornbills will play a vital role in the maintenance and regeneration of rain forests in Central Africa as forest fragmentation increases and terrestrial vertebrates decline in numbers.

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

Key words: *Bycanistes albotibialis*; Cameroon; *Ceratogymna atrata*; hornbills; rain forest; satellite tracking; seed dispersal.

ANIMALS ARE WELL RECOGNIZED FOR THEIR CRITICAL ROLE IN SEED DISPERSAL OF TROPICAL RAIN FOREST TREES (Howe & Smallwood 1982, Howe 1984, Wunderle 1997, Jansen *et al.* 2012, Karubian *et al.* 2012), and vertebrate assisted seed dispersal, a key process that drives forest diversity and genetic structure, has been negatively impacted by human activities such as fragmentation and habitat degradation (Wang & Smith 2002). As humans continue to modify tropical landscapes, it is crucial to understand how these changes may affect the range and movements of important seed dispersers. Long distance seed dispersers, including large bodied mammals and birds, are particularly important for maintaining tropical tree populations (Howe 1984, 1986, Holland *et al.* 2009, Ruxton & Schaefer 2012, Mueller *et al.* 2014). However, in Central African rain forests, the spatial and temporal scale of long distance movements by large avian frugivores remains

poorly understood, despite their significant influence as dispersers on forest ecosystems and community structure.

In the southern rain forests of Cameroon, large hornbills in the genus *Ceratogymna* (Gonzalez *et al.* 2013) are important seed dispersers (Whitney & Smith 1998, Poulsen *et al.* 2002), both quantitatively they disperse 20 percent of the major tree species (Whitney *et al.* 1998) and qualitatively over 80 percent of seeds they ingest move well beyond the canopy of the parent tree (Holbrook & Smith 2000). *Ceratogymna* hornbills have been shown to track fruit resources (Whitney & Smith 1998) and make large scale movements, *e.g.*, up to 290 km (Holbrook *et al.* 2002). These movements are generally larger than the ones recorded for South African (Lenz *et al.* 2011, Mueller *et al.* 2014) or Asian hornbills (Kinnaird & O'Brien 2007), which also play a major role in seed dispersal in their respective landscapes. Holbrook *et al.* (2002) provided important insights on the extent of West African hornbill movements, suggesting hornbills may not only play a fundamental role in dispersing seeds within forest reserves,

but also help maintain regional tree species diversity by dispersing seeds from primary forest to secondary forests and agricultural areas. As a result of hunting pressures, the southern rain forests of Cameroon are losing many of their largest frugivores, particularly elephants and many primate species (Muchaal & Ngandjui 1999, Chapman *et al.* 2006, Wang *et al.* 2007, Maisels *et al.* 2013). Given these declines of mammalian frugivores, hornbills are likely to play an increasingly vital role in the general maintenance of tropical forests and the potential for forest regeneration in many parts of the Central Africa.

While numerous factors contribute to the movement patterns of seed dispersers in tropical forests (Fleming 1992, Schaik *et al.* 1993, Jordano 2000), Leighton and Leighton (1983) offered three hypotheses to explain correlations between cyclical declines in vertebrate dispersers and reduced fruit production. They postulated that species that did not switch their diet would need to move to find adequate resources and would exhibit either migratory behavior, nomadic behavior, or large home range expansions. To explore Leighton and Leighton's hypotheses, we used satellite telemetry to examine the movements of two of the largest African frugivorous hornbills, *Ceratogymna atrata* (Black-casqued Hornbill, BC) and *Bycanistes albotibialis* (White-thighed Hornbill, WT), over 3 yr in southern Cameroon. We characterized hornbill movements and habitat use in relation to both natural and human altered landscapes, measured the extent of their movements across multiple seasons, and assessed habitat preferences in relation to mature and human altered rain forests. We hypothesize that if: (1) species show migratory behavior, the timing of movements should be seasonal and should be in a similar direction, with individuals returning to the same areas; (2) hornbills are nomadic, there should be no consistent directionality of movement and birds may not necessarily return to the same geographic localities from which they came; and (3) ranges of hornbills simply expand and contract seasonally, directed long distance movements should not be observed.

METHODS

STUDY AREA. Southern Cameroon is characterized by semi-deciduous lowland tropical forest (Letouzey 1968), and ranges in elevation from 400 to 800 m, with an annual rainfall of 1600 mm that is bimodal with a large peak occurring in September-October and smaller peak in April-May. The study region encompasses the Dja Biosphere Reserve and surrounding areas, and includes intact mature forest, disturbed secondary forest, and northern savanna forest ecotone. The study region varies considerably with respect to carbon biomass, with the highest levels in intact mature forests and lowest levels in anthropogenically transformed areas including deforested or degraded lands (Mitchard *et al.* 2009, Saatchi *et al.* 2011).

HORNBILL CAPTURE AND SATELLITE TRACKING. We captured 15 hornbills using pulley-mounted mist nets installed in the canopy near actively fruiting trees, which allowed us to capture individuals as they arrived to feed. We attached three to four mist nets

(227 mm mesh, 12 m × 2.8 m) to each other top to bottom to create a single stacked net as previously described (Holbrook & Smith 2000). Net height depended on the fruiting tree in question, but generally ranged between 20 and 40 m. We fitted the dorsum of each bird with a GPS-enhanced solar backpack PTT (Platform Transmitter Terminal) using a 9/16" kevlar ribbon and secured it using polyester thread (Kenward 2001). We fitted ten adults and one juvenile *B. albotibialis* with an average body mass of 987 g with transmitters weighing 22 g each (Model PTT 100, Microwave Technology Inc., Columbia, MD, U.S.A.), or 2.2 percent of the birds' body mass. We fitted three adults and one juvenile *C. atrata* with an average body mass of 1077 g with transmitters (Model 30GPS, North Star Science and Technology LLC, King George, VA, U.S.A.) weighing 30 g each, or 2.8 percent of the birds' body mass. Because each transmitter weighed less than 3 percent of the bird's mass, it was unlikely to affect bird movement and/or survivorship (Cochran 1980). We programmed transmitters to collect no fewer than two fixed points daily and continually tracked and measured distance and directionality. Transmitters attached to females and males were programmed with a duty cycle (the time the transmitter actively sends a signal to the satellite) of 10 d for females and 6 d for males; the extended cycle for females helped to conserve battery power during periods of nesting, in which females remain in cavities for up to 3 mo.

Of the 15 hornbills fitted with transmitters, we successfully analyzed movement data for eight individuals. Long-term data were not available for the remaining individuals either due to the hornbill removing the transmitter, death of an individual due to hunting, battery failure, or other unknown reasons. Of the eight transmitters for which long-term data were obtained, five were deployed on *B. albotibialis* (three males and two females), and three on *C. atrata* (two males and one female). For each data point received, there was an accompanying estimated error based on the quality of the satellite signal. For all transmitters and location data, we analyzed only those returned data with estimated errors of <250 m, ensuring equality between location data from different transmitter types. We collected and analyzed data from start dates through March 2012.

TEMPORAL AND SPATIAL VARIATION IN HORNBILL MOVEMENT PATTERNS. We estimated the area that hornbills utilized using a convex hull estimate (after removing 5% of outlier points) using the *adehabitatHR* package in R (Downs & Horner 2009, R Development Core Team 2011), as well as a minimum convex polygon method (Worton 1995, Fig. S1). We report the convex hull estimate as the best estimate of area utilized, as minimum convex polygon estimates were less accurate due to a high number of outlying points relative to the inner points (Worton 1995). Individual tracking periods ranged from 269 to 1134 (mean = 748) days per individual. We estimated range sizes using 2082 (mean = 560) locations for *B. albotibialis* and 1027 (mean = 342) locations for *C. atrata*.

To examine the trajectories and distances traveled by each individual between GPS points, we used *adehabitatLT* (Calenge 2006) in R. We then plotted these data to track each individual

across the landscape. The trajectories sampled are the angles traversed by the animal as it moves between locations. We overlaid these trajectories on a map of forest cover to assess how frequently hornbills visited forested areas as measured by biomass (see below). To determine the percent of time hornbills spent moving relative to the time spent resting at a single location, we used the *adehabitatHR* package (Calenge 2006) in R. We also analyzed the distance traveled per bird per month to assess whether certain seasons were characterized by extensive bursts of movement.

To determine the ability of hornbills to traverse natural or anthropogenic features of the landscape, we determined whether birds crossed major rivers, roads, or villages. We utilized a roads data base that was constructed by digitizing satellite images from 2005 to 2010 and mapping with a GPS unit on the ground in areas where cloud cover precluded the use of satellite images (WRI 2012). Anthropogenic features such as villages and paved or unpaved roads in the vicinity of the Dja were further verified by on the ground observation. Rivers were mapped with synthetic aperture radar, which is an effective tool for delineating water bodies in forests with persistent cloud cover such as those found in southern Cameroon (Arnesen *et al.* 2013).

To examine whether seasonal rainfall patterns could help explain movements during an annual cycle, we tested for correlations between rainfall and movement using the R library *acf* (R Development Core Team 2011) at various time lags (0 time lag as well as monthly lags up to ± 9 mo between rainfall and movement). Precipitation data were obtained from NOAA's Climate Prediction Center and are the quantitative estimate of precipitation combining METEOSAT, Global Telecommunication System data, and ground station precipitation data. Precipitation estimates were available every 10 d, which is similar to the duty cycles of our satellite tags (Xie & Arkin 1997).

HABITAT PREFERENCES. We analyzed satellite images of the study region to determine the environmental characteristics of sites frequented by hornbills. A high resolution biomass layer was used that contained values ranging from 0 to 454 Mg/ha (Baccini *et al.* 2008). From field observations and previous research in the area (Holbrook & Smith 2000, Holbrook *et al.* 2002, Smith *et al.*

2013), we defined 'disturbed' habitats as having biomass values between 1 and 120 Mg/ha and excluded 0 values as this was the value given to water bodies (Baccini *et al.* 2008). We created a mask to identify these anthropogenically altered habitats and calculated the Euclidean distance from each individual hornbill location to altered habitats. We ran a *t* test in R (R Development Core Team 2011) to determine whether the two species' proximities to disturbed areas were significantly different.

RESULTS

TEMPORAL AND SPATIAL VARIATION IN HORNBILL MOVEMENT PATTERNS. The spatial extent of the area that the two hornbill species used varied widely from 365 to 71,645 ha, with a mean area of 14,773 ha (Table 1). *Ceratogymna atrata* movements varied more than 30 fold (412 13,971 ha; mean 5604 ha), but were nevertheless smaller and much less variable than those of *B. albotibialis*, which varied 200 fold (365 71,645 ha; mean 20,274 ha). Although sample sizes for each species are limited, female ranges were on average four times larger (mean of 45,897 ha for *B. albotibialis*, 13,971 for *C. atrata*) than those of males (mean of 3192 ha for *B. albotibialis*, 1420 ha for *C. atrata*). Individuals showed considerable variation in the distance traveled and the amount of area used (Fig. 1). For example, from the points where they were tagged, adult male hornbill WT 37 traveled only 27 km spanning an area 365 hectares in size, while male hornbill BC 07 traveled 38 km spanning 412 ha values almost an order of magnitude smaller than other individuals. It is doubtful that these small range sizes were due to low sample size because each individual was tracked for at least 36 mo. For hornbills traversing these larger areas (>100 ha), data suggest that 'burst movements', defined here as movements occurring in a time period of less than 15 d, represented a large percentage of the total area covered (Fig. 2). For example, WT 39 traveled over 223 km in only 14 d between 29 October and 12 November 2009. We also found that species differed in cardinal direction traveled; the majority of *C. atrata* individuals moved in a south or southeast direction, while *B. albotibialis* individuals (with the exception of individual WT41) moved in a northeastern direction during initial movements (Fig. 1).

TABLE 1. Characteristics and movement summaries of *Bycanistes albotibialis* and *Ceratogymna atrata* during study period.

Species	Hornbill	Age	Sex	Convex Hull (ha)	Distance Per Day (km)	#Locations	#Days	Tracking Period
<i>B. albotibialis</i>	WT 33	Adult	Female	20,149	2.13	280	364	9/11/2009 7/10/2010
	WT 34	Adult	Female	71,645	0.80	641	647	7/3/2009 4/11/2011
	WT 37	Adult	Male	365	0.69	967	974	7/1/2009 3/1/2012
	WT 39	Adult	Male	6,098	1.56	651	683	9/10/2009 7/25/2011
	WT 41	Adult	Male	3,112	1.45	263	269	9/11/2009 6/7/2010
<i>C. atrata</i>	BC 03	Juvenile	Male	2,428	1.5	483	1007	6/23/2009 3/26/2012
	BC 07	Adult	Male	412	3.6	324	1134	2/15/2009 3/25/2012
	BC 09	Adult	Female	13,971	4.7	220	906	9/18/2009 3/12/2012

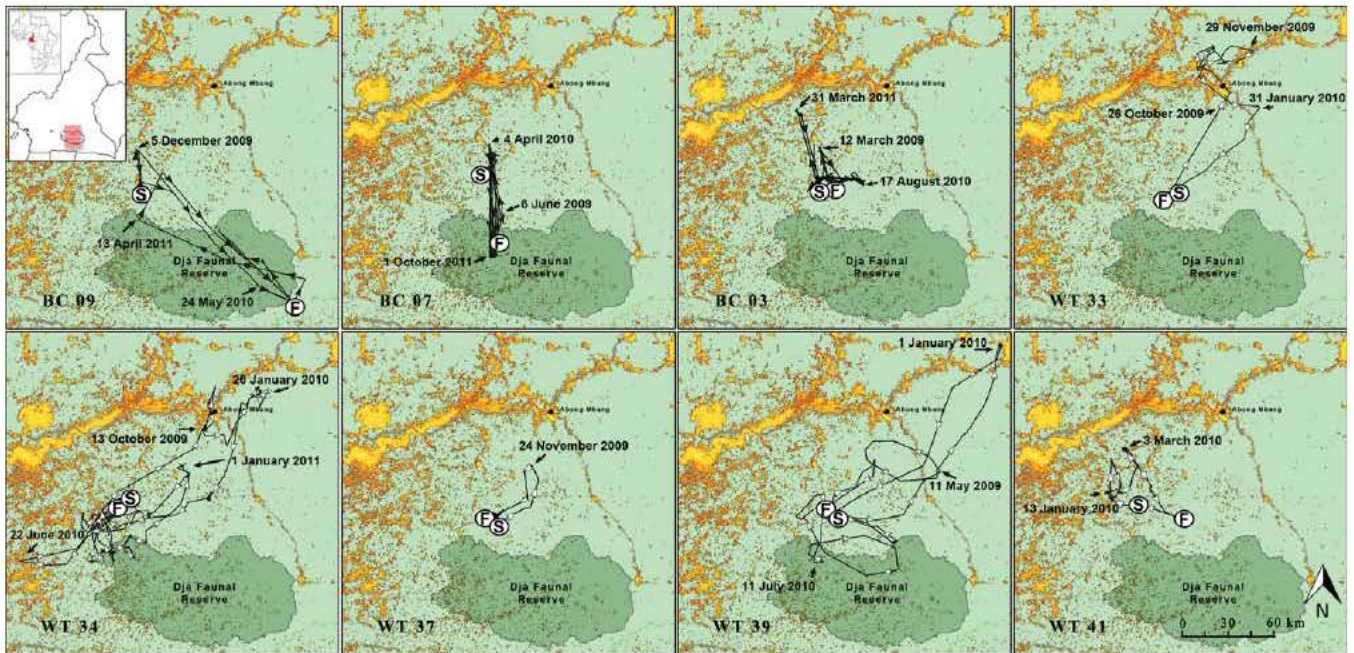


FIGURE 1. Hornbill movements relative to the Dja Biosphere Reserve, Cameroon. *Bycanistes albotibialis* (White-thighed Hornbills, WT) movement depicted by white arrows, *Ceratogymna atrata* (Black-casqued Hornbills, BC) are depicted by black arrows. Start dates indicated by S and end dates by E. Yellow regions reflect areas of low biomass and light green areas depict areas of higher biomass, with highest biomass estimated in the Dja Reserve.

We found no consistent annual or monthly relationship between precipitation and burst movement, even when accounting for potential lag times. However, when we pooled data across all individuals of both species, we found a pattern of increased burst movements during the major dry season (December, January, and February) of the first year ($N = 8$). Additionally, in the following year's main dry season, all but one of the individuals (WT 37) showed some burst movements ($N = 6$). However, during the final year of tracking, we did not observe these same burst movements from any of our remaining tracked individuals ($N = 4$) during the major dry season, despite precipitation being similar in magnitude and timing. In general, hornbills demonstrated great variability in their movements, often associated with large distances traveled, but with little evidence of synchronous seasonal movements. However, movements were not nomadic as many individuals returned to the location where they had been originally tagged (Fig. 1).

The two species of hornbills differed in their movement patterns with respect to proximity to human infrastructure such as villages or major roads. The major roads considered here are high traffic national and regional roads such as the Cameroon N10. These roads are either paved or large enough to create forest gaps that are 110 m wide on average (standard deviation: 13 m). *Bycanistes albotibialis* crossed major roads frequently and passed close to villages (Fig. 1), while *Ceratogymna atrata* never crossed major anthropogenic features, such as roads or large villages. *Ceratogymna atrata* also tended to avoid anthropogenic breaks in the forest, major rivers, although individuals did cross the Dja and

Nyong Rivers, an average of 6.44 times/year and 7.25 times/year, respectively.

HABITAT PREFERENCES. Hornbills showed marked differences in landscape use, with the mixture of primary and disturbed habitats used (as defined by biomass). *Bycanistes albotibialis* was found in fragmented landscapes more often than *C. atrata* individuals (Fig. 3, Welch Two Sample t test, $t = 26.93$, $P < 0.01$) and moved greater distances from the initial tagging locations to access fragmented areas. For every geolocation recorded for *B. albotibialis* ($N = 2082$), individuals were always located within 10 km of these fragmented habitat types. In contrast, *C. atrata* locations were recorded at significantly greater Euclidian distances from disturbed forest habitats (Welch Two Sample t test, $t = -22.04$, $P = 2.2 \times 10^{-16}$).

DISCUSSION

Large forest hornbills are important members of the Central African seed dispersing community. The two species examined disperse the seeds of 18 and 20 percent of the tree flora, respectively, and deposit only a small percentage of seeds beneath parent trees (Whitney *et al.* 1998, Holbrook & Smith 2000). The importance of hornbills and other avian seed dispersers is expected to increase in the future as populations of mammalian dispersers, such as elephants and primates, decline (Muchaal & Ngandjui 1999, Chapman *et al.* 2006, Wang *et al.* 2007, Maisels *et al.* 2013). Mammalian seed dispersers, particularly duikers and

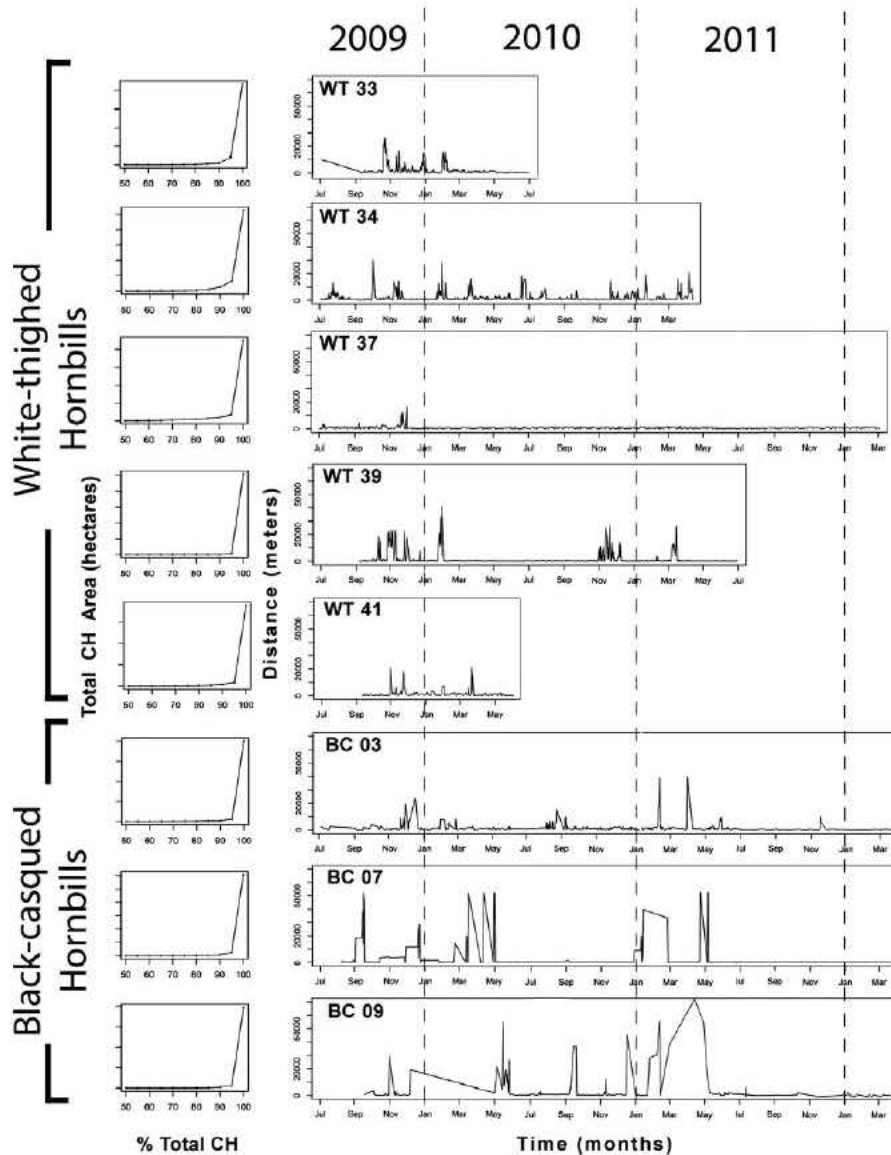


FIGURE 2. Hornbill movements through time and percent utilization of home range in southern Cameroon from 2009 to 2011. Left panels show the percent of total home range area used in calculating the convex hull on the x -axis compared with the total area. Right panels show individuals movement patterns through time, with peaks representing burst movements.

elephants, typically avoid roads (Laurance *et al.* 2006, Buij *et al.* 2007, Blake *et al.* 2008). This, combined with recent increases in human population, anthropogenic barriers, and illegal poaching, threatens to seriously diminish the role of effective mammalian seed dispersal (Wright *et al.* 2007). Previous studies on the overlap between bird and mammal fruit consumers indicate that while the fruit diet shared by hornbills and primates can be substantial (38% [Astaras & Waltert 2010, Poulsen *et al.* 2001, Mitani 1999, 1–3]), the degree of overlap with elephants is significantly less [8%, (Mitani 1999, Yumoto & Maruhashi 1995)]. Thus, the potential for hornbills to provide seed dispersal services typically performed by primates is considerably greater than those provided by elephants. Faced with further mammalian habitat loss

and human encroachment, avian species may represent one of the few remaining effective seed dispersers in the region.

We do not know how changes in the types of seed disperser community may affect forest composition a topic worthy of further study. However, in many regions, avian species represent the only dispersers that have yet to be extirpated by hunting. Mammalian seed dispersers such as elephants are classified as 'Vulnerable' on the Red List and primates, including chimps and bonobos, are listed as 'Endangered' (IUCN 2014). The Red List classifies WT and BC hornbills as 'Least Concern', and movements of hornbills are generally less impeded by fragmentation than those of large mammals. However, in at least one of these species (*C. atrata*), effective seed dispersal is still likely to be

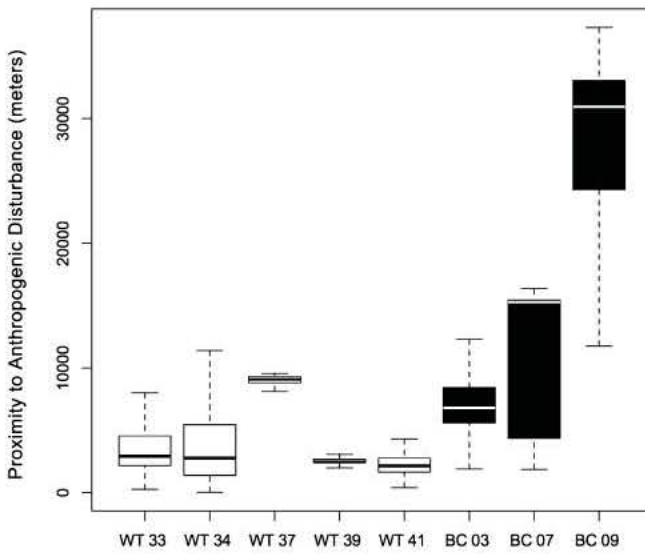


FIGURE 3. Individual hornbill locations and their proximity to anthropogenic areas (disturbed habitat), which includes villages, roads, and agricultural areas. Horizontal bars within boxplots represent median of proximity to anthropogenic disturbance, and boxes extend to the first and third quartiles. Whiskers indicate full extent of data.

limited by anthropogenic activities, given the tendency of this species to avoid human dominated landscapes and roads. An emerging issue is the hunting of hornbills while this practice was quite rare in the region in the 1980s and 1990s, with fewer primates and duiker remaining, the hunting and selling of hornbills for food is becoming more common (T. Smith, pers. obs.), as is illegal international trade (Trail 2007).

Movements in response to resource scarcity may be categorized in various ways (Leighton & Leighton 1983); these include true migratory movements, nomadic movements, or expansions of range size. Our results show little support for true migratory behavior in hornbills. Movements did not occur synchronously or in significant association with any particular temperature or precipitation cues. However, seasonal and inter annual fruiting patterns are a distinctive characteristic of the region (Whitney & Smith 1998, Holbrook & Smith 2000, Stauffer & Smith 2004, French & Smith 2005). Further work will be necessary to determine if these complex fruiting cycles drive long distance movements of large frugivores.

There was evidence of burst or irruptive movements consistent with those seen in relation to fluctuations in food abundance (Newton 2008). Irruptive movements typically occur from areas of low food abundance to areas with greater food availability, generally north to south in northern latitudes, as in boreal finches and owls (Newton 2008). The directionality observed in the first year of this study could be in response to food availability, but without quantitative data on resources one can only speculate. Interestingly, the movements observed by Holbrook *et al.* (2002) were in a different direction (southward), suggesting the directionality of long distance movements may vary between years.

Previous research also found that *C. atrata* and *B. albotibialis* numbers are greater in regions with high fruit availability than low fruit availability (Whitney & Smith 1998). But as fruit abundance was not quantified in this study, it was not possible to examine movement patterns as a function of fruit abundance. Nevertheless, previous studies do suggest that hornbill species move in response to fruit availability and support the keystone role that these species play in dispersing seeds. Given that burst movements occurred predominantly in the dry season when fruit availability is generally low suggests that hornbills may undertake large distance movements in search of fruit resources. However, additional research will be necessary to fully understand the main drivers of long distance movements and inter annual variation in directionality.

While movements were not synchronous between individuals, hornbills did return to previous locations, suggesting they were not strictly nomadic. Returning to nesting habitat may be the result of a lack of suitable nesting habitat in other parts of these species' ranges, as hornbills require nesting cavities, in particular ecological regions (Newton 1994). Hornbills did tend to return to areas where they previously bred and were initially tagged. The smaller ranges observed for males as compared with ranges for females may result from the need for males to return sooner to defend nesting cavities (Stauffer & Smith 2004). The amount of areas used by hornbills varied by orders of magnitude, and was significantly larger than ranges previously reported for these species (Holbrook & Smith 2000). In fact, the range estimates for hornbills we recorded are some of the largest reported of any tropical frugivorous bird (Howe 1986, Holbrook *et al.* 2002, Kitamura *et al.* 2008, Kitamura 2011, Mueller *et al.* 2014).

Roads are important barriers to movements of seed dispersing mammals and birds in the tropics (Benítez López *et al.* 2010). Both species of hornbills studied here are capable of dispersing seeds over long distances across natural barriers such as rivers, making them important for maintaining genetic diversity of tree populations. *Bycanistes albotibialis* crossed major paved roads, suggesting it is unencumbered by barriers to dispersal that may inhibit terrestrial mammals (Laurance *et al.* 2006, Buij *et al.* 2007, Blake *et al.* 2008). The fact that this species can cross anthropogenic barriers and inhabit secondary forests (Stauffer & Smith 2004) indicates a potentially vital role for this species in seed dispersal and forest regeneration in a region that is likely to see greater anthropogenic change in the future. However, unlike *B. albotibialis*, *C. atrata* avoided disturbed habitat and roads, a pattern similar to that found in Red knobbed Hornbills (*Aceros cassidix*) studied in Sulawesi (Kinnaird *et al.* 1996).

Hornbills have the potential to move across heterogeneous habitats and distribute seeds over a large area in both intact (especially *C. atrata*) and in fragmented forests (*B. albotibialis*). While further research will be required to fully quantify the extent that these species can promote long distance seed dispersal and gene flow and aid in forest regeneration, the conservation importance of both species is likely to increase as the ecological contributions of mammalian dispersers to maintaining forest health

diminish with further hunting and accelerating anthropogenic alteration to habitats.

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SUPPORTING INFORMATION

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

FIGURE S1. Minimum convex polygon and characteristic hull representations of areas utilized by hornbills relative to the Dja Biosphere Reserve, Cameroon.

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