Movement Behaviour And Seed Dispersal Patterns Of Trumpeter Hornbills (*Bycanistes bucinator)* In Fragmented Landscapes

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To my father.

“Remember that the best relationship is one in which

your love for each other exceeds your need for each other.”

Dalai Lama
2004

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CONTENT

1 SUMMARY

Long-distance seed dispersal is a crucial process allowing the dispersal of fleshy-fruited tree species among forest fragments. In particular, large frugivorous bird species have a high potential to provide inter-patch and long-distance seed transport, both important for maintaining fundamental genetic and demographic processes of plant populations in isolated forest fragments. In the face of increasing worldwide forest fragmentation, the investigation of long-distance seed dispersal and the factors influencing seed dispersal processes has recently become a central issue in ecology. In my thesis, I studied the movement behaviour and the seed dispersal patterns of the trumpeter hornbill (*Bycanistes bucinator*), a large obligate frugivorous bird, in KwaZulu-Natal, South Africa. I investigated (i) the potential of trumpeter hornbills to provide long-distance seed dispersal within different landscape structures, (ii) seasonal variations in ranging behaviour of this species, and (iii) the potential of this species to enhance the functional connectivity of a fragmented landscape. I used high-resolution GPS-data loggers to record temporally and spatially fine-scaled movement data of trumpeter hornbills within both continuous forests and fragmented agricultural landscapes during the breeding- and the non-breeding season. First, combining these data with data on seed-retention times, I calculated seed dispersal kernels, able to distinguish between seed dispersal kernels from the continuous forests and those from the fragmented agricultural landscapes. The seed dispersal distributions showed a generally high ability of trumpeter hornbills to generate seed transport over a distance of more than 100 m and for potential dispersal distances of up to 14.5 km. Seed dispersal distributions were considerably different between the two landscape types, with a bimodal distribution showing larger dispersal distances for fragmented agricultural landscapes and a unimodal one for continuous forests. My results showed that the landscape structure strongly influenced the movement behaviour of trumpeter hornbills, and this variation in behaviour is likely reflected in the shape of the seed dispersal distributions. Second, for each individual bird I calculated daily ranges and investigated differences in daily ranging behaviour and in the process of range expansion comparatively between the breeding- and the non-breeding season. I considered differences in habitat use and possible consequences resulting for seed dispersal function during different seasons. I found that within the breeding season multi-day ranges were built from strongly overlapping and nearly stationary daily ranges which were almost completely restricted to continuous forest. In the non-breeding season, however, birds assembled multi-day ranges by shifting their range site to a generally different area, frequently utilizing the fragmented agricultural landscape. Thereby, several small daily ranges and few large daily ranges composed larger multi-day ranges within the non-breeding season. Seasonal differences in ranging behaviour and range assembly processes resulted in important consequences for seed dispersal function, with short distances and less spatial variation during the breeding season and more inter-patch dispersal across the fragmented landscape during the non-breeding season. Last, I used a projection of simulated seed dispersal events on a high-resolution habitat map to assess the extent to which trumpeter hornbills potentially facilitate functional connectivity between plant populations of isolated forest fragments. About 7% of dispersal events resulted in potential between-patch dispersal and trumpeter hornbills connected a network of about 100 forest patches with an overall extent of about 50 km. Trumpeter hornbills increased the potential of functional connectivity of the landscape more than twofold and seed dispersal pathways revealed certain forest patches as important stepping-stones for seed dispersal among forest fragments. Overall, my study highlights the overriding role that large frugivorous bird species, like trumpeter hornbills, play in seed dispersal in fragmented landscapes. In addition, it shows the importance of fine-scaled movement data combined with high-resolution habitat data and consideration of different landscape structures and seasonality for a comprehensive understanding of seed dispersal function.

2 GENERAL INTRODUCTION

Human activities have a massive impact on the natural environment causing alterations to the climate, biogeochemical cycles, land cover and species distribution (Vitousek *et al.* 1997a, MEA 2005a). Humans' increasing awareness of their large impact on the environment has caused considerable interest in potential ecological consequences of anthropogenic activities (Chapin *et al.* 2000, Loreau *et al.* 2001, Hooper *et al.* 2005, MEA 2005a). Human activities strongly threaten the world's diversity of life and cause changes in species distribution and community compositions (Baillie *et al.* 2004, MEA 2005a). Overall, the human footprint dramatically affects biodiversity.

Biodiversity, human well-being and ecosystem functions

Biodiversity is the variability among all living organisms on all levels of biological organisation, encompassing genetic diversity of a species within or between populations, species diversity in species communities, diversity of communities and of entire ecosystems (CBD (article II) 1992). Loss of biodiversity could cause concern for moral and ethical reasons, but also has high potential to severely affect human well-being (Chapin *et al.* 2000, MAE 2005b, Díaz *et al.* 2006).

Biodiversity is inextricably linked to human well-being through its contribution to ecosystem functioning (MEA 2005a, Turner *et al.* 2007). Ecosystem functions provide various services fundamental for humanity (Chapin *et al.* 2000, MEA 2005a, Díaz *et al.* 2006). One way to describe these services is to categorize them into cultural, provisioning, supporting and regulating services (MEA 2005c). Cultural services encompass all non-material benefits to humans, like spiritual enrichment and reflection, recreation and aesthetic appreciation. Provisioning services are products from the ecosystem which humans obtain, such as food, fresh-water, fuel, fibre, and genetic resources. Maintaining a diversity of species and genes could include information on traits and functions potentially important in the future, e.g. for medicine or improved food resources. Regulating services emanate from regulating processes of ecosystems, such as pollution degradation, climate regulation, water purification, disease control, pollination and seed dispersal. For the production of these ecosystem services, the supporting services are necessary, such as oxygen production, primary production, soil formation and maintenance of material cycles like the carbon, hydrologic and nutrient cycles. These services are the foundation for human well-being and emanate from ecosystem functions (MEA 2005b). Alteration of ecosystem processes has strong potential to affect the functions providing services to humanity, and thus can have severe consequences for human well-being (MEA 2005b, Díaz *et al.* 2006).

Biodiversity is strongly linked to ecosystem functioning (Chapin *et al.* 2000, Loreau *et al.* 2001, Hooper *et al.* 2005 & 2012). Ecosystem functions are based on the functional characteristics of the species included in the ecosystem. Species loss could result in the loss of a specific functional trait from the ecosystem and may degrade ecosystem functioning. In general, a high diversity of species implies in a high functional diversity (Tilman *et al.* 1997). Functional diversity can increase the resilience of ecosystems in two ways - with functional redundancy and response diversity. Functional redundancy means that different species contribute similarly to a certain ecosystem function and can therefore be substituted for one another with little impact on ecosystem processes (Walker 1992, Lawton & Brown 1993). Response diversity means that functionally similar species respond differently to disturbance and thus could compensate for each other’s decline (Elmqvist *et al.* 2003). Thus, biodiversity can considerably influence the resilience of an ecosystem and its ability to provide ecosystem services under a changing environment (Chapin *et al.* 2000, Balvanera *et al.* 2006, Hooper *et al.* 2012). Therefore, a major focus of recent ecological research is to describe the link between biodiversity and ecosystem viability (Chapin *et al.* 2000), to identify the major threats to biodiversity (Sala *et al.* 2000, Thomas *et al.* 2004) and to understand the natural processes maintaining biodiversity and ecosystem functioning under global environmental changes (Bascompte & Jordano 2007, Montoya *et al.* 2010).

Threats to biodiversity

Current species loss is estimated to be 100- 1,000 times higher than the natural background extinction rate (Pimm *et al.* 1995, Barnosky *et al.* 2011) and human activities are the leading cause of the largest part of current species loss (Vitousek *et al.* 1997a, MEA 2005a). The major threats to biodiversity are overexploitation, spread of invasive species, nutrient loading and pollution, climate change, and habitat alteration (CBD (chapter 2) 2006). Overexploitation, e.g. as a result of hunting and collecting of species, can lead to species loss or to alteration in abundance of species (Peres & Palacios 2007). Invasive species, whether intentionally introduced or not, can have severe effects on native species through predation, parasitism, competition for resources (space, nutrition, light) or the interruption of mutualisms (pollination, seed dispersal). Thus, an introduction of invasive species could lead to biotic exchange and may initiate strong alterations of community composition (Vitousek *et al.* 1997b). Pollution and nutrient load occur in regions of vast agriculture, industry or mining and could be either directly lethal for species or create an unsuitable environment.

Climate change is increasingly considered one of the strongest drivers of biodiversity loss next to habitat alteration (Sala *et al.* 2000, Travis 2003, Thomas *et al.* 2004). The tremendous speed of current climate change will have long-term consequences and likely result in a rearrangement of global climatic conditions, e.g. some climates disappearing entirely and new ones emerging (Williams *et al.* 2007). This can lead to loss of unique habitats and constraints on many others. Species with low ranges of climate tolerance will need to either adapt to the new environmental conditions or shift their range to track their climatic niche (Parmesan & Yohe 2003, Berg *et al.* 2010, Walther *et al.* 2010). Species need to keep pace with climates as they move (Pearson 2006). However, the pace of climate change will be more rapid than some species' migration capacity (Thomas *et al.* 2004). Species with low adaptability and/or dispersal capacity will then be challenged by the need of range adjustment and low likelihood of reaching distant suitable habitats, ultimately resulting in increased extinction rates (Walther *et al.* 2010).

Many human activities lead to habitat modification. For instance, urbanisation, industrial development, expansion of infrastructure and increasing agriculture combine to cause expansive habitat alterations in the form of degradation, loss or fragmentation. Habitat degradation and loss refer to a decline in the ability of an ecosystem to retain all species: Habitat degradation refers to destructive impacts affecting only some species. In contrast, habitat loss concerns almost all species in the focal habitat (Groom & Vynne 2006). Habitat fragmentation, however, alters the spatial configuration of a habitat area and creates a composition of smaller and more or less isolated habitat patches, often coinciding with a decline in habitat area. Habitat fragmentation has strong potential to negatively affect population dynamics and species' demographic and genetic patterns (Wilcove *et al.* 1986, Saunders *et al.* 1991, Fahrig 2003).

Habitat fragmentation as threat to biodiversity in tropical forests

Habitat fragmentation and loss are the major drivers of current and predicted biodiversity loss (Vitousek *et al.* 1997a, Sala *et al.* 2000, Travis 2003, Morris 2010). More than 75% of the Earth's ice-free land is affected by human land use and residence (Ellis & Ramankutty 2008). Tropical and subtropical forest ecosystems are particularly affected by habitat loss and fragmentation (Foley *et al.* 2005, Mayaux *et al.* 2005, Wright 2005). The majority of the world's biodiversity hotspots are located in the tropics (Myers *et al.* 2000, Mittermeier *et al.* 2004). About 50% of all described species inhabit tropical forests (Dirzo & Raven 2003) and tropical forest ecosystems play a disproportionately large role in global carbon and energy cycles and are thus essential for climate regulation (Brown & Lugo 1982, Foley *et al.* 2005). Tropical forests in particular face a multitude of threats to their existence, e.g. for demographical, political and cultural reasons (see Lambin *et al.* 2003 and references). Population growth in tropical regions is particularly high; consequently, humans rapidly need more space for living and agriculture (Wright & Landau 2006, Wright 2007). Additionally, a lack of policy frameworks to support sustainable development and natural resource protection, political instability, poverty and inequality make tropical countries vulnerable to over-exploitation, either through commercial operations, e.g. timber production (Achard *et al.* 2002, Geist & Lambin 2002), or local practices, e.g. hunting or medicinal plant harvesting.

Tropical forest regeneration cannot keep up with recent and predicted future deforestation, resulting in the decline and fragmentation of forests (Wright & Muller-Landau 2006). Additionally a large proportion of formerly forested landscapes have been permanently occupied by human activities, e.g. urban and agricultural areas, making re-colonization for displaced species almost impossible. This often leads to permanent forest fragmentation and results in isolated populations of species remaining in single habitat patches which are separated from one another by a "*matrix* of habitats unlike the original" (Wilcove *et al.* 1986) (Fahrig 2003).

Plant dispersal in fragmented landscapes

Habitat fragmentation may confine species to relatively small areas within their previous ranges. Organisms then have to cross the above-mentioned *matrix* to reach other areas of suitable environmental conditions. For many species, habitat fragmentation results in limited dispersal and connectivity among populations (Saunders *et al.* 1991). Restricted dispersal and a loss of exchange among populations can have severe genetic and demographic consequences (Howe & Miriti 2004). Reduced gene flow could lead to a decrease in genetic diversity within a population, which in general reduces a species' ability to adapt to changing environmental conditions (Cain *et al.* 2000, Nathan 2006). Further, given that climate change is predicted to affect the distribution of tropical forests (Eeley *et al.* 1999, Mittermeier *et al.* 2004), dispersal is particularly important for species that will need to adjust their ranges to their preferred climate niche (McLachlan *et al.* 2005, Pearson & Dawson 2005). Consequently, habitat loss and fragmentation may increase species' susceptibility to climate change, first by limiting their ability to track climate variations across space (Travis 2003, Thomas *et al.* 2004), and second by diminishing their adaptability to changing environmental conditions (Nathan 2006). In general, susceptibility of species to habitat fragmentation depends largely on their ability to move among remaining habitat patches, which makes immobile species more sensitive to fragmentation (Nathan *et al.* 2011). This is especially true for plants, which have no capacity for relocation (Nathan 2006). Long-distance movements of propagules cannot be executed by the plant itself, and so plants have developed strategies for passive seed-transport, through both biotic and abiotic means.

Seed dispersal

seed dispersal is an important ecosystem function. It facilitates gene flow, thereby influencing the genetic structure within and among plant populations, allows for range expansion, re-colonisation and dispersal to un-colonised habitats. It is a crucial process for seedling recruitment, for maintaining the natural regeneration of forest ecosystems (Herrera 2002, Wang & Smith 2002, Sekercioglu 2006) and consequently for biodiversity conservation (Bascompte & Jordano 2007).

Seed dispersal & landscape connectivity

Successful seed dispersal fundamentally depends on propagules being moved into a habitat appropriate for their establishment (Schupp 2010). In landscapes with a patchy distribution of suitable habitat sites, such as fragmented forest landscapes, successful seed dispersal occurs either as within-patch or between-patch dispersal. Within-patch dispersal is important for gene flow and recruitment within populations; between-patch dispersal facilitates movement of propagules across fragmented landscapes thereby enhancing landscape connectivity (Cain *et al.* 2000, Nathan *et al.* 2008).

Landscape connectivity is the degree to which the landscape facilitates or hinders movements of organisms between landscape elements (Taylor *et al.* 1993). In the case of plants, landscape connectivity refers to the movement of propagules as the mobile unit. However, forest fragmentation reduces the connectivity of populations of forest patches (Wilcove *et al.* 1986). Fragmentation affects both, the structural connectivity given in given in the physical linkage between landscape elements, e.g. number and spatial distribution of patches, and the functional connectivity which refers to the flow of ecological processes among forest patches, such as seed dispersal (Bélisle 2005). Whether seed-transport results in within-patch dispersal, between-patch dispersal or dispersal into the matrix is determined by the dispersal mode and the dispersal distance.

Short- versus long-distance dispersal

The process of seed dispersal can be classified into two forms: short-distance dispersal and long-distance dispersal (Cain *et al.* 2000). The exact scale of each form is not always easy to determine and depends on the study system. Short distance dispersal is generally considered to be dispersal of several metres from the parental tree. Long-distance dispersal results in dispersal across larger distances (Nathan *et al.* 2003), e.g. more than 100 m (Cain *et al.* 2000). Long- and short-distance dispersal typically facilitate different ecological outcomes. The former plays an important role in determining the germination and survival probability of plants, which generally increases with distance to the parental tree (Janzen 1970, Connell 1971, Howe & Smallwood 1982). The latter is crucial for colonisation of new sites and for maintenance of genetic diversity through facilitating exchange of individuals among spatially separated populations (Cain *et al.* 2000, Clark 2005, Nathan 2006). Consequently, in regions where forests are increasingly fragmented, long-distance seed dispersal becomes increasingly important (Trakthenbrot *et al.* 2005). Nevertheless, in most plant species long-distance dispersal events are rather rare and most seeds are dispersed over short distances (Willson 1993a). In general, the dispersal distance depends largely on the seed dispersal mechanism; hence, different seed dispersal mechanisms lead to different seed dispersal outcomes.

Dispersal modes

The major dispersal methods that have evolved are wind-, water-, animal- and self-dispersal (Howe 1982). Self-dispersing plants (autochory) move their seeds without the help of an external vector. As a result, dispersal is limited to rather short distances (Vittoz & Engler 2007). Water-dispersal (hydrochory) plays an important role for hydrophytes but also for some terrestrial plant species, such as trees of floodplain forests (Schneider & Sharitz 1988) and riparian forests (Hampe 2004). The major seed dispersal modes for most tree species are wind- and animal-mediated (anemochory and zoochory). Wind-dispersed seeds are typically rather small; larger seeds are typically dispersed by animals. While wind dispersal can displace seeds over very large distances (Nathan & Muller-Landau 2000, Levin *et al.* 2003, Higgins *et al.* 2003, Tackenberg *et al.* 2003), vertebrates usually facilitate larger dispersal distances than wind dispersal (Willson 1993b; Clark *et al.* 2005). Many tree species in the boreal and temperate forests are wind-dispersed, whereas animal-mediated seed dispersal is particularly prevalent in tropical regions (Howe & Smallwood 1982).

Animal-mediated seed dispersal

In tropical and subtropical forests, the seeds of up to 90% of all woody species are dispersed by animals (Howe & Smallwood 1982, Jordano 2000). An important characteristic of animal seed dispersal is directed dispersal (Schupp *et al.* 2002). Animals usually generate non-random movements and display habitat preferences, leading to spatially inconsistent seed dispersal patterns (Clark *et al.* 1999). This may result in directed dispersal to sites especially favourable for seed survival and establishment (Howe & Smallwood 1982, Wenny 2001). This could be a vital factor for successful seed dispersal within fragmented landscapes where suitable habitat patches are scattered across the landscape and are not randomly distributed (Wenny & Levey 1998, Cain *et al.* 2000, Gómez 2003, Breitbach *et al.* 2012).

Animal-mediated long-distance seed dispersal

Animal-mediated seed dispersal occurs across all spatial scales and the displacement distances are often related to the body size of the disperser (Westcott & Graham 2000, Jordano *et al.* 2007, Wotton & Kelly 2012). For instance, invertebrates disperse seeds mostly over a few metres, e.g. ants (Gómez & Espadaler 1998) or slugs (Türke *et al.* 2010) and beetles (De Vega *et al.* 2011). Vertebrate seed dispersers, in contrast, can reach much larger distances. Tropical fish species are important dispersers for some tropical plants and can disperse a variety of seeds over distances of up to several kilometres (see Pollux 2011). Likewise, large reptiles can account for a major proportion of regional long-distance seed dispersal (Blake *et al.* 2012). However, the majority of vertebrate seed-disperser species are frugivorous mammals and birds (Stiles *et al.* 2000). Among frugivores, large-bodied species are considered to be particularly important for long-distance seed dispersal due to their physiological and behavioural traits. In general, large-sized frugivores are likely to exhibit a wider dietary breadth (Peters 1983) and tend to have wider gape widths compared to small frugivores, which allows them to swallow fruits and seeds of a wide range of sizes. Additionally, gut retention times tend to be longer and ranges may be larger relative to smaller animals (Herrera 1984). Large-bodied vertebrates can thus disperse a high quantity of seeds over large distances (Jordano *et al.* 2007) and are often the exclusive dispersers of large-seeded plant species (Cramer *et al.* 2007). For instance, elephants in Asia and Africa are crucial long-distance seed dispersers for a variety of fruiting plants (Campos-Arceiz *et al.* 2008, Blake *et al.* 2009) and in most tropical regions primates, terrestrial herbivores and large bird species are significant long-distance seed dispersers (Poulsen *et al.* 2002, Russo *et al.* 2006).

The importance of large-bodied birds

Bird species represent a large proportion of vertebrate frugivores in many terrestrial ecosystems (Sekercioglu 2006, Forget *et al.* 2011). Birds are particularly important seed dispersers in tropical forests because many tropical fruiting tree species are mainly dispersed by birds (Howe & Smallwood 1982, Herrera 2002, Levey *et al.* 2002). Depending on their physiological and behavioural traits, different bird species contribute differentially to the seed dispersal pattern (Dennis & Wescott 2007, Jordano 2007, Spiegel & Nathan 2007). In general, large bird species have higher potential to disperse a larger number and variety of seeds over greater distances than small birds (Herrera 1984, Holbrook & Smith 2000, Westcott & Graham 2000, Jordano *et al.* 2007, Spiegel & Nathan 2007).

Although, forest fragmentation is assumed to affect birds less than other taxonomic groups due to their high mobility (Price 2006, Corlett 2007, Peres & Palacios 2007) there is strong evidence that particularly large-bodied bird species are prone to extinctions and population declines compared to small-bodied birds, resulting in serious consequences for plant recruitment (Cramer *et al.* 2007, Peres & Palacios 2007). Large frugivorous birds could have high potential to counter the dispersal limitations of tree species in fragmented tropical forests; hence, birds might play an increasing role in fragmented landscapes (Holbrook *et al.* 2002).

Factors affecting movements of seed-dispersing birds

Whether birds facilitate long-distance seed dispersal depends on their movement behaviour. The movement behaviour of frugivorous birds is in turn influenced by several different factors (Nathan & Muller-Landau 2000).

Spatial effects of landscape configuration

The spatial distribution of resources (e.g. fruiting trees, perches or nesting sites) has a large influence on the movement patterns of seed-dispersing bird species (Levey 1988, Graham 2001, Bélisle & Desrochers 2002, Russo *et al.* 2006). Resource distribution depends largely on the composition and configuration of the landscape. Within fragmented forest landscapes, habitat patches are spatially scattered and the probability and the frequency of inter-patch movements of birds can be strongly influenced by the spatial configuration of these patches (Graham & Blake 2001, Price 2006). Fragment characteristics (e.g. habitat type and size) as well as characteristics of the matrix are relevant factors facilitating inter-patch flights of birds (Magrach *et al.* 2012). The vicinity of forest fragments to large continuous forests also affects the visitation rate of birds to those forest fragments, e.g. fragments closer to the forest might be visited more often (Watson *et al.* 2004). Moreover, structures like *stepping stones* and *habitat corridors* within the *matrix* are suggested to be important elements enhancing a bird species' mobility and thus facilitating long-distance and between-patch seed dispersal by birds (Levey *et al.* 2005, Neuschulz *et al.* 2011).

Temporal effects

Movement behaviour of frugivorous birds can also vary over time due to seasonality of environmental or species traits. First, seasonal fluctuations in resource distribution, e.g. the fruiting period of tree species, may lead to seasonal changes in the movement behaviour of frugivorous birds (Whitney & Smith 1998, Levey *et al.* 2005). In fragmented landscapes, changes in resource availability could vary among habitat patches, which may initialize inter-patch movements and enhance habitat connectivity (Levey *et al.* 2005). Second, seasonal differences in resource requirements may lead to shifts in an animal's movement behaviour, e.g. depending on its reproductive stage (Wiktander *et al.* 2001). Availability of suitable nesting sites and the rearing of nonmobile offspring could lead to periodical alterations of the ranging behaviour of the parent birds. Nesting birds often follow a central-place foraging strategy restricted to the surroundings of the nesting site and switch to a more flexible foraging behaviour when they are not breeding (Stearns 1992, Rosenberg & McKelvey 1999). This could explain why some bird species tend to have smaller ranges during the breeding-season and larger ranges during the non-breeding season (Rolando 1998, Suryadi *et al.* 1998, Novoa *et al.* 2006). Consequently, forest fragmentation might affect a bird's ranging behaviour differently during the course of the year and may be an important determinant of seasonally different ranges. This could in turn lead to seasonal variation in seed dispersal processes, e.g. resulting in shorter dispersal distances during the breeding season than during the non-breeding season.

Temporal differences in social behaviour could add to seasonal differences in seed dispersal patterns. For instance, the foraging group size could affect seed dispersal distribution (Karubian & Duãres 2009). A large group of birds needs more food resources, and thus might forage in a larger area than a single bird. Additionally, movements of a large foraging group may result in clumped seed-deposition underneath fruiting trees and roosting sites. Consequently, both seed clumping and dispersal distance could increase with increasing foraging group size (McConkey & Drake 2006).

Measuring seed dispersal

An investigation of factors influencing seed dispersal function requires data on seed dispersal patterns. However, measuring animal-mediated seed dispersal is challenging, since tracking seed movements by animals is difficult for most natural systems (Jordano 2000, Wang & Smith 2002, Nathan *et al.* 2003, Bullock *et al.* 2006). A common method used to quantify seed dispersal distances is to estimate the seed dispersal kernel; this is the frequency distribution of dispersal distances of seeds relative to the distance from the source (Levin *et al.* 2003). To do so, one needs data on seed movements. Different approaches are available to measure seed trajectories, each operating from one of two perspectives. The *target-* or *seed deposition site-based* perspective traces a seed back from its deposition site to its putative source. The *source-based* perspective follows a seed from the parental plant to its deposition site (Jordano 2007).

Target-based tracking of seed dispersal

The *target-based* design is built on seed-traps. Seed-traps capture the seed rain at certain places away from the seed source. This allows for the analysis of seed rain patterns and also for incorporation of their source (Clark *et al.* 1999, Nathan *et al.* 2002). Nevertheless, this method is limited when the number of potential seed sources is large and/or when seed shadows of conspecifics overlap (Godoy & Jordano 2001). Further, it is the arrangement of seed traps relative to the seed source which determines the range within seed dispersal distances can be detected (Jones *et al.* 2005). Finally, when more than one disperser can be considered, drawing conclusions regarding the seed dispersal vector is not possible unless the seed source and seed-trap are monitored (Jordano & Schupp 2000). Consequently, this methodology is not feasible for tracking seed movements by animals.

Resource-based tracking of seed dispersal

Tracking seed movements from their source can be achieved either by re-locating the seed post-dispersal or following the seed in real time. Relocating seeds after dispersal requires some markings to recover the seeds. These can be physical markers (e.g. thread tags, metal plates or magnets; e.g. Sork 1984) or radio transmitters (e.g. Hirsch *et al.* 2012). These methods are unsuitable for small seeds, however, and can cause difficulties when fruits and seeds are ingested (e.g. for fruit choice, ingestion, digestion or defecation/regurgitation) (Levey & Sargant 2000). Thus, tracking seeds is particularly difficult when the seed dispersal is by birds. Even though small seeds could be marked by application of chemical markers, e.g. fluorescent particles (Levey & Sargant 2000), all of the above-mentioned techniques bear limitations in detecting long-distance seed dispersal, because the effort for seed recovery increases exponentially with search radius (Hirsch *et al.* 2012).

Following seeds in real time requires direct observation of the seed disperser, the feeding behaviour, the movements and the seed deposition. Consistent direct observation, however, is for most mobile avian frugivores impractical (Jordano *et al.* 2007). Additionally, when the focal animal visits different individuals of the same species, again seeds need to be individually identifiable. The parental tree could be identified genetically, however, genetic analysis are complex and labour intensive and thus might be rather unsuitable for estimating long-distance seed dispersal (Nathan 2005).

Modelling seed dispersal

Dispersal models have also been used to quantify seed dispersal patterns, in particular inverse and mechanistic models (Nathan & Muller-Landau 2000). Inverse models fit a mathematical function to observed data and thereby describe dispersal patterns. (Nathan *et al.* 2003). Seed-trap data can be used for inverse modelling of seed dispersal kernels. Therefore, parameter values are estimated for dispersal function which result in the best fit to the sampled seed-deposition pattern. From the resulting model the seed dispersal kernel can then be calculated (Clark *et al.* 1999, Nathan & Muller-Landau 2000, Bullock *et al.* 2006). The drawback to this method, however, is that the dispersal process itself is not taken in to account and remains unknown.

Mechanistic models predict seed dispersal based on an understanding of the traits of the components of the seed dispersal process. This facilitates prediction of seed dispersal distances independently of the observed data (Nathan *et al.* 2003). Mechanistic models are effective for seed dispersal by wind, since the factors influencing wind dispersal are easier to identify and to measure (e.g. wind speed, seed release height) (Nathan *et al.* 2001, Nathan *et al.* 2003, Tackenberg 2003). Animal movement is complex, however, since it is not determined only by abiotic factors and vegetation (see above) and its influences are in general difficult to measure (Nathan & Muller-Landau 2000, Westcott *et al.* 2005). Mechanistic models of seed dispersal by animals usually predict seed dispersal kernels using a combination of seed retention times and displacement rate of animals (Murray 1988, Sun *et al.* 1997, Westcott *et al.* 2005, Russo *et al.* 2006). Seed disperser movements and seed retention times are measured independently. Seed retention times can be measured with feeding trials of animals in captivity (e.g. Sun *et al.* 1997, Whitney 1998). Displacement rates of animals can be collected by direct or remote tracking of individual animals.

Tracking birds

Animal movement data can be recorded by either direct mapping of frugivore locations (Whitney *et al.* 1998, Russo *et al.* 2006, Holbrook 2011) or by using a remote tracking device (Westcott & Graham 2000, Holbrook *et al.* 2002, Westcott *et al.* 2005, Holland *et al.* 2009).

Direct observations carry some limitations, particularly for rapid, long-distance movements (Jordano *et al.* 2007). Changes in the movement behaviour, e.g. from short-distance to long-distance movements and from open to dense vegetation, could result in differential visibility of the focal animal. Thus, the quality of direct observations can vary increasingly with increasing heterogeneity in the animal's use of space. Remote tracking of animals can overcome these limitations. Radio transmitters and Argos satellite tags attached to the animal are frequently used to record bird movements. A high-frequency (VHF)-radio tag sends a radio signal to a terrestrial receiver. By following the signal or by triangulation, one can determine an animal's location. This tracking method is suitable for animals staying in a certain area, since following the animals with the receiver can be difficult and labour-intensive (e.g. Holbrook & Smith 2000, Wotton & Kelly 2012). Argos satellite tags send periodic signals via Argos satellites to receiving stations around the globe. The animal's location can then be calculated from the signal input. This method provides position data that are typically of low spatial accuracy (Soutullo *et al.* 2007), but animals can be located anywhere on the globe. Thus, this method is particularly suitable for migratory birds (Tomkiewicz *et al.* 2010). However, both methods bear limitations when recording accurate location data of wide ranging non-migratory bird species.

Animal tracking using GPS (Global Positioning System) techniques arose in the 1990s and has been well developed since then (Rempel *et al.* 1995, Cagnacci *et al.* 2011). A GPS tag calculates an animal's location using position data from a satellite network. Location data can be stored on-board the tag and is then available through remote data access (satellite, cell phone or ad hoc wireless download). These tags provide a large amount of precise location data but in the beginning were relatively heavy and thus limited to larger animals (Tomkiewicz *et al.* 2010). The recent development of miniaturized GPS-data loggers allows researchers to track the movements of even relatively small animals in hitherto unreached temporal and spatial resolution (Cagnacci *et al.* 2011, Recio *et al.* 2011). This offers opportunities to obtain high-quality location data which allow a detailed analysis of the movement behaviour and an assessment of the consequences of habitat fragmentation on the seed dispersal function of frugivorous birds.

Tracking seed dispersal across spatial and temporal scales

Seed dispersal function has increasingly gained attention in ecological research, but studies of seed dispersal by birds at scales relevant for long-distance seed dispersal are rare and analysing the effect of spatial and temporal factors remains challenging (Carlo *et al.* 2013, Morales *et al.* 2013). Whereas several studies investigate seed dispersal by birds under changing environmental conditions (see Markl *et al.* 2012 for review), only a few address temporal and spatial variations in long-distance seed dispersal of large frugivorous bird species.

Seed dispersal under changing environments is often studied by investigation of differences in the occupancy of dispersed seeds or disperser species related to different habitat types. For instance, some studies analyse the variation of the number and the spatial distribution of dispersed seeds between different habitats (Herrera & Garcia 2010, Carlo *et al.* 2013), or investigate changes in the abundance and the movement behaviour of bird species under landscape fragmentation (Neuschulz *et al.* 2011). Studies considering both, the plant and the disperser species (e.g. Cordeiro & Howe 2003, Gómez 2003, Spiegel & Nathan 2007) are conducted on a rather small scale (Cortes & Uriarte 2013) and do not incorporate different levels of fragmentation. Experimental studies on habitat fragmentation can directly address the effects of landscape characteristics on seed dispersal function, such as the effect of landscape corridors on bird movements (Levey *et al.* 2005), or the patch size relative to spatial configuration (Uriarte *et al.* 2011). However, experimental landscapes may be either too small to incorporate long-distance seed dispersal or seed dispersal events cover an area too large to allow for replication or experimental manipulation (Debinski & Holt 2000). Additionally, experimental designs may sometimes be unfeasible, e.g. in complex terrains or nature conservation areas.

Species-specific seed dispersal

Although large frugivorous birds may play an overriding role in seed dispersal processes in fragmented landscapes, little is known about the effect of landscape fragmentation on the movement behaviour and the resulting seed dispersal distribution of such birds (Cain *et al.* 2000, Nathan *et al.* 2003, Nathan 2006). The difficulties in measuring long-distance seed dispersal have resulted in a deficit of studies analysing the long-distance seed dispersal potential of large bird species per se and under different environmental conditions. Species-specific studies have, to date, mostly obtained movement data to calculate seed dispersal distributions only in one landscape type (Holbrook & Smith 2000, Graham 2001, Westcott *et al.* 2005, Sun *et al.* 2007, Herrera & Garcia 2010, Holbrook 2011) or estimated seed dispersal kernels only generally, e.g. for heterogeneous landscapes (Gómez 2003, Herrera *et al.* 2011). Additionally, studies on bird movement mostly consider movement data either for one particular season, e.g. breeding or non-breeding season (Suryadi *et al.* 1998, Datta 2003, Novoa *et al.* 2006, Haffner *et al.* 2009). Longer-term studies mostly estimated seed dispersal potential from movement data averaged across seasons (e.g. Holbrook & Smith 2000) and the process of seasonal range shifts might be blurred. Since the animal tracking method and study design always differs among studies, results are limited in their comparability with each other and cannot be generalized for other species (Horne *et al.* 2007, Kitamura 2011). Consequently, detailed knowledge on the temporal and spatial factors influencing the seed dispersal potential of large frugivorous bird species remains elusive. However, this knowledge is a crucial step to better understand their role in ecosystem functioning and, ultimately, biodiversity conservation (Trakhtenbrot *et al.* 2005, Montoya *et al.* 2008).

Aims and structure of the thesis

In my thesis I investigated the influence of forest fragmentation on the movement behaviour and seed dispersal potential of a large frugivorous bird species in subtropical Africa. I chose the trumpeter hornbill (*Bycanistes bucinator*) as model organism. Due to its large body size, high abundance and high mobility, it is probably one of the most important seed dispersers in its range. During five field trips with a total duration of 13 months, I caught 54 adult trumpeter hornbills. I captured birds during three different seasons, two within the non-breeding season with one at high fruit abundance and one at low fruit abundance (Bleher *et al.* 2003) and a third one during the breeding season. Because female trumpeter hornbills enclose themselves in a nesting cavity during the whole breeding cycle, only male birds were equipped with a high resolution GPS-data logger. I was able to successfully track 33 individuals, each over an average period of 19 days. The centre of my field research was Oribi Gorge Nature Reserve in KwaZulu-Natal, South Africa. The reserve contains an almost unaltered natural closed forest (Pooley 1994) and is surrounded by heterogeneous and intensively used farmland. Consequently, this region was particularly suitable for investigating my research question as it enabled a direct comparison between the movement behaviour and the seed dispersal distributions of an important avian seed-disperser in both large continuous forests and in heavily fragmented agricultural landscapes. Additionally, I conducted feeding experiments with trumpeter hornbills in captivity in Germany, to obtain data on seed-retention times.

My thesis consists of three independent chapters. Each chapter is structured like a journal publication, with an abstract and an introduction, followed by a section on the methodology, a paragraph presenting the results and a discussion. Supplementary information and all references are cumulated in an appendix and a common reference list at the end of the thesis. General synthesis and conclusions are given in a last chapter following the three major research chapters.

In chapter 3, I determined the seed dispersal potential of trumpeter hornbills. To do so, I combined fine-scale movement data with seed retention times of trumpeter hornbills to calculate species-specific seed dispersal kernels. To investigate the effect of landscape structure on seed dispersal distances of trumpeter hornbills, I used high resolution landscape data from satellite imagery and compared seed dispersal kernels while birds moved within continuous forest with those from the fragmented agricultural landscape. For this chapter, I contributed to the study question and design. I conducted the majority of and supervised all field work. I developed all analysis on data quality, draw detailed habitat maps and drafted the manuscript. Wolfgang Fiedler contributed to field work and sampling methods. Claudia Grünewald supervised feeding experiments with trumpeter hornbills at the Max Planck Institute of Ornithology in Radolfzell, Germany. Katrin Böhning-Gaese and Tanja Caprano developed analytical methods. Tanja Caprano implemented the sampling procedures of dispersal events and curve fitting. Katrin Böhning-Gaese, Wolfgang Fiedler and Martin Wikelski contributed to the study design and manuscript writing.

In chapter 4, I investigated seasonal variations in ranging behaviour of trumpeter hornbills between the breeding- and the non-breeding season. To do so, I calculated daily ranges for each individual and investigated differences in range size, the variation in size, the underlying habitat type and the spatial distribution of daily ranges between the breeding and the non- breeding seasons. I focused on the process of range expansion of trumpeter hornbills during the non-breeding season and tried to deduce ecological consequences for seed dispersal processes in relation to the reproductive stage of trumpeter hornbills. I conducted the majority of and supervised all of the field work. Wolfgang Fiedler contributed to field work and the manuscript. I conducted all analyses and wrote the manuscript. Thomas Müller assisted in analytical methods and statistics. Thomas Müller and Katrin Böhning-Gaese contributed to study design and manuscript writing.

In chapter 5, I aimed to illustrate the potential of trumpeter hornbills to facilitate functional connectivity among plant populations of isolated forest fragments. A projection of simulated seed dispersal events on a habitat map displayed spatially explicit seed dispersal paths. This allowed to elucidate the probability of between-patch seed transport by trumpeter hornbills and additionally provided important information on forest patches, critical as stepping-stones linking the connectivity network. In this study I was involved in the study design, was leading data preparation of all spatial layers and was involved in the analysis. Further, I supervised the remote sensing analysis disentangling suitable from non-suitable habitat. Also involved in the study design were Thomas Müller and Katrin Böhning-Gaese. Tanja Caprano implemented the sampling procedures of dispersal events, Thomas Müller performed frequency and graph analysis and wrote the first draft of the manuscript and all authors contributed substantially to revisions.

CHAPTER 3

SEED DISPERSAL DISTRIBUTION OF TRUMPETER HORNBILLS IN A FRAGMENTED LANDSCAPE

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Lenz, J., Fiedler, W., Caprano, T., Friedrichs W., Gaese, B. H., Wikelski, M. & Böhning-Gaese, K. (2011) Seed dispersal distributions by Trumpeter Hornbills in fragmented landscapes.

3.1 Abstract

Frugivorous birds provide important ecosystem services by transporting seeds of fleshy fruited plants. It has been assumed that seed dispersal kernels generated by these animals are generally leptokurtic, resulting in little dispersal among habitat fragments. However, little is known about the seed dispersal distribution generated by large frugivorous birds in fragmented landscapes. We investigated movement and seed dispersal patterns of trumpeter hornbills (*Bycanistes bucinator*) in a fragmented landscape in South Africa. Novel GPS loggers provide high-quality location data without bias against recording long-distance movements. We found a very weakly bimodal seed dispersal distribution with potential dispersal distances up to 14.5 km. Within forest, the seed dispersal distribution was unimodal with an expected dispersal distance of 86 m. In the fragmented agricultural landscape, the distribution was strongly bimodal with peaks at 18 and 512 m. Our results demonstrate that seed dispersal distributions differed when birds moved in different habitat types. Seed dispersal distances in fragmented landscapes show that transport among habitat patches is more frequent than previously assumed, allowing plants to disperse among habitat patches and to track the changing climatic conditions.

3.2 Introduction

Over recent decades, tropical and subtropical forests have become smaller and more fragmented (Foley *et al.* 2005, Mayaux *et al.* 2005). This results in increasing difficulties for plant and animal species to move among these fragments. The isolation of forests and forest fragments, and limited exchange of individuals, can have severe demographic and genetic consequences (Howe & Miriti 2004, Begon *et al.* 2006, Groom *et al.* 2006). Exchange of individuals among fragmented populations is important to allow organisms to adapt to changing environmental conditions (Cain *et al.* 2000, Nathan 2006). This problem is further accelerated by global climate change, which forces organisms to track changes in the geographical position of their preferred climatic niche (Pearson & Dawson 2005, McLachlan *et al.* 2005). Dispersal limitations are particularly pressing for organisms that cannot disperse by themselves, such as fruit-bearing trees (Nathan 2006).

Most tropical and subtropical tree species are dispersed by frugivorous animals (frequently birds) (Herrera 2002, Levey *et al.* 2002). For these trees, dispersal among forest fragments requires the movement of birds among these fragments. To be efficient seed dispersers, birds have to move large distances and should be able to cross the 'matrix habitat', often farmland, which separates the forest fragments. Large fruit-eating bird species have the potential to move within fragmented landscapes and to fly between patches of forest (Powell & Bjork 1995, Chaves-Campos *et al.* 2003, Price 2006). Species that should be able to act as seed dispersers among forest fragments in an agricultural landscape are hornbills in Southeast Asia and Africa, and toucans in the Neotropics (Kemp 1995*,* Graham 2001*,* Holbrook & Smith 2000). Nevertheless, to our knowledge no study has so far investigated seed dispersal of large frugivorous birds such as hornbills in a fragmented landscape containing only small and distant patches of suitable habitat

To quantify the seed dispersal pattern of trees, one possible approach is to track the movement patterns of the birds using radio-telemetry, to measure gut passage times (GPTs) of seeds, and to combine both distributions to calculate an average seed dispersal distribution (Murray 1988). So far, this approach has been used very successfully for quantifying short-distance seed dispersal patterns within habitats (i.e. within forests (Murray 1988, Sun *et al.* 1997, Westcott & Graham 2000, Holbrook & Smith 2000, Westcott *et al.* 2005*,* for a definition of short- and long-distance seed dispersal see Nathan 2005).

In contrast, little is known about long-distance seed dispersal patterns among forests or forest fragments (Cain *et al.* 2000*,* Nathan *et al.* 2003*,* Nathan 2006). For example, movement patterns of hornbills have been studied within a tropical rainforest in Cameroon (Holbrook & Smith 2000). Some data demonstrate that in periods of fruit scarcity in the forest, birds appear to start long-distance movements of up to 290 km (Holbrook *et al.* 2002). A telemetry study on toucans demonstrated that these birds move readily among forest patches through farmland (Graham 2001). Nevertheless, to our knowledge no quantitative data on long-distance movement patterns and seed dispersal among forests and forest fragments exist for hornbills or toucans. Furthermore, it is not known whether seed dispersal distributions differ if a bird is moving within continuous habitat (e.g. within a large forest) or among patches of suitable habitat (e.g. forest patches in an agricultural matrix).

An important region for studying large-scale movement patterns of birds is South Africa. The few forests occur mostly along the east coast and are heavily fragmented. These forests are a global hotspot for tree diversity (Mittermeier *et al.* 2004) and are expected to suffer profoundly from global climate change (Eeley *et al.* 1999). The Trumpeter Hornbill. The trumpeter hornbill (*Bycanistes bucinator*) is the largest obligate frugivorous bird in South Africa and the species is abundant along the east coast (Kemp 1995, Bleher *et al.* 2003). We predicted trumpeter hornbills to be the most promising long-distance seed dispersal agents in eastern South Africa. To assess whether the tree diversity along the east coast can be conserved under climate change, one prerequisite is to demonstrate whether trumpeter hornbills are able to disperse seeds among forest fragments.

We used a novel telemetry device-GPS loggers (e-obs GmbH, Munich, Germany, Holland *et al.* 2009) to track movement patterns of trumpeter hornbills in large remnants of continuous forest and in the agricultural landscape containing little suitable habitat. We conducted feeding trials of captive hornbills to asses GPTs, and combined movement patterns and GPTs to derive seed dispersal distributions. To assess how habitat influenced movement patterns and seed dispersal distributions, we quantified seed dispersal distributions at times when birds moved within continuous forests and at times when they foraged in the agricultural landscape with few, small and distant patches of suitable habitat.

3.3 Materials and Methods

3.3.1 Study site and species

Forests occur in South Africa mostly along the east coast. The study area lies within one of the recognized global hotspots of biodiversity: the Maputaland-Pondoland-Albany hotspot, which contains nearly 600 tree species (the highest tree diversity of any of the world's temperate forests) (Mittermeier *et al.* 2004). Climate change is expected to have severe consequences for South Africa, and in particular for the forests along the east coast, which are expected to shift their altitudinal and latitudinal position (Eeley *et al.* 1999). At the same time, these forests are heavily fragmented for both natural and anthropogenic reasons (Eeley *et al.* 1999, Wethered & Lawes 2005). Large natural forests lie in deep gorges (for example Oribi Gorge Nature Reserve (Pooley 1994)) and on steep slopes. They are surrounded by areas that are highly populated and intensively used for agriculture.

The centre of the study area was located in Oribi Gorge Nature Reserve (range: 30.1718 E–30.3088 E; 30.6938 S30.7268 S), approximately 100 km south of Durban and 20 km inland from Port Shepstone. The gorge consists of natural subtropical coastal scarp forest (Pooley

1994), which has the highest species richness of the main forest types in KwaZulu-Natal (Eeley et. *al.* 2001). About 7 km northwards of Oribi Gorge lies the large forested valley of the Mzimkhulu River, and to the southwest of Oribi Gorge the smaller Mbumbasi Nature Reserve, which also contains a larger area of forest: Both nature reserves are surrounded by intensively used farmland, especially sugarcane plantations. Within the agricultural matrix, there are small patches and strips of natural forest at sites that cannot be used for agriculture, such as rocky outcrops, along creeks and in deep valleys. In addition, the farmhouses in this agricultural area have large gardens that contain indigenous and exotic fruit-bearing trees.

The trumpeter hornbill is the largest obligate frugivorous bird in South Africa (Kemp 1995). Even during the breeding season, 89 per cent of its food items are fruits (Kemp 1995). The trumpeter hornbill is a medium-sized hornbill, with an average body weight of 550 g for females and 720 g for males. Trumpeter hornbills have a large gape width, which allows them to swallow and also to transport large seeds. In Oribi Gorge, trumpeter hornbills are among the most abundant frugivores (Bleher *et al.* 2003).

3.3.2 Trapping and tracking of Trumpeter Hornbills

Trumpeter hornbills were caught using canopy mist nets in fruiting fig (*Ficus* spp.) or mahogany trees (*Trichilia* spp.), or using free-standing nets placed in flying routes to and from these trees. The birds were weighed, measured and ringed. Only males were fitted with GPS loggers, because females enclose themselves in cavities during breeding and we were worried loggers could interfere with their breeding behaviour. A logger weight of 27 g is below the generally accepted threshold of 3–5% body weight (Kenward 2001) (males weighed on average 743 g; range 600–835 g). GPS loggers were attached like a backpack. We used Teflon strings with predetermined breakage points as backpack straps, allowing loggers to drop-off eventually.

The GPS loggers measure the position of the bird with GPS quality at predetermined times. In our case, they were programmed to measure the position in time intervals of 15 min during daytime, the activity period of the hornbills. At night, the loggers were switched to standby to save battery energy. The data are stored in the logger on the bird and can be downloaded to a handheld base station through a radio link. Using yagi antennas, handheld as well as fixed on the roof of a car, we improved the range for a successful download to distances up to 2 km. The battery of the loggers lasted on average 18 days for data sampling (maximum 26 days). A data download is possible also after the GPS logger stopped recording locations, because the battery saves energy for a last download process. Once we released the birds, we searched for them, systematically starting from the trapping point and continuously extending the area. Successful data downloads led us to new habitat patches used by the birds for foraging or for spending the night.

We tested the precision of the location data by placing loggers in the open and under tree canopies, and measuring the distance between the true location and the location recorded by the logger.

3.3.3 Feeding trials

To determine GPTs, we made feeding trials on two captive trumpeter hornbills (one male, one female), housed at the Max-Planck Institute for Ornithology, Radolfzell, following established methods (e.g. Westcott *et al.* 2005*,* Spiegel & Nathan 2007). The birds were kept in three inter-connected cages of about 3-4 m area (3 m height) and were tame, tolerating the presence of observers close to and in the cage without signs of distress. We fed each individual five differently sized types of fruit/seed: cocktail tomatoes (median seed size 0.0002 g), grapes (0.020 g), tangerines (0.20 g), lychees with small seeds (0.28 g) and lychees with large seeds (2.04 g). Birds ingested these fruits readily; lychees are also consumed in the wild (B. Peckham 2009, personal communication). We conducted two feeding trials per bird and fruit type. Fruits were fed in the morning; non-consumed fruits were removed after 18 min during the experiment and the night before the birds were offered seedless food. All seeds were defecated except the large lychee seeds, of which 90 per cent were regurgitated. We recorded the time and place of each defecation on the floor of the cage. Faeces were collected after defecation, passed through a sieve and inspected for seeds. Defecations were collected until all ingested seeds were recorded or until no seed was detected for a 2.5 h time period after the last seed was recorded in the faeces. We determined the GPT of each seed for each experiment. We defined the starting point of the gut passage as the mid-point between start of fruit presentation at the beginning of the experiment and the removal of non-consumed fruits. We then determined for each experiment and each seed the time interval between this mid-point and the time the seed was defecated. In case the seeds were regurgitated, we calculated the time between swallowing and regurgitation of the seeds. We calculated for each experiment the median and maximum GPT of the seeds. As we conducted two feeding trials per fruit type and bird (n = 20 experiments), we were able to test whether median and maximum GPT per trial differed between the five fruit/seed size types, between defecated and regurgitated seeds, and between the two individuals.

3.3.4 Data analysis

We included in all analyses only days for which at least 30 valid coordinates were available (76.9% of relocations of a day in summer season and 63.9% of a day in winter season). This reduced sample size by on average 1.4 days per bird (from a mean number of 18.2 to a mean number of 16.8 days per bird). To test whether birds had to adapt to the GPS loggers, we tested whether the birds flew shorter distances on the first days on which they carried loggers. We calculated for each bird the cumulative flight distance per day. We tested whether the flight distance on the first (second, third, etc.) day differed significantly from the mean flight distance averaged over all later days. We found that from the fourth day on, daily flight distances did not differ significantly from those of the later days (Wilcoxon one-sided signed-rank test: p = 0.1). We conducted all the following analyses excluding the first 3 days the birds carried GPS loggers. This reduced the sample size again from a mean number of 16.8 to a mean number of 12.5 days per bird. For this analysis and all following analyses, we used the open-source software R (R Development Core Team 2010).

We first calculated displacement distributions of birds. We randomly selected starting points in the movement track of each bird and measured the distance to the location each bird had 15, 30, 45, 60, 75, 90, 105, 120, 135 or 150 min later, following established methods (e.g. Westcott *et al.* 2005, Spiegel & Nathan 2007). The time intervals (15, 30, 45 min, etc.) were drawn from a uniform distribution. The maximum time interval of 150 min represented the maximum GPT (see §3). Thus, we randomly selected a starting point in the movement track of each bird, then randomly selected a movement time interval from the uniform distribution (15, 30, 45 min, etc.) and finally calculated the Euclidean distance between the chosen starting point and endpoint. We randomly drew 1000 displacement distances per individual bird. We chose starting points such that the earliest starting point was about 1 h before sunrise and the latest endpoint about 1 h after sunset. Displacement distances were thus calculated uniformly over the activity period of the hornbills. We determined the displacement distribution for each of the birds separately and then calculated for each time interval (15, 30, 45 min, etc.) the mean and standard error across the birds.

We then combined the individual displacement distributions of each bird with the mean GPT distribution. The test of median and maximum GPT per feeding trial showed that there were no significant differences in median and maximum GPT between the five fruit/seed size types, between defecated and regurgitated seeds, nor between the two individuals (see §3). We therefore determined a mean GPT distribution across the 20 feeding trials. We calculated the mean proportion of seeds that were defecated or regurgitated on average 15, 30, 45, 60, 75, 90, 105, 120, 135 or 150 min (each+7.5 min) later across the 20 feeding trials. These proportions were 12.1, 19.9, 20.8, *13.7*, 12.7, 12.9, 2.9, 2.8, 0.4 and 1.6 per cent of the seeds, respectively (figure 1).We then repeated the procedure described above, but now the time intervals (15, 30, 45 min, etc.) were drawn not from a uniform distribution but from the distribution of GTPs (i.e. after randomly selecting a starting point, 12.1 per cent of the distances were calculated for a time interval of 15 min, 19.9 per cent for an interval of 30 min, etc.) This procedure weights the displacement distribution with the GPT distribution. To evaluate whether bird displacement and seed dispersal distributions differed between habitat types, we calculated both distributions over time periods when birds moved within large continuous forests and over time periods when they foraged in the agricultural landscape.

To evaluate habitat cover, we used the latest KwaZulu-Natal Land-Cover dataset (GeoTerraImage, www.geoterraimage.com; preliminary 2005, modified 2008). We defined 'continuous forests' as the large continuous forest of Oribi Gorge Nature Reserve (1930 ha), the densely wooded parts of the Mzimkhulu River valley 7 km to the north of Oribi Gorge and the forest within Mbumbasi Nature Reserve (trees and bush cover 70%; 880 ha). These three forests are the largest natural forests within about 30 km of Oribi Gorge. The agricultural landscape was defined as the following habitat types: all types of farming (e.g. sugarcane, exotic plantations), old cultivated fields, bush land, grassland, wetlands, roads and expanses of water. Within the agricultural landscape, patches of natural forest are small (156 ha) and there are tree rows, isolated trees and farm gardens frequented by the hornbills. The rest of the habitat types (e.g. suburban areas, rural communities) were subsumed under an 'other habitat types' category.

We identified in the movement track of each bird time periods with a minimum duration of 150 min (representing the maximum GPT; see §3) in which all locations were in the same habitat type, either 'continuous forest' or 'agricultural area'. We then selected starting points randomly in the 'continuous forest' and in the 'agricultural area' sub datasets (all birds) and calculated seed dispersal distributions for the two habitat types separately, using the same procedure as described above. We drew 100 displacement distances randomly per individual bird and habitat type.

To describe the dispersal distributions in the two habitat types mathematically, we fitted five different probability density functions (normal, logistic, Cauchy, Student t and Weibull) to the dispersal distance distributions, separately for the two habitat types types (Russo *et al.* 2003, Clark *et al.* 2005). We estimated parameters of each distribution based on maximum likelihood using R package BBLME2010 (Bolker 2009, R Development Core Team 2010, version 2.11.1). To identify the best-fitting model for the bimodal distribution in the agricultural landscape, we first partitioned the data into two unimodal distributions, based on visual inspection (see also Russo *et al.* 2006, Levey *et al.* 2008). We first fitted distributions to the first and the second peak separately and then tested all possible linear combinations of the five functions using the parameters estimated from the separate fits as starting points. We applied the Akaike information criterion (AIC) to assess model fit.

3.4 Results

We caught 10 male and 8 female trumpeter hornbills in two field seasons. Of the males, six were caught in July 2008 and four in April 2009; both were non-breeding seasons. We were able to relocate all 10 tracked birds. We obtained data for a mean number of 18.2 days per bird (range 6–26 days; the bird with only 6 days of recording lost his backpack). After eliminating days with less than 64 per cent valid location data and after dropping the first 3 days' data, an average of 12.5 days per bird (range 2–22 days were available).The analyses are based on a mean number of 675.6 locations per bird (minimum 193, maximum 955). Median measurement error of the logger location was 8.0 m (25% quartile: 4.5 m; 75% quartile: 14.0 m; n = 142 locations, 71 in the open, 71 under tree canopies). The distribution of measurement errors shows a peak at about 5.6 m (see electronic supplementary material, figure S1).

Mean median GPT in the 20 feeding trials was 57 min, mean maximum GPT was 77 min and the absolute maximum GPT was 155 min (Fig. 3.1). Median and maximum GPT per fruit/seed size type and trial did not differ between the five fruit/seed size types or the two individuals (two-factor ANOVAs, median GPT: fruit/ seed type: F4,14 = 2.2, p = 0.12; individual: F1,14 = 1.5, p = 0.24; maximum GPT: fruit/seed type: F4,14 = 2.0; p = 0.15; individual: F1,14 = 3.4, p = 0.086). Median and maximum GPT did not differ between regurgitated and defaecated seeds (two-factor ANOVAs, median GPT: digestion mode: F1,16 = 2.6, p = 0.12; individual: F1,16 = 0.3, p = 0.61; maximum GPT: digestion mode: F1,16 = 0.9; p = 0.35; individual: F1,16 = 0.9, p = 0.35). This shows that GPTs were rather independent of fruit seed size, digestion mode and individual, and may be representative for natural fruits more generally.

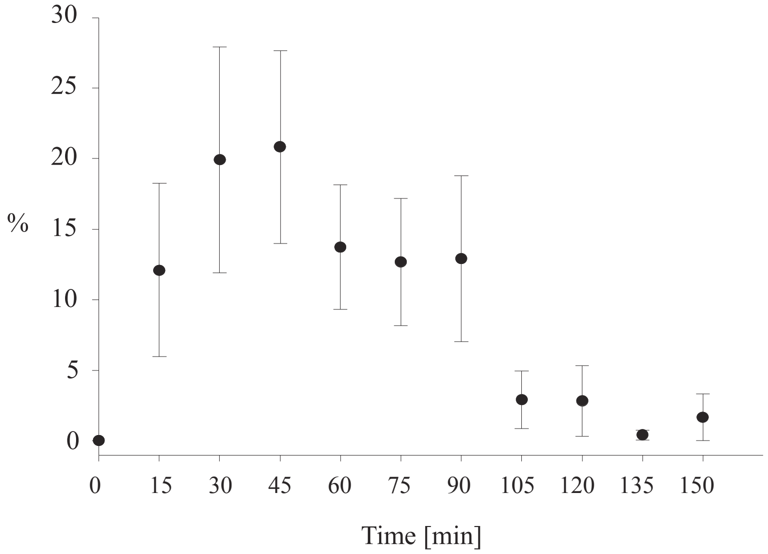

Figure 3.1: *Distribution of average gut passage times (GPTs) of two trumpeter hornbills. Mean percentage of seeds (+s.e.) defaecated in each 15 min interval. n = 20 feeding trials.*

The movement tracks differed widely among individuals. Some birds stayed in Oribi Gorge Nature Reserve or in the surrounding area; others moved between Oribi Gorge Nature Reserve and the coast (Fig. 3.2). The displacement distribution averaged across the 10 birds is shown in figure 3a. It was very slightly bimodal with a very slight first peak at about 25 m, and a higher second peak at about 630 m. Weighting the displacement distribution (Fig. 3.3a) with GPT (Fig. 3.1) yielded the potential seed dispersal distribution, averaged over the 10 hornbills (Fig. 3.3b). It was also very weakly bimodal with a slight first peak at about 25 m and a second slightly higher peak at about 630 m. The seed dispersal distances of the individuals showed a similar pattern; 9 of the 10 birds had a bimodal seed dispersal distribution (electronic supplementary material, figure S2). Maximum potential seed dispersal distance was 14.5 km. Overall, the largest spatial extent over which a bird moved within the study period was 37 km.

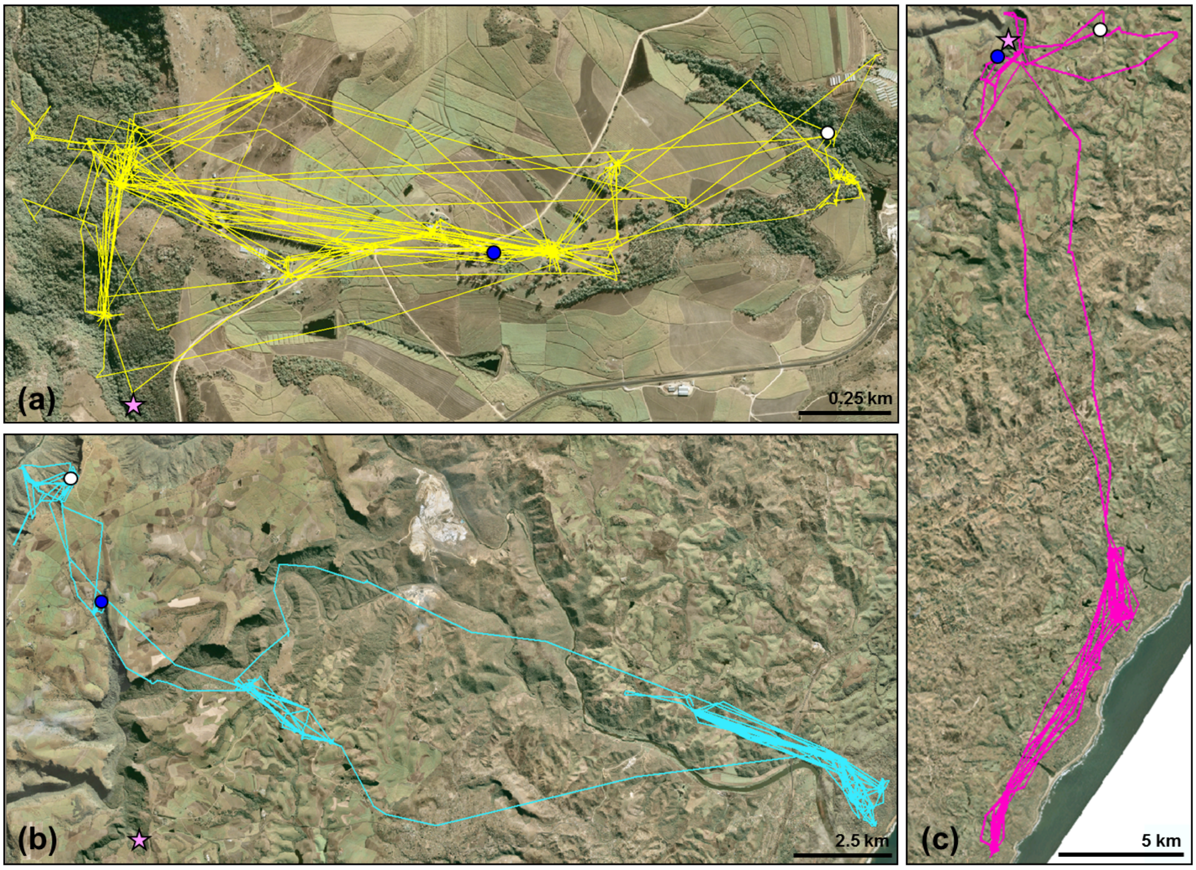

Figure 3.2: *Movement tracks of three different trumpeter hornbills that moved at different spatial scales. Presented are the tracks of each bird during the whole tracking period. The starting point of each track is marked with a white circle and the endpoint with a blue one. The pink star shows the southern entry to Oribi Gorge Nature Reserve. Coloured lines represent hornbill movements tracked (a) from 4 to 25 August 2008 (n = 21 days), (b) from 9 July to 3 August 2008 (n = 25 days) and (c) from 15 to 31 July 2008 (n = 16 days). (Compare electronic supplementary material, figure S2.)*

Seed dispersal distributions differed considerably among habitat types. The seed dispersal distribution in the forest was based on seven birds and the one in the agricultural area on nine birds, as not all birds spent 2.5 h continuously in each of the two habitat types. Birds spent on average 30 per cent of their time in the three larger forests (range 0–99%, *n* = 10 birds), 50 per cent in agricultural areas (range 1–85%) and the remaining 20 per cent in other habitat types (range 0–80%). The seed dispersal distribution in continuous forest was unimodal with a best fit by the Weibull function with an expected mean seed dispersal distance of 86 m and a maximum seed dispersal distance of 3016 m (Fig. 3.4a and Tab. 3.1). The seed dispersal distribution in the agricultural area was strongly bimodal (Fig. 3.4b). This distribution was fitted best by two different functions that had similar AIC values (Δ AIC ≤ 2). The first function was a linear combination of the Weibull function for the first peak and a normal function for the second peak; the second function was a linear combination of two normal functions for both peaks (Tab. 3.1). The first, larger peak was placed at about 18 m and the second, smaller peak at about 512 m dispersal distance; maximum seed dispersal distance was 8914 m (Fig. 3.3b).

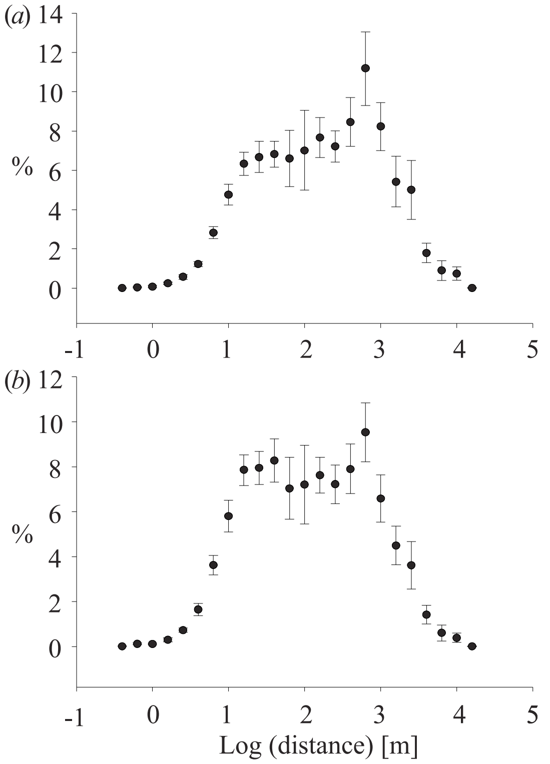

Figure 3.3: *(a) Displacement distribution and (b) seed dispersal distribution averaged over 10 trumpeter hornbills. Mean percentage of displacement events (±s.e.) and seed dispersal events (±s.e.) for each distance class, respectively. The seed dispersal distribution (b) is generated by combining GPTs (Fig. 3.1) and the displacement distribution (a).*

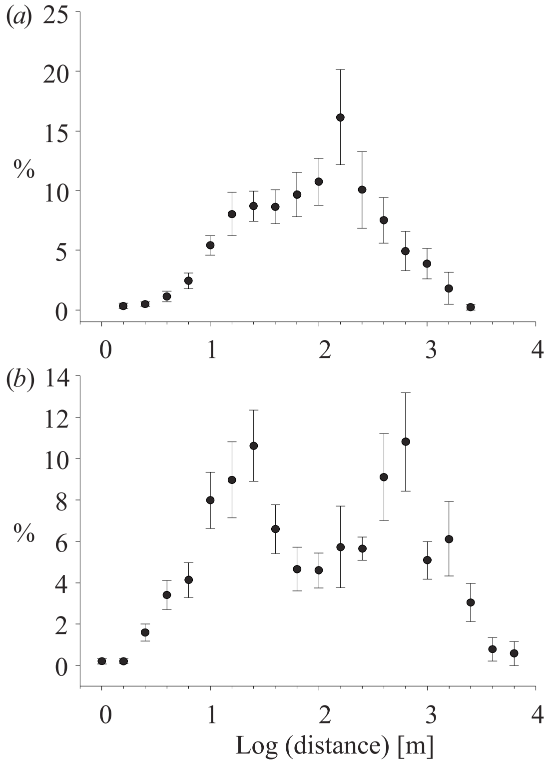

Figure 3.4: *seed dispersal distribution in (a) continuous forest (n = 7 birds) and (b) agricultural landscapes with little natural habitat (n = 9 birds). Mean percentage of dispersal events (±s.e.) for each distance class.*

3.5 Discussion

Our data showed that movement patterns of trumpeter hornbills in fragmented landscapes with a patchy occurrence of forests resulted in very slightly bimodal seed dispersal distribution with a maximum seed dispersal distance of 14.5 km. Seed dispersal distributions differed among habitat types, with a unimodal seed dispersal distribution within continuous forests and a strongly bimodal distribution in agricultural areas.

The distribution of measurement errors of the loggers demonstrates that the first peak in the movement and seed dispersal distributions of the birds was not caused by measurement error. The peak in the measurement error distribution at 5.6 m (electronic supplementary material, figure S1) is located at a considerably smaller distance than the first peak of the dispersal distribution at about 25 m (Fig. 3.3a,b).

In general, it has been assumed that the seed dispersal kernels generated by mobile animals in continuous landscapes are more or less leptokurtic with a peak close to the seed source, followed by a rapid decline and a long tail. Such a pattern in a fragmented landscape would result in little dispersal among fragmented habitat patches, and would make long-distance dispersal events and transport of seeds among fragmented habitat patches exceedingly rare. The novel GPS data loggers we used allowed us to quantify the movement behaviour of the birds precisely without bias with regard to movement distances. That is, at times in which birds moved large distances, the number and quality of the location data were as high as at times with short movement distances. Rare long-distance flights of the birds between gorges or to coastal areas could be located with the same high probability as short-distance flights. The data generated by the GPS loggers showed that the movement patterns of trumpeter hornbills were more complex than previously anticipated. Different movement behaviour of the birds in the two habitat types resulted in distinctly different dispersal distributions for continuous forests and the fragmented agriculture landscape (Fig. 3.4a,b). Seed dispersal distances averaged over the 10 individuals (Fig. 3.3b) were similar to those of the agricultural habitat (Fig. 3.4b), probably because birds spent on average 50 per cent of their time in agricultural areas and only 30 per cent in continuous forests (and 20% in other habitat types).

The seed dispersal distribution within large continuous forests was unimodal, with a best fit by the Weibull function and an expected dispersal distance of 86 m. For seed dispersal by birds in continuous forests, previous studies found, in general, leptokurtic distributions (Westcott & Graham 2000, Westcott *et al.* 2005, Morales & Carlo 2006). Some of these dispersal kernels were distinctly leptokurtic with only a small proportion of seeds dispersed over long distances. Nevertheless, some studies also showed a small second peak at longer dispersal distances (Murray 1988, Sun *et al.* 1997, Holbrook & Smith 2000, Russo *et al.* 2006). Dispersal distributions for Asian hornbills also showed that these birds have a high potential for transporting seeds across the landscape and for occasional long-distance dispersal (Kinnaird & O'Brien 2007). Comparisons of these seed dispersal distributions with those of the trumpeter hornbills presented here are difficult because of differences in the scaling of the dispersal distances. The fact that dispersal distributions in continuous forest were unimodal can also explain why bird (i) was the only individual that did not have a bimodal seed dispersal distribution (electronic supplementary material, figure S1, bird (i)). This bird was the only bird that spent almost all its time (99%) within the continuous forest of Oribi Gorge.

In contrast, movement and seed dispersal distributions in agricultural areas were bimodal, with a first peak at about 18 m and a second peak at about 512 m. Here, the first peak was best fitted by a Weibull or a normal function and the second peak by a normal function. Goméz (2003) found a bimodal seed dispersal pattern for jays within and between oak forests, but with much smaller dispersal distances than trumpeter hornbills. Other seed dispersal kernels measured in heterogeneous landscapes have been leptokurtic in most cases (Spiegel & Nathan 2007, Levey *et al.* 2008). In agricultural areas, trumpeter hornbills often moved only short distances within and between the crowns of neighbouring trees while foraging within a forest fragment or a farm garden, probably resulting in the first peak in their displacement distribution. However, the birds made equally likely long-distance flights with a preferred distance of about 512 m, resulting in a surprisingly high probability that seeds were transported to such distinct long-distance classes. It is possible that the first peak at about 18 m is caused by the mean size of forest fragments or farm gardens in the study area, and the second peak at about 512 m by the mean distance between suitable habitat patches. To answer this question requires a larger sample size of birds, and more detailed analyses of the habitat choice, size and spatial distribution of suitable habitat patches, and of the movement tracks of the birds and is beyond the scope of the present study.

Table 3.1: *Best fitting probability density functions to seed dispersal distributions within continuous forest and the agricultural landscape (Fig. 4a, b). Fit of the Weibull function to the seed dispersal distribution within continuous forest (all other functions differed by Δ AIC > 9 from the best model). The two best fitting linear combinations of two probability density functions to the bimodal seed dispersal distribution within the agricultural landscape (all other linear combinations differed by Δ AIC > 3 from the best model); a = linear combination parameter.*

continuous forest

function	parameters (+ s.e.)		r^2	AIC	ΔAIC
Weibull	shape = 3.544 (+ 0.09)	scale = 2.151 (+ 0.02)	0.832	1864.5	—

agricultural landscape

function	parameters (+ s.e.) first peak		second peak		a	r^2	AIC	ΔAIC
Weibull/ normal	shape = 3.859 (+ 0.184)	scale = 1.401 (+ 0.029)	mean = 2.710 (+ 0.031)	s.d. = 0.441 (+ 0.023)	0.493 (+ 0.022)	0.877	2225.2	—
normal/normal	mean = 1.275 (+ 0.025)	s.d. = 0.375 (+ 0.018)	mean = 2.716 (+ 0.023)	s.d. = 0.438 (+ 0.022)	0.498 (+ 0.021)	0.878	2227.2	1.9

Here, we would like to emphasize that seed dispersal distributions differed considerably between continuous forests and agricultural areas. Seed dispersal distributions in agricultural areas were more complex than in forests. Furthermore, modal and maximum seed dispersal distances were much larger in agricultural areas (maximum 8914 m) than in forests (maximum 3016 m). This shows that landscape structure strongly influences the movement behaviour, and thus the movement and seed dispersal pattern, of trumpeter hornbills. Previous radio-tracking studies of frugivorous birds within continuous habitats might have, in general, underestimated the ability of large birds to cope with large distances between forests in fragmented, agricultural areas. Trumpeter hornbills regularly moved between forest fragments and between the large continuous forests in the study region. These birds therefore have the potential to disperse seeds over large distances and among patches of suitable habitat. This also allows seeds to move between patches and to reach new sites. The high-mobility, frequent, long-distance flights and the high abundance of these birds suggest that trumpeter hornbills play an essential role for long-distance seed dispersal among the fragmented forests of eastern South Africa.

To conclude, our results show that seed transport among habitat patches might be more frequent than previously assumed. The long seed dispersal distances quantified here emphasize the ability of large frugivorous birds to disperse seeds among habitat patches in fragmented landscapes and their crucial role in allowing plants to adapt to global climate change.

3.6 Acknowledgement

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CHAPTER 4

PROCESSES OF SEASONAL RANGE EXPANSION OF A LARGE FRUGIVOROUS BIRD

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4.1 Abstract

Studies on the ranging behaviour of birds often suggest that ranges vary seasonally with larger ranges in the non-breeding compared to the breeding season. However, due to limitations in tracking methods very little is known about the underlying processes driving seasonal differences in ranging behaviour, especially in fragmented, heterogeneous landscapes. Such knowledge is particularly important if movements deliver essential ecosystem functions such as seed dispersal. We provide the first study comparing daily ranging behaviour between the breeding and non-breeding season of a frugivorous bird and give detailed insights into the process of range expansion during the non-breeding season. We tracked movements of 31 male trumpeter hornbills (*Bycanistes bucinator*) across a fragmented landscape of eastern South Africa using high temporal resolution GPS data-loggers. We found that larger seasonal ranges in the non-breeding season were mostly driven by location shifts of daily ranges across the landscape, rather than increasing mean daily range size. Birds in the breeding season were highly stationary, while birds in the non-breeding season shifted their daily ranging areas across the landscape and showed highly clustered space use at the regional scale. During the breeding season hornbills were mostly located in large continuous forests; birds in the non-breeding season used frequently forest patches within the agricultural landscape and residential areas. The movement behaviour of hornbills in the non-breeding season results in important consequences for seed dispersal of plant species, with more inter-patch dispersal across the agricultural matrix in the non-breeding than in the breeding season. Our findings provide detailed information on seasonal differences in ranging behaviour of frugivorous birds and lead to a better understanding of the processes of seasonal range assembly.

4.2 Introduction

Investigations of animal movement patterns provide knowledge of ranging behaviour and space use which is particularly important if movements deliver essential ecosystem functions (Howe 1998, Nathan 2008). For example, movements of frugivorous birds play a crucial role in population dynamics of trees since frugivores disperse seeds away from the parent tree with corresponding demographic and genetic benefits (Herrera 2002, Gómez 2003, Howe & Miriti 2004, Nathan 2006). Large bird species are critically important especially where forest habitats are fragmented or degraded because they are capable of long-distance movements needed to disperse seeds between the patchy, isolated forest remnants (Westcott and Graham 2000, Jordano *et al.* 2007). In combination with their, compared to small birds, long gut retention time large frugivorous birds are in principle able to transport seeds over long distances (Spiegel and Nathan 2007, Lenz *et al.* 2011).

However, the ecosystem functions these birds provide may vary with season since ranging behaviour may be highly variable in the course of the year (Rolando *et al.* 1998). Especially the breeding status of birds significantly influences their use of space (Suryadi *et al.* 1998, Novoa 2006). Previous studies show that birds have relatively smaller seasonal ranges when nesting and feeding young and increase their ranges during the non-breeding season (Suryadi *et al.* 1998, Grant and Liechtfield 2003, Novoa 2006). However, surprisingly little detail is known about the ranging behaviour of frugivorous birds in the non-breeding season.

When investigating the processes that generate ranges over a whole season it is important to examine ranges with finer temporal resolution, for example, by focussing on ranging behaviour at the daily scale. The increase of ranges in the non-breeding season compared to the breeding season could be either due to larger daily ranges or due to greater variability of locations of daily ranges with little change in daily range size. In the latter case birds would follow a rather nomadic movement pattern where shifts in daily range locations lead to generally larger seasonal ranges. Distinguishing between these strategies is important as they would result in fundamentally different movement patterns. Switching the location of daily ranging sites leads to relatively few long-distance movements, which in turn affects ecosystem functioning such as long-distance seed dispersal.

However, data availability for such fine-scaled analyses has so far been limited for birds (Otis and White 1999, Horne *et al.* 2007), because of technological hurdles (Tomkiewicz 2010). Recent progress in miniaturizing GPS tracking devices has made them suitable for large birds and finally offers the opportunity to obtain regular location data of a bird's movement in high temporal and spatial resolution (Kie *et al.* 2010, Tomkiewicz 2010, Lenz *et al.* 2011). We used GPS data loggers to track movements of trumpeter hornbills (*Bycanistes bucinator*) along the fragmented agricultural landscape of the eastern coast of South Africa. Among frugivorous African and Asian birds, hornbills belong to the major seed dispersers of fruiting trees (Whitney *et al.* 1998, Kinnaird and O'Brien 2007, Kitamura 2011). Studies on hornbill movement within the course of the year report increasing ranges for the non-breeding season (Poonswad and Tsuji 1994, Suryadi *et al.* 1998, Holbrook *et al.* 2002, see Kinnaird and O'Brien 2007). However, so far no quantitative analysis of seasonal changes of daily range size of frugivorous birds exists. To our knowledge, we provide the first study investigating range expansion and seasonal differences in daily ranging behaviour of a large frugivorous bird species. We compared the mean and variance in the size of the daily ranges in the breeding and non-breeding season. Further we calculated the cumulative area increase of daily-ranges across several days to compare range expansion during the breeding and non-breeding season. We also performed seasonal comparisons of clustering and dispersion of locations among daily ranges. In a last point we examined if hornbills used continuous forest and fragmented agricultural landscape differently in the two seasons and draw conclusions on potential important ecological consequences for seed dispersal of large frugivorous birds.

4.3 Methods

4.3.1 Study area

The study area was situated at the East Coast of South Africa within the province KwaZulu-Natal, within one of the recognized global hotspots of biodiversity, i.e. the Maputaland-Pondoland-Albany hotspot (Mittermeier *et al.* 2004). The region is characterized by a highly heterogeneous landscape with a mixture of forests, agricultural, and residential areas. Oribi Gorge Nature Reserve, the centre of the study area, is mostly covered by natural subtropical coastal scarp forest (Pooley 1994) holding the highest species richness of the main forest types in KwaZulu-Natal (Eeley et. al. 2001). The only other large forested areas close to Oribi Gorge are the smaller Mbumbasi Nature Reserve in the south and the forested valley of the Mzimkhulu River in the north. Forests are embedded in an intensively used agricultural matrix, mostly consisting of sugar cane and nut plantations, interspersed by residential areas (cf. Fig. 4.1). Within the agricultural matrix, non-arable sites like rocky outcrops and wet sides close to streams provide small patches and strips of natural forest and residential areas and farm gardens contain indigenous and exotic fruit-bearing trees.

We evaluated habitat cover in ArcView GIS 10.0 (Environmental Systems Research Institute, Inc. 19992010) using the latest KwaZulu-Natal Land Cover dataset (Geoterraimage, preliminary 2005; modified 2008; < www.geoterraimage.com >) together with high resolution satellite imagery (Quickbird imagery, GISCOE 2005; <http://www.giscoe.com>). We defined "continuous forests" as Oribi Gorge Nature Reserve, the densely wooded parts of the Mzimkhulu River valley and Mbumbasi Nature Reserve (trees and bush cover > 70%, see Lenz *et al.* 2011). All other habitat types were grouped to "non-forested habitat" (for example all types of farming, rural and residential areas, gardens of farmsteads and small forest patches (< 156 ha) within the agricultural matrix (see Lenz *et al.* 2011).

4.3.2 Study species

The trumpeter hornbill belongs to the most abundant frugivores in Oribi Gorge (Bleher *et al.* 2003). Within South Africa, it is with an average body weight of 565 g for females and 720 g for males (Kemp 1995) the largest obligate frugivorous bird species. Even during the breeding season 89% of its food items are fruits (Kemp 1995). Due to its large gape width it is able to swallow also large fruits. Breeding period of trumpeter hornbills in Natal in South Africa is from October to January and nesting lasts for at least 94 days (Kemp 1995, Roberts *et al.* 2005). Females enclose themselves in a nesting cavity and she and the juveniles are fed by the male. Juveniles stay for about 6 month with their parents (Kemp1995). Trumpeter hornbills are monogamous and generally move in pairs during the breeding season. However, during the non-breeding season they may form large flocks consisting of both, juveniles and adult individuals (Kemp 1995).

4.3.3 Trapping and tracking

We caught trumpeter hornbills in three different seasons in the years 2008 to 2011. We did not track females because data loggers might interfere with their breeding behaviour. We conducted trapping sessions during the breeding season in 2010 and 2011 (November–December), and during two different periods within the non-breeding season (April–May 2009 and 2010 and July–August 2008 and 2009). Individuals were tracked only either within the breeding or the non-breeding season, never during both seasons. We used free-standing nets placed in flying routes and canopy mist nets at fruiting trees (e.g. of the species *Ficus* spp., *Trichilia dregeana* or *Protorhus longifolia).* Birds were fitted with a GPS-data logger (E-Obs GmbH; Munich, Germany; <www.e-obs.de>). Data loggers were below the generally accepted threshold of 3–5% body weight (Kenward 2001) (males weighed on average 775 g; range 600–880 g, n = 35). GPS-data loggers were attached as a backpack between the wings of the bird. We used Teflon strings with an implemented predetermined breakage point as straps, allowing the data loggers to drop off eventually. After the procedure the animals were released at the trapping location.

We recorded a bird's position every 15 min over the daytime period. Data loggers were programmed to start sampling shortly before and stop sampling shortly after daytime. At night, during the hornbill's inactive phase, data loggers were programmed to switch to standby to save battery energy. Every 15 min, data loggers measured the location of the bird, the accuracy of the location measurement as well as the speed of the bird using the Global Positioning System GPS. We downloaded the data remotely via radio link to a handheld receiver. To relocate tagged birds we searched systematically through habitats appropriate for trumpeter hornbills for foraging or roosting and placed stationary receivers at suitable locations. The battery of the data loggers lasted on average 19 days. To insure that we included only non-biased movement data we did not use the first three days of tracking (see Lenz *et al.* 2011). We also considered only days with at least 30 locations and used only data of birds with a minimum of two days of tracking data.

4.3.4 Data Analysis

Calculating ranges

We calculated daily ranges for each individual using the Brownian bridge movement model (BBMM) developed by Horne *et al.* (2007). The BBMM considers the time dependence between successive locations and thus accounts for the order of locations and the time interval in between them (Bullard 1999, Horne *et al.* 2007). Consequently, the BBMM makes explicitly use of autocorrelated movement data which might contain important biological information (De Solla *et al.* 1999, Otis and White 1999, Blundell *et al.* 2001).

All analysis was done in R version 2.13.0 (R development core team 2010). We calculated a Brownian bridge kernel for each bird and tracking day using the R package adehabitat (Calenge 2006). We selected the 95 % isopleths for daily range calculation (Seaman 1999). Calculation of Brownian bridge kernels requires two smoothing parameters, *Sigma1* and *Sigma2*. *Sigma1,* the Brownian motion variance, accounts for the average speed of the animal. We used the average above ground speed per bird per day, recorded by the data loggers, and calculated *Sigma1* with Horne's *et al.* (2007) maximum likelihood based algorithm (implemented in adehabitatHR, Calenge 2006). The second smoothing parameter

Sigma2 is related to the precision of the locations and therefore we used the average measurement error per bird per day, also recorded by the data loggers. Because the movement behaviour of the birds varied between and within individuals, we calculated both smoothing parameters for each bird and day separately.

To obtain comparable data quantity among tracking days we calculated daily ranges per bird by randomly sampling 30 locations out of each tracking day's total number of locations without replacement. We chose 30 locations since this provided the best compromise of available data and minimum data requirements for home range calculations (White and Garrott 1990, Seaman 1999). To avoid sampling bias we repeated this procedure 10 times and calculated mean areas of daily ranges for each bird and day.

Comparing daily range size and variance

We tested if daily range sizes differed between the breeding and the non-breeding season. We log-transformed the sizes of the daily ranges and used linear mixed models (function lmer in R, library lme4, Bates *et al.* 2011) with a fixed effect of season, incorporating random effects for both the individual and the tracking year. We also tested whether variances of daily range sizes differed between the seasons. We calculated the variance among daily range sizes for each hornbill and again used linear mixed models with a fixed effect of season, accounting for different years with a random effect. We tested for the significance of the fixed effects using Markov chain Monte Carlo (MCMC) methods (function pvals.fnc in R, library languageR, Baayen 2008).

Range expansion and stationarity of daily range locations

To test if range expansion over several days differed between seasons, we calculated the cumulative area of multi-day ranges for birds in the breeding and in the non-breeding season. We expected that cumulative multi-day range sizes increased faster from day to day in the non-breeding than in the breeding season. Because an increase in cumulative multi-day range size indicates that birds used rather different areas each day, we used this increase as a measure of variability in spatial location of daily ranges. We calculated the cumulative area increase across daily ranges from one up to nine days. We chose nine days because most birds provided at least nine days of movement data. We randomly drew nine daily ranges without replacement per individual and calculated cumulative areas by overlaying up to nine of these daily ranges. We repeated the procedure 1000 times per bird and obtained average cumulative multi-day range sizes from one to nine days. We used linear mixed models (described above) to test whether the interaction between number of days over which multi-day ranges were calculated and season had a significant effect on cumulative multi-day range size. A significant interaction term indicates a different range expansion among seasons. We calculated a random intercept and random slope model and included birds and tracking year as random effects for intercept and slope.

Characterizing patterns of locations among tracking days

To understand seasonal differences in ranging behaviour we also examined for each bird the spatial clustering or dispersion of locations among days. We analysed for each individual the spatial position of each day's locations relative to all other locations (Mueller *et al.* 2011). We treated the locations of a particular day as a statistical point pattern and calculated the bivariate k function between each day's location point pattern and the location point pattern built up of all other locations of the particular individual. The bivariate k function (Rowlingson and Diggle 1993) calculates the expected number of points of pattern A (locations of one day) within a distance s of an arbitrary point of pattern B (locations of all other days), divided by the overall point density in pattern A (function k12hat, R library splancs, Rowlingson *et al.* 2008). Values near zero indicate randomness, above zero spatial dispersion, and below zero spatial clustering of location point patterns across daily ranges. A pattern of dispersion indicates that locations of daily ranges are evenly distributed within the total range, thus birds use each site within the total range with the same intensity. A clustering among days indicates that birds use different areas in their total range with different intensity, i.e. that daily ranges are concentrated at certain sites within the total range. We calculated for each individual the mean and the range of estimates for the bivariate k-function at different spatial lags (s).

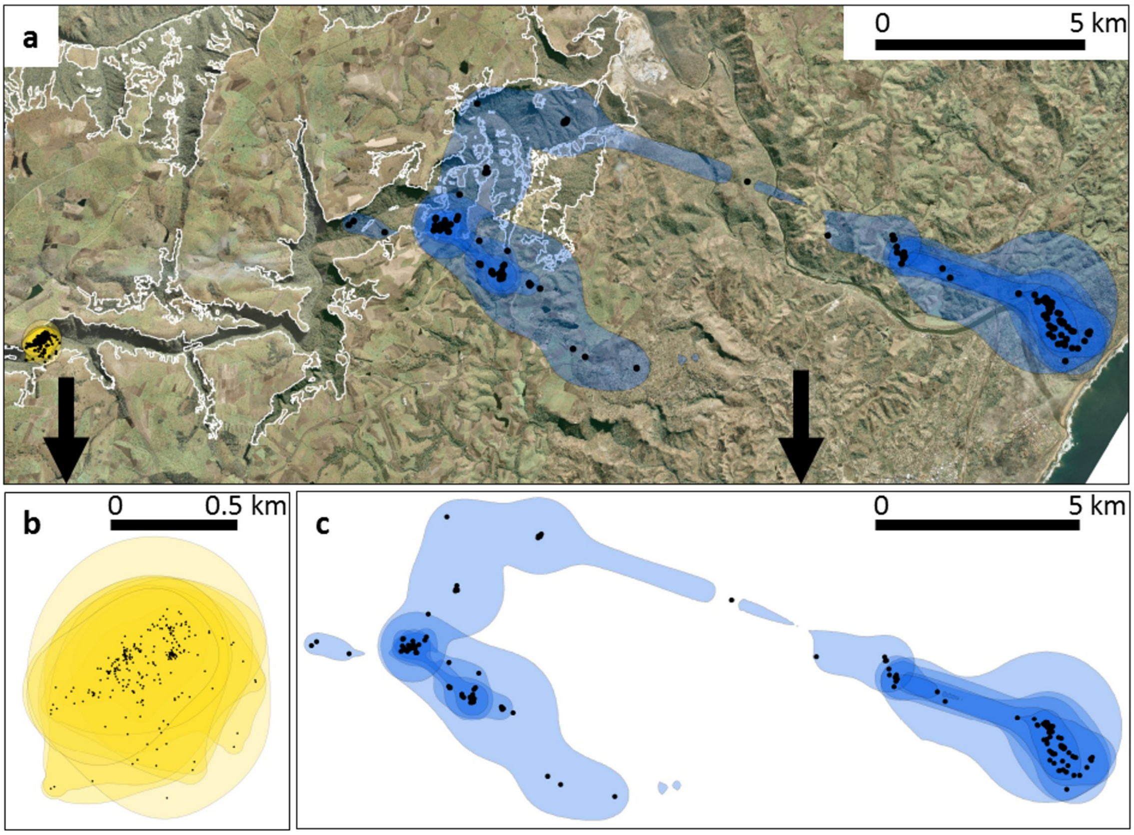

Figure 4.1: *Transparent polygons depict nine daily ranges of a single bird in a. the breeding season (yellow) and b. (of a different bird) in the non-breeding season (blue). The underlying satellite image shows the fragmented landscape of the study area with white markings bordering the continuous forest.*

4.5 Results

We collected location data of 31 male trumpeter hornbills and after the refinement of data (see methods) our analysis was based on 29 male birds ($n_{\text{breeding season}} = 9$; $n_{\text{non-breeding season}} = 20$) with movement data of on average 14 days (range 2–52) and 43 locations (range 30–54) per day. In total we had data from 457 tracking days ($n_{\text{breeding season}} = 165$; $n_{\text{non-breeding season}} = 292$) and 19,781 locations ($n_{\text{breeding season}} = 7{,}645$; $n_{\text{non-breeding season}} = 12{,}136$). Averaged measurement error as retrieved trough the GPS modules over all data-loggers was 17 m (breeding season = 18 m, non-breeding season = 16 m). Median size of the 95% kernel of the daily ranges was for birds tracked in the breeding season 41.9 ha (range 1.8–418.8 ha) and for those tracked during the nonbreeding season 164.4 ha (range 1.5–3520.67 ha). Daily range sizes in the breeding season ranged about three orders of magnitude and those in the non-breeding season about four orders of magnitude. When log-transforming daily range sizes and accounting for the random effects of individuals and years, mean daily ranges were not significantly different between seasons (mean($\log_{10}$) $_{\text{breeding season}}$ = 36.0 ha, mean($\log_{10}$) $_{\text{non-breeding season}}$ = 129.4 ha, $P_{\text{MCMC}} = 0.452$, Fig.2a). Median of variances of daily range sizes of birds in the breeding season was 1.25 (range 1.07–1.95), of birds in the non-breeding season 1.68 (range 1.10–6.99). With log-transformed daily range sizes and incorporating the random effect of individuals, variances of daily ranges were significantly different between seasons (mean($\log_{10}$) $_{\text{breeding season}}$ =1.32, mean($\log_{10}$) $_{\text{non-breeding season}}$ = 2.00, $P_{\text{MCMC}} = 0.025$; Fig. 4.2b) with daily range sizes being more variable in the non-breeding season.

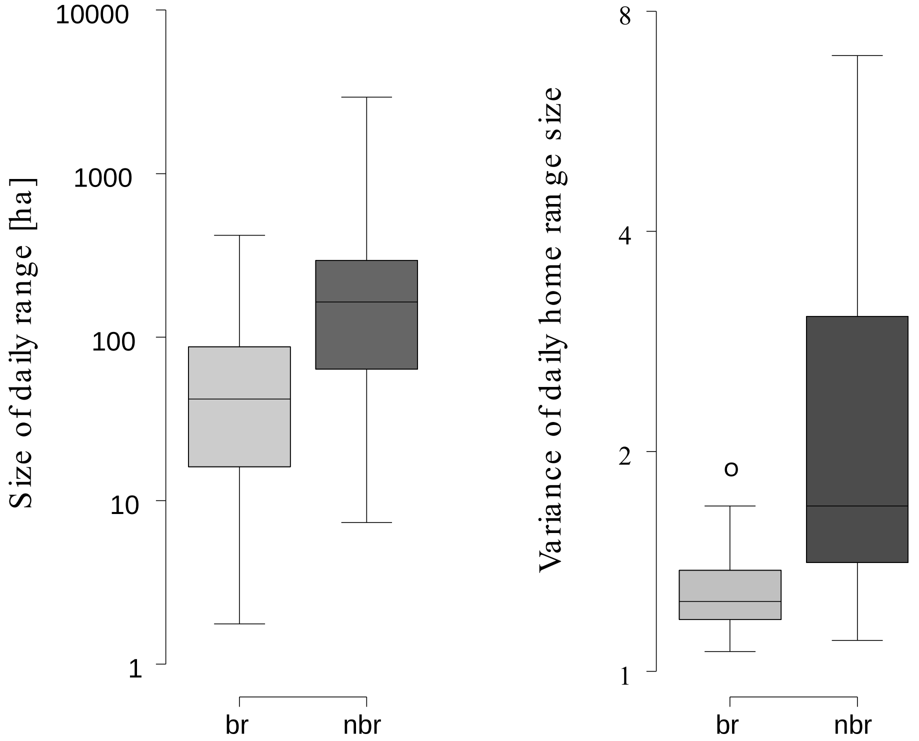

Figure 4.2: *Differences (median and ±SD) in size of daily ranges (a) and of variances in daily range size (b) for birds in the breeding season (br, light grey, n = 8) and bird in the non-breeding season (nbr, dark grey, n = 23).*

Cumulative area of multi-day ranges of up to nine days resulted in no significant increase of range size for birds in the breeding season, whereas hornbills in the non-breeding season increased their cumulative range with days significantly (Tab. 4.1, Fig. 4.3). Consequently, spatial variation in the location of daily ranges was significantly greater in the non-breeding season than in the breeding season (e.g. Fig. 4.1). During the non-breeding season we often observed nomadic movement behaviour of hornbills: The birds stayed in a specific area for a couple of days with overlapping daily ranges, moved to a different region and stayed there for a few days, and so forth (see Fig. 4.1b). After a while birds tended to return to previously visited areas.

Table 4.1: *Effect of the number of days and season on multi-day range sizes of trumpeter hornbills. We calculated cumulative area of multi-day ranges from one to nine days. Linear mixed model incorporating the tracking year and the individual as random factors for intercept and slope.* $n_{\text{breeding season}} = 8$ *birds,* $n_{\text{non-breeding season}} = 17$ *birds; significance code:* $p < 0.001$****,* $p < 0.01$***,* $p < 0.05$**.*

Fixed effects	**Estimate**	**SE**	**Random effects**	**SD**
(Intercept)	6.17***	0.21	Individual	0.47
Days	0.06	0.01	Individual × days	0.01
Days × non-breeding	0.03***	0.01	Year	0.36
			Year × days	0.00

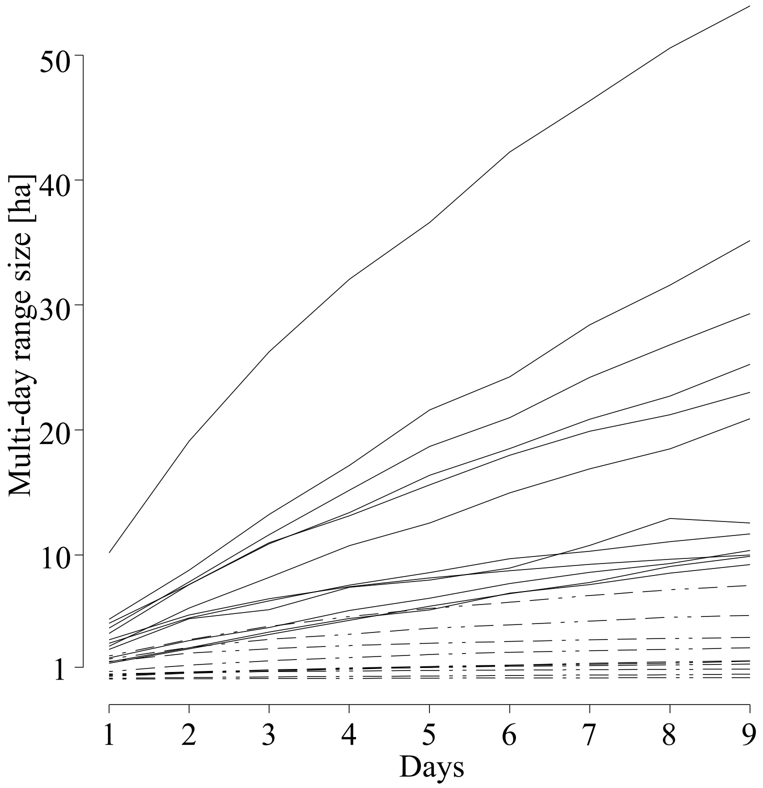

Figure 4.3: *Mean of 1000 bootstrap estimates of cumulative area of multi-day ranges from one to nine randomly chosen days. Dashed lines = breeding season (n = 7 birds), solid lines = non-breeding season (n = 14 birds).*

Results of the bivariate k function showed that trumpeter hornbills created a rather spatially clustered pattern among daily ranges (Fig. 4.4). Nevertheless, clustering was much stronger for birds in the non-breeding season. Only one bird tracked during this season showed a ranging behaviour rather matching the pattern of the birds in the breeding season, for all other birds the pattern was specifiable in accordance to season (Fig. 4.4). This shows that in the non-breeding season daily ranges were concentrated at certain sites in the total range, whereas hornbills in the breeding season distributed their daily ranges more evenly over the total range area. 94% of locations in the breeding season were located within continuous forest and only 6% were found in other habitats (for a typical example see Fig. 4.1). In contrast only 32% of locations in the non-breeding season were within closed forests and 68% were located in other habitats.

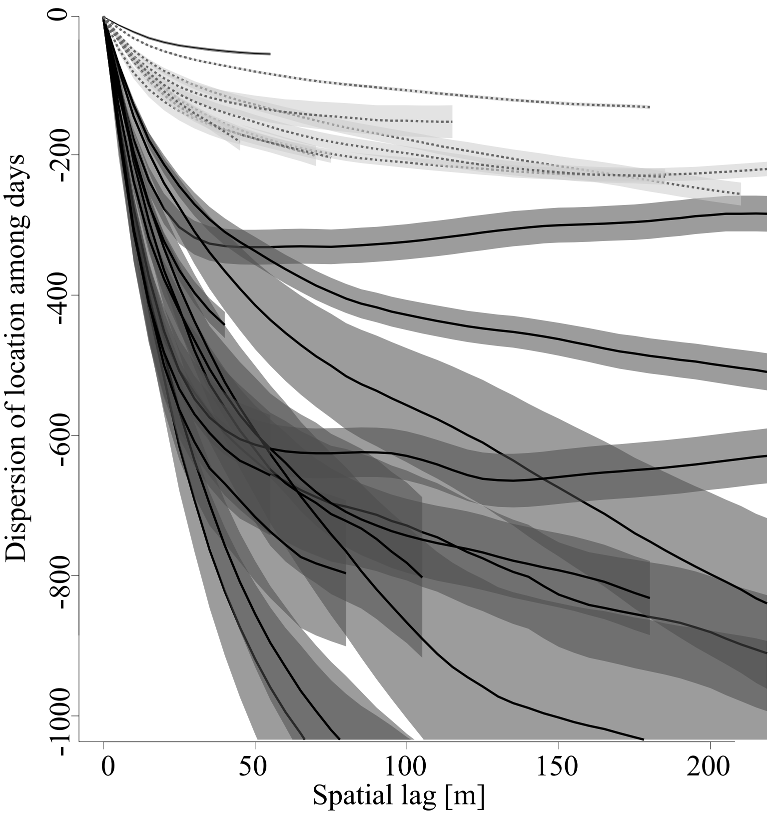

Figure 4.4: *Dispersion of locations among daily ranges. Bivariate k-function estimates between each day's location data and the location data of all other days of a particular individual as a function of spatial lag. Breeding season (dashed lines, light grey, n = 7 birds), non-breeding season (solid lines, dark grey, n = 14 birds). Lines show the mean and shaded areas the range of all estimates. Values above zero would indicate spatial dispersion and negative values spatial clustering between locations of different days. For birds in the non-breeding season it is shown that daily ranges clustered at different sites whereas daily ranges for birds in the breeding season where more evenly distributed in their total range (cf. Fig. 4.1).*

4.6 Discussion

Our approach to investigate changes in ranging behaviour on a daily basis provided new insights into the underlying process of range expansion. Range expansion during the non-breeding season happened mostly because hornbills shifted the location of daily ranges in the non-breeding season and not because of greater daily range sizes. In the non-breeding season daily ranges of trumpeter hornbills were more variable in size and location compared to the breeding season.

In the breeding season, hornbills had small daily ranges that were similar in size among days. Furthermore, cumulative multi-day range sizes did not increase significantly within our nine day window (Fig. 4.3), demonstrating that daily ranges did not change their spatial location among days. In addition, we observed that in the breeding season birds spent almost all time exclusively within continuous forest. Considering that a male bird has to gather food for its female and offspring in the breeding season and hence has large food requirements, small ranges in combination with highly stationary spatial location were rather surprising. However, there are a number of possible causes that might explain the small and stationary daily ranges of the breeding season: A feeding hornbill has to visit the nest at least once every 12h (Kemp 1995, Roberts *et al.* 2005, Kinnaird and O`Brien 2007). Foraging within farmland to reach widely scattered food resources would cause higher energetic cost in the breeding season (Graham 2001). Thus ranging behaviour might be constrained due to central place foraging (Rosenberg 1999). Our results suggest that birds found sufficient food resources within these small ranges. Within the forest many trees of different species can occur within a small area; thus birds may reach different food resources easily. In addition, trumpeter hornbills might reach their food requirements by adding other food resources than fruits, like insects and small amphibians, to their diet during that season (Kemp 1995). Likewise, helpers, trumpeter hornbills functioning as additional feeders, could cover the demand on food items of the female and the offspring (O' Brien 1997). Agricultural areas might provide no appropriate nesting trees or sites are not suitable because of a scattered distribution of food resources. Our study hence demonstrates the importance of continuous forest for trumpeter hornbills as suitable breeding habitat, providing suitable nest sites and sufficient food resources.

Our findings support the general notion that seasonal range sizes of frugivorous birds increase during the non-breeding season. While mean daily range sizes were not significantly larger in the non-breeding than in the breeding season, we found an increase of multi-day ranges with days, demonstrating that hornbills expanded their range during the non-breeding season by shifting locations of daily ranges (Fig. 4.3). To understand the process of range expansion during the non-breeding season we examined the spatial relation of locations between daily ranges and thus the process of how several daily ranges aggregated to a larger multi-day range. The analysis of the spatial position of each day’s locations point pattern relative to all other locations of a particular bird showed that daily ranges were clustered within multi-day ranges (Fig. 4.4). This means that several daily ranges were located at specific sites, whereas other sites were rarely used. Consequently hornbills in the non-breeding season did not increase their range size continuously from day to day, but with shifts of the general location of daily ranges to a different area every couple of days. We found that usually small daily ranges were located over several days within the same area; whereas large daily ranges resulted from movements to a different general area (e.g. see Fig. 4.1b), explaining the large variance in daily range sizes in the non-breeding season. Nomadic movements for hornbills were reported by Kemp (1995) and Kinnaird and O'Brien (2007) and seasonal shifts in abundance of hornbills were detected for several regions (Kinnaird *et al.* 1996, Rainey and Zuberbühler 2007, Kemp *et al.* 2011). In contrast to our findings, those shifts persisted for longer than only a few days and indicate a general and broader seasonal shift in foraging ground and tracking of fruit resources via seasonal migrations (Whitney and Smith 1998). On a daily basis, Nova *et al.* (2006) report for partridges (*Perdix perdix hispaniensis*) an increase of daily movement distances with increasing mobility of the offspring. For blackbirds (*Turdus merula*) daily ranges were larger on days on which the birds were not feeding young and were smaller on days when the birds fed young (Neitscher 2010). However, range expansion of trumpeter hornbills was not significant on a day-based resolution, but due to nomadic movement, hornbills assembled daily ranges to a larger overall range.

Several reasons might explain the range expansion via nomadic location shifts of daily ranges. Almost all hornbills tracked in the non-breeding season frequently used the agricultural landscape and foraged within the smaller forest patches, residential areas, and farm gardens. Because trees occur in the agricultural landscape only in a scattered distribution, finding enough and different kinds of food resources might only be possible by the regular switching of locations hornbills exhibited in the non-breeding season. This switching behaviour is possible across large scales during the non-breeding season, because birds are not bound to a nest site and do not need to follow a central place foraging strategy. However, while greater dispersion of food resources in the agricultural matrix might explain differences in movements compared to the forest, it does not explain why hornbills leave the continuous forest in the first place and expand their range in the non-breeding season. First the small ranges in the breeding season might not allow collecting sufficient resources, might lead to weight loss and may be tolerated by hornbills only over the rather shorter time periods of the breeding season. Second, it is likely that there are genuine advantages of the range expansion and dispersion during the non-breeding season. Hornbills may find new fruit resources and new suitable nest sites. Hornbills form large communal flocks in the non-breeding season and may benefit from each other's knowledge of resource distributions. Thirdly, unmated hornbills may search for mating partners across a wider range. Overall, social interaction may play an important role for range expansion of trumpeter hornbills during the non-breeding season.

Finally, the strong seasonal differences in ranging behaviour should also have ecological consequences for plant species dispersed by trumpeter hornbills. During the breeding season seed dispersal by hornbills would be constrained to large, continuous forests and not reach the smaller patches in the agricultural matrix. In addition, the small daily ranges would cause short-distance seed dispersal limited to the close neighbourhoods of the parental trees and seed transport through breeding birds would concentrate seed deposition at the nesting tree (Howe 1989, Kitamura *et al.* 2004, Kitamura 2011). These patterns should especially limit seed dispersal for trees fruiting exclusively in September to December, the breeding season of trumpeter hornbills, for example red beech (*Protorhus longifolia*) (Pooley 1994). Limitations of seed dispersal in the breeding season could lead to reduced meta-population dynamics causing genetic isolation and difficulties for plants species to adapt to changing environmental conditions (Nathan 2006).

In the non-breeding season, daily ranges were mostly located within the agricultural landscape, but often included more than one forest patch. This behaviour should allow inter-patch dispersal for tree species fruiting during the non-breeding season of trumpeter hornbills.

However, there is the possibility that seed dispersal in the agricultural landscape maybe limited due to low seed survival and seedling establishment (e.g. Cordeiro and Howe 2001). In addition, dispersal activity that includes residential areas might be problematic since birds could function as dispersal vectors also for exotic plant species.

Conclusions

Our focus on a day-based resolution of ranging behaviour revealed that range expansions of trumpeter hornbills in the non-breeding season were mostly due to shifts in the location of daily ranges and not due to larger daily ranges per se. During the breeding season birds seemed to be constricted to large forested areas and thus seed dispersal during this time of the year would lead to short dispersal distances almost only within continuous forests. Also in the non-breeding season trumpeter hornbills tended to have small daily ranges and large distance movements occurred only when birds moved across the matrix of the agricultural landscape to a general different region. Most daily ranges included multiple forest patches and, thus, inter-patch dispersal might be frequent during this season. The small daily ranges of trumpeter hornbills in the breeding season could indicate how limitations in movement ability of large frugivorous birds, e.g. due to landscape fragmentation, could affect the dispersal ability of plants. Seasonal changes in ranging behaviour of animals could cause crucial alterations in ecosystem functions and understanding the processes of range variation helps to determine the ecological consequences of those seasonal differences.

4.7 Acknowledgement

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CHAPTER 5

LARGE FRUGIVOROUS BIRDS FACILITATE FUNCTIONAL CONNECTIVITY OF FRAGMENTED LANDSCAPES

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5.1 Abstract

Facing increasing habitat fragmentation and climate change, between-patch dispersal of seeds by frugivores becomes ever more important for fleshy-fruited plants. However, to date, methodological hurdles have limited our understanding of between-patch dispersal on the landscape scale. We made use of newly available tracking devices and combined movement data of 32 trumpeter hornbills (*Bycanistes bucinator*) with gut-passage times and high-resolution habitat data to examine functional connectivity in a fragmented landscape in South Africa. Although potential between-patch dispersal events were rare (on average 7%), they could cover distances of up to 15 km. Hornbills visited over 100 forest patches and connected a habitat network with an extent of about 50 km. They increased the potential functional connectivity of the landscape more than twofold and we identified critical stepping-stones for seed dispersal pathways. Without these stepping-stones the network would likely disintegrate into separated components and lead to isolation of forest fragments. We demonstrate how high resolution movement and landscape data can be used for spatially explicit mapping of potential seed dispersal pathways and connectivity networks, which will be critical for maintaining and managing ecosystem functions in the face of global change.

5.2 Introduction

Seed dispersal by frugivorous animals is critical for ecosystem functioning especially in the tropics since most tropical and many subtropical trees depend on seed dispersal by frugivorous animals, often birds (Howe & Smallwood 1982, Herrera 2002, Levey *et al.* 2002, Forget *et al.* 2011). Since tropical forests become increasingly fragmented into small patches (Foley *et al.* 2005, Mayaux *et al.* 2005) frugivores play an even more important role as they have the potential to facilitate seed dispersal among forest fragments (i.e., patches). Otherwise, the isolation of forest fragments limits the exchange of propagules which can have severe demographic and genetic consequences (e.g. Howe & Miriti 2004). In addition, gene flow among fragmented populations is important to allow trees to adapt to changing environmental conditions (Cain *et al.* 2000, Nathan 2006). Especially under climate change it will be critical that species are able to adjust their ranges and move distances that allow them to keep track with their preferred climatic conditions (Loarie *et al.* 2009, Hof *et al.* 2012, McConkey *et al.* 2012, Kremer *et al.* 2012). For animal-dispersed plant species in fragmented landscapes this is only possible by between-patch movements of frugivores (Damschen *et al.* 2008). Assessing how frequently frugivorous birds move seeds between forest fragments and identifying between patch pathways through the landscape will thus be key to manage for allowing tropical trees to adjust to and track climate change.

If a bird ingests tree seeds in a fragmented landscape, in principle, three scenarios are possible: Seeds could be moved until they reach a different forest patch. This constitutes *between-patch dispersal* and facilitates not only gene flow and recruitment, but it also allows range adjustments in the wake of climate change. Ideally each patch is connected frequently and to many other patches via seed dispersal by frugivores to safeguard from fragment isolation and allow range adjustments. Secondly, a seed could be moved from the parent tree but is deposited in the same patch where it originated. *Within-patch dispersal* allows for recruitment away from the parent tree but no long-distance movement or gene flow among patches. Finally, dispersal fails, if ingested tree seeds are moved outside the patch where they originated but are deposited in the inhospitable matrix habitat.

Several studies demonstrate that large fruit-eating bird species such as hornbills in Southeast Asia and Africa, and toucans in the Neotropics are able to fly between forest patches of fragmented landscapes and have the potential to act as long-distance seed dispersers (Kemp 1995, Powell and Bjork 1995, Holbrook and Smith 2000, Graham 2001, Chaves-Campos *et al.* 2003, Price 2006, Kays *et al.* 2011, Lenz *et al.* 2011). In addition, previous studies have investigated seed dispersal patterns of trees by combining distributions of movement data of birds and gut passage times (GPTs) of seeds (Price 2006, Kays *et al.* 2011, Lenz *et al.* 2011). This approach has been used mostly for quantifying short-distance seed dispersal within forest patches (Murray 1988, Sun *et al.* 1997, Holbrook & Smith 2000, Westcott & Graham 2000, Westcott et al 2005).

However, to date, long-distance dispersal among habitat patches has been difficult to quantify and has been less studied (but see Gómez 2003, Spiegel & Nathan 2007), in particular because movement data for birds was not available in the high temporal and spatial resolution necessary to track between-patch movements. To our knowledge, no study so far used movement data and GPTs for quantifying the frequency of between-patch dispersal and spatially explicit mapping of seed dispersal paths among forest patches and for quantifying the degree to which large frugivorous bird movements could increase landscape connectivity.

We demonstrate how newly available high-resolution data from miniaturized GPS tracking devices can be used to assess how large frugivorous birds facilitate functional connectivity of fragmented landscapes.

We studied seed dispersal by trumpeter hornbills (*Bycanistes bucinator*) along the eastern coast of South Africa. Trumpeter hornbills are the largest obligate frugivorous birds in South Africa and reach high abundances in the coastal and riverine forests of KwaZulu-Natal (Kemp 1995, Bleher *et al.* 2003). The forest fragments of south eastern South Africa are a global hotspot for tree diversity (Mittermeier *et al.* 2004), but after decades of human land-use these forests are today heavily fragmented and only few natural forest patches remain (Eeley *et al.* 2001). The study area is thus ideal to investigate seed dispersal in fragmented landscapes.

We tracked movement patterns of hornbills and used data on feeding trials of captive birds to asses GPTs. We combined distributions of movement patterns and GPTs to derive potential seed dispersal events (Lenz *et al.* 2011). We also used high resolution habitat data to classify the landscape into forest patches (i.e., habitat that allows natural recruitment of tree seeds) versus matrix habitat. We evaluated whether potential seed transport happened to a different forest patch (*between-patch dispersal*), within the same patch (*within-patch dispersal*), or into the habitat matrix (*failed dispersal*).

We conducted our analyses with two goals in mind: (1) We aimed to investigate questions related to the frequency of between-patch dispersal: How often do dispersal events occur that constitute between-patch dispersal compared to within-patch and failed dispersal? Is landscape configuration, i.e. between-patch distance critical for dispersal events? Are there seasonal differences in the frequency of between-patch dispersal events? Overall, we expected less between-patch dispersal in the breeding season when birds are bound to nest sites and ranging behaviour may be significantly reduced compared to the non-breeding seasons. (2) We asked questions related to the location of potential dispersal pathways through the landscape. Are there forest patches that represent critical stepping-stones for landscape connectivity? Finally we aimed to quantify the increase in landscape connectivity, comparing landscape connectivity with and without between-patch seed dispersal by hornbills.

5.3 Methods

5.3.1 Study area and habitat

The study area lies at the east coast of South Africa in KwaZulu-Natal centred around the Oribi Gorge Nature Reserve approximately 100 km south of Durban and 20 km inland from Port Shepstone. The area features subtropical coastal scarp forest with some of the highest tree diversity on earth (Mittermeier *et al.* 2004).

Large natural forests lie in deep gorges and on steep slopes (e.g., Oribi Gorge Nature Reserve, Mbumbasi Nature Reserve). These nature reserves are surrounded by intensively used farmland, especially sugarcane plantations. Within the agricultural matrix, there are small remnant patches and strips of natural forest. In addition, the farmhouses in the agricultural areas often have large gardens that contain indigenous and exotic fruit-bearing trees. Climate change is expected to have severe consequences for these forests making significant altitudinal and latitudinal shifts of tree species necessary (Eeley *et al.* 1999).

To map and distinguish habitat that is suitable for natural recruitment of indigenous fruit-bearing trees from areas that are unsuitable, we used the KwaZulu-Natal Land-Cover dataset based on SPOT satellite imagery (GeoTerraImage, Pretoria, South Africa) as a base layer. We defined as suitable habitat areas that were categorized as forest (indigenous), dense thicket and bush (70 – 100 % canopy closure) and medium bush (< 70% canopy closure; in the following all termed forest). For all other land-cover classes successful natural establishment of a dispersed seed is very unlikely (e.g., sugarcane plantations, rural areas, farm gardens, roads) and we grouped them collectively as matrix habitat. Since the land cover data set has a rather coarse resolution of 20 m we acquired high resolution Quickbird imagery (GISCOE, Gauteng, South Africa) for the entire study area (a total of 142 Quickbird scenes) with a resolution of 60 cm to refine our habitat map. This imagery allowed a much finer delineation of habitat edges. We visually inspected all locations hornbills had visited (see description on hornbill movements below) and used on-screen digitizing to (1) adjust edges of all forest patches hornbills had visited and (2) to correct for possible habitat misclassification of the coarser base layer.

5.3.2 Hornbill movement and gut passage time

Trumpeter hornbills are the largest obligate frugivorous birds in South Africa and are among the most abundant frugivores in the study area (Kemp 1995). From 2008 to 2011 we caught trumpeter hornbills throughout the study region, around Oribi Gorge nature reserve and around the coastline, during the breeding and non-breeding seasons. We equipped male birds with backpack style GPS loggers. We did not track females since the data logger may interfere with their breeding behaviour. GPS loggers were programmed to measure the position of birds in 15 min intervals throughout the day. At night, when hornbills do not move, we did not record any positions. GPS relocations were downloaded remotely via VHF receivers. Since it was not necessary to recapture birds and we were able to relocate all birds and download their data, we achieved a representative sample of movement distances without a bias in favour of short distances (as is the case with traditional ground-based telemetry methods).

Hornbills almost exclusively feed on fruits even throughout the breeding season and their large gape width allows them to swallow and transport also large seeds (Kemp 1995). We used GPT data of feeding trials from Lenz *et al.* (2011). They determined the distribution of GPTs for trumpeter hornbills (median: 57 min; minimum: 15 min; maximum: 155 min) and they also did not find any significant difference among different fruit types and sizes or bird individuals in GPTs. Hornbills tend to pass small seeds through the gut and regurgitate large seeds.

5.3.3 Frequency and limitation of between-patch dispersal

To quantify the frequency of and identify limiting factors for between-patch dispersal we calculated potential seed dispersal distributions by combining the individual displacement distributions of each bird with the GPT distribution. We used only days for which we had at least 30 relocations and eliminated the first three days of tracking when movement distances were shorter (see Lenz *et al.* 2011). We randomly selected a thousand starting points in the movement track of each bird. We then drew a time interval from the distribution of GPTs (ranging from 15 min to 150 min) to identify an endpoint on the bird's movement track and calculated the Euclidean distance between each starting point and endpoint Westcott *et al.* 2005, Spiegel and Nathan 2007, Lenz et al 2011). Since seed dispersal cannot originate from the habitat matrix, starting points were only allowed when they were located in a forest patch. For each event, we then recorded whether it ended in a different patch than where it had originated, in the same patch, or in the habitat matrix. This procedure weighted the distribution of movement distances with the GPT distribution and allowed us to model how often dispersal events occurred that constituted between-patch dispersal compared to within-patch dispersal and failed dispersal. Please note, that we did not track seeds directly, nor did we assess the likelihood whether seeds that had been moved by hornbills established themselves. Thus, in this paper, we investigate potential, rather than actual functional connectivity.

We also investigated effects of landscape configuration and seasonality. We compared between-patch dispersal distances with patch-to-all-other-patches distances and patch-to-nearest-patch distances. To calculate those distances we used patch centroids for all those patches that had been visited by hornbills. If distance among patches mattered and dispersal occurred mostly from one patch to the nearest neighbouring forest patch, we expected shorter distributions of successful between-patch dispersal events compared to patch-to-all-other-patches distances. Accordingly, we expected similar distributions of between-patch dispersal events compared to patch-to-nearest-patch distances. Finally, we compared seasonal differences in the frequency of between-patch dispersal. Since birds are bound to the proximity of the nesting site in the breeding season we expected less between patch dispersal in the breeding season than in the non-breeding season.

5.3.4 Functional connectivity and mapping dispersal pathways

To calculate the degree to which hornbills raised functional connectivity in the landscape we used all tracking data and identified every potential seed dispersal path, i.e. every movement within 150 minutes that ended in a different forest patch than where it had originated. We mapped all these possible connections and generated a spatially-explicit, binary, non-directed graph network (Calabrese & Fagan 2004). Using node and link weighted network measures (Rayfield *et al.* 2011) we compared landscape connectivity with and without between-patch seed dispersal by hornbills. Specifically, we calculated the integral index of connectivity (*IIC,* eq. 1, (Rayfield *et al.* 2011, Saura 2008, Saura & Rubio 2010) as:

$$IIC = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n}\frac{a_i \cdot a_j}{1+nl_{ij}}}{A_L^2}$$

eq. 1

where n is the total number of nodes (i.e., forest patches) in the landscape, a_i and a_j are the area sizes of nodes i and j, nl_{ij} is the number of links in the shortest path (topological distance) between patches i and j, and A_L is the total landscape area. This index calculates whether two seeds randomly placed within the landscape fall into the same forest patch or forest patches that are connected via dispersal links. The index accounts for both, topology and area size of patches. We used the software Conefor Sensinode 2.2 (Rayfield *et al.* 2011) to calculate *IIC*. We calculated the total landscape area used by hornbills with an alpha convex hull (disc radius: 3 km) encompassing all hornbill relocations.

We identified critical stepping stones for seed dispersal by calculating betweenness centrality for each patch, i.e. the number of geodesics or shortest paths going through a patch (library "igraph" in R Development Core Team 2010) and identifying those forest patches in the upper five percentile of betweenness centrality.

5.4 Results

We tracked 32 birds, 10 in the breeding and 22 in the non-breeding season with a total of 543 tracking days and 23,794 relocations. For the frequency analyses we refined the data (see methods) and had data of 31 birds, 9 in the breeding and 22 in the non-breeding season with a total of 461 tracking days. Overall, 7% of all potential dispersal events constituted between-patch dispersal. However, that proportion varied by season, with only 4% of all dispersal events in the breeding season being predicted to be between-patch dispersal compared to 8% in the non-breeding season (Fig. 5.1). 20% of all dispersal events were predicted to end in the habitat matrix (failed dispersal). That means that in total about 27% of all dispersal events left a forest patch and 73% of all potential dispersal events occurred within the same forest patch. Again, that proportion varied by season with almost all potential dispersal events, i.e. 93%, in the breeding season being within-patch dispersal, compared to only 67% in the non-breeding season.

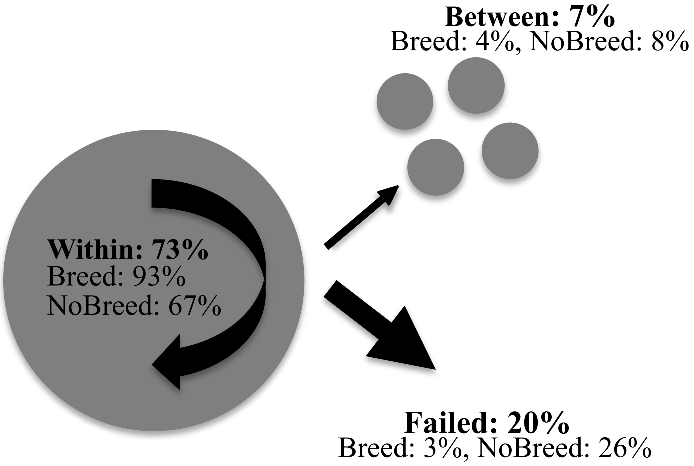

Figure 5.1: *Proportion of potential between-patch dispersal compared to within-patch dispersal and failed dispersal ending in the landscape matrix. Potential between-patch dispersal occurred on average to four different patches. Breed: Breeding season, NoBreed: Non-breeding season.*

Between-patch dispersal (median = 1,513 m, min = 77 m, max = 14,790 m, Fig. 5.2) had the longest distances, compared to failed dispersal (median = 584 m, min = 7 m, max = 13,980 m, Fig. 5.2) or within-patch dispersal (median = 68 m, min = 0 m, max = 5,103 m, Fig. 5.2). Likewise patch-to-all-other-patches distances (median = 15,110 m, min = 75 m, max = 48,710 m, Fig. 5.3) were considerably greater than between-patch dispersal distances. However, patch-to-nearest-patch distances were slightly shorter (median = 728 m, min = 75 m, max = 5,413m, Fig. 5.3) than successful between-patch dispersal distances. All between-patch dispersal across distances greater than 3 km happened in the non-breeding season (non-breeding season: median = 1,722 m, min = 77 m, max = 14,790 m; breeding season: median = 858 m, min = 207 m, max = 2,240 m).

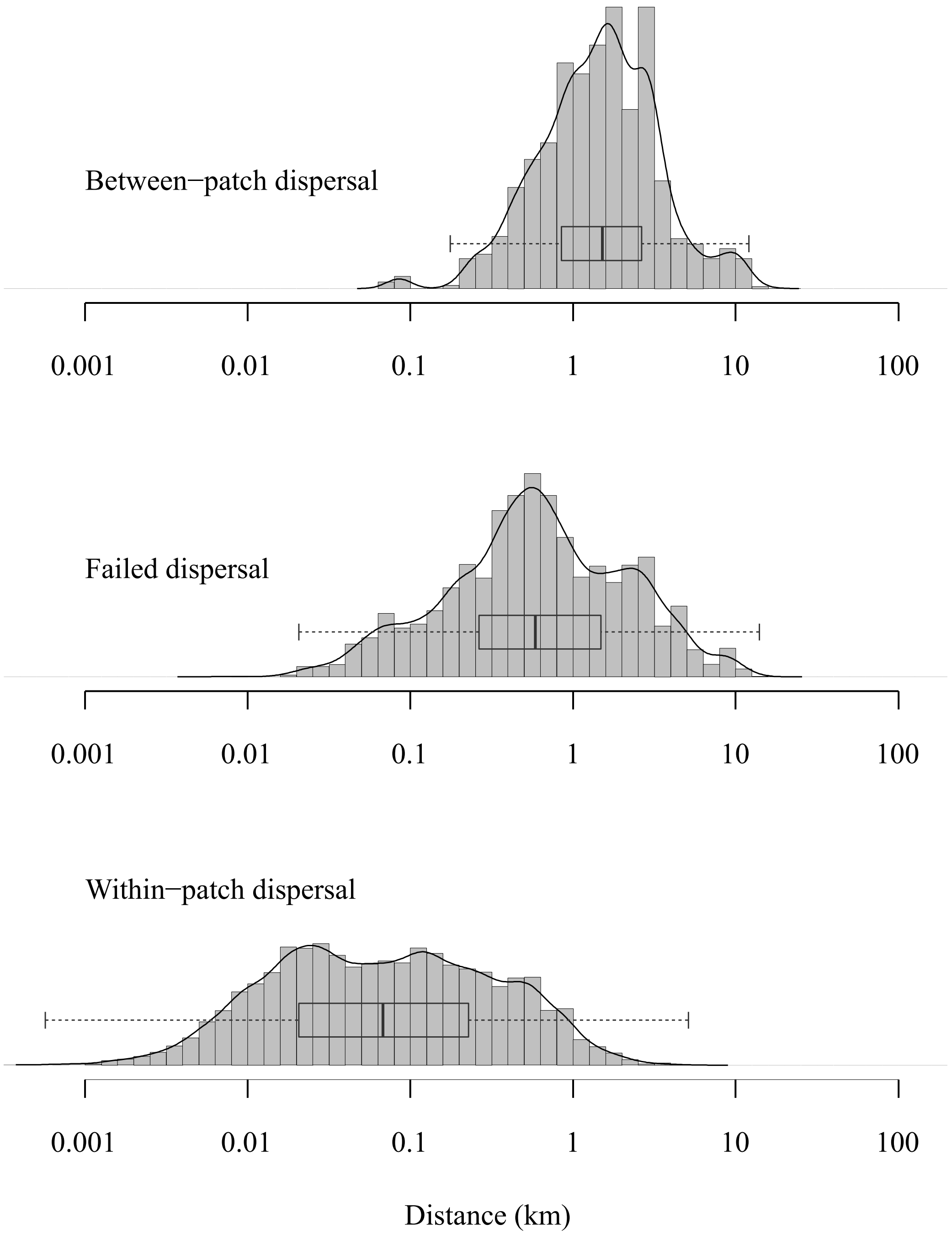

Figure 5.2: *Distribution of potential between-patch dispersal distances compared to failed dispersal distances (i.e., dispersal events that leave a forest patch but end in the habitat matrix) and potential within-patch dispersal distances. Boxplots indicate range, quartiles and median of distributions.*

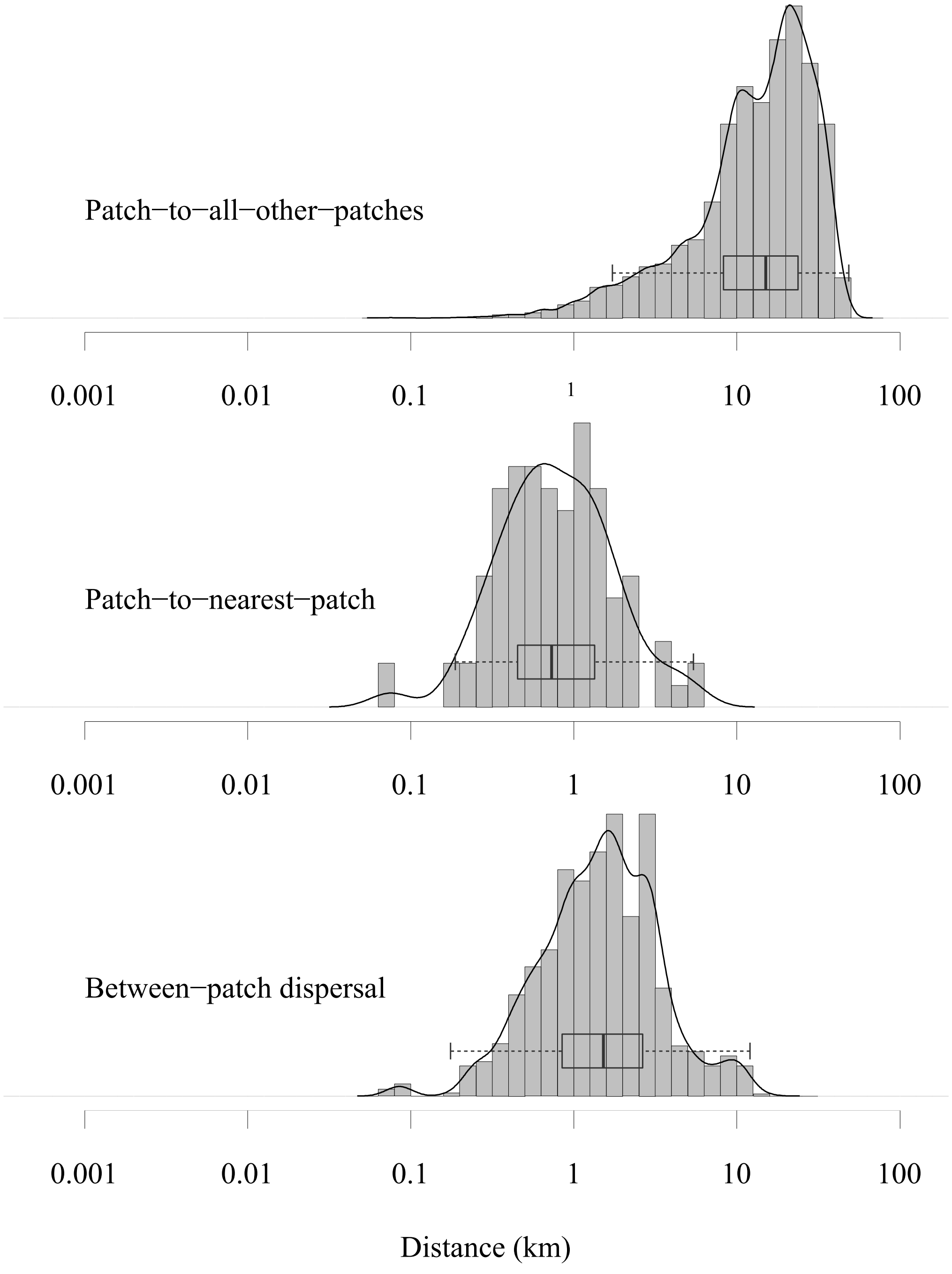

Figure 5.3: *Patch-to-patch distances compared to nearest-patch distances and potential between-patch dispersal distances. Boxplots indicate range, quartiles and median of distributions.*

The graph analysis showed that out of 103 forest patches visited by hornbills 100 patches were connected via hornbill movements within the range of GPTs (max = 150 min). We detected 233 links among forest patches that were potential seed dispersal paths (Fig. 5.4). Three patches were isolated with no potential seed dispersal to or from the other 100 patches. Potential seed dispersal paths ranged from Oribi Gorge Nature Reserve along three corridors all the way to the coast (Fig. 5.4). The main, central corridor included Mbumbasi nature reserve located in between Oribi Gorge and the coast (Fig. 5.4). The habitat matrix between forest patches along these corridors consists mostly of residential areas and farmlands. For example, Mbumbasi nature reserve is surrounded by densely populated areas closely covered with rural built-up providing almost no natural forest stripes. Northwards of Oribi Gorge lays the forested valley of the Mzimkhulu River, which was less visited by the trumpeter hornbills. Importantly movement happened in both directions, and hornbills that were caught at the coast (Fig. 5.4) moved all the way to Oribi Gorge and vice versa. Overall, dispersal movement of hornbills connected a network of forest patches that spans about 50 km in north-south and 30 km in east-west direction (compared to capture locations that spanned 29 km and 11 km respectively, Fig. 5.4).

On average, each patch was connected to 4.5 other patches via dispersal links. However the standard deviation was high with 5.2 dispersal links. 15 out of the 103 patches had connections to only one or no other patch. Likewise the betweenness centrality varied widely among patches with a median of 1 and a maximum of 3304. The overall network diameter, i.e. the longest topological distance from one end to the other of the network, was 9 links.

We identified five forest patches in the upper 5 percentile of betweenness centrality that were stepping-stones having a great number of geodesics (shortest paths) from all nodes (i.e., forest patches) to all others that pass through that node (Fig. 5.4). The two nature reserves in the area, Oribi Gorge and Mbumbasi Nature Reserve, were two of these critical stepping-stones facilitating dispersal in all directions. Additionally we identified three smaller patches as stepping-stones (Fig. 5.4), one in direct neighbourhood of Oribi Gorge and two located close to the coast. The two patches at the coast were critical for connectivity towards the larger patches of forest in the southern part of the study area (Fig. 5.4). The forest area of the 103 visited forest patches covered 73% of the entire landscape area measured as alpha convex hull around all hornbill relocations. The connectivity of the landscape measured as *IIC* without hornbill dispersal was 10%. If the links among patches of the sample of between-patch dispersal events of hornbills were included (Fig. 5.4), that probability increased more than two-fold to 24%.

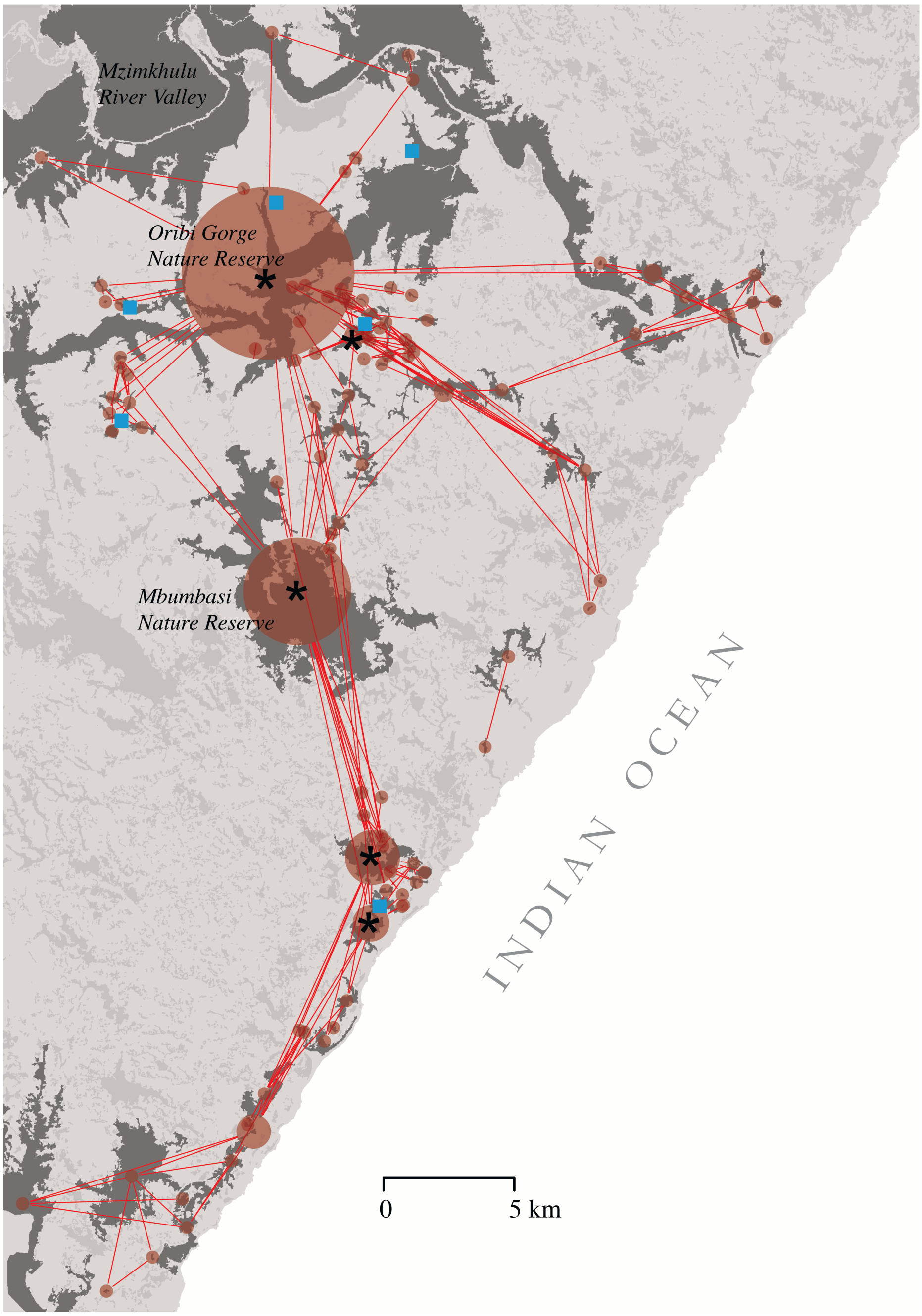

Figure 5.4: *Map of the study area at the east coast of South Africa in KwaZulu-Natal and seed dispersal by hornbills. Forest patches (grey) and graph-network of potential seed dispersal pathways (red). Dark grey: patches visited by the tracked hornbills, light grey: other forest patches, blue: capture locations of hornbills, *: stepping-stones for seed dispersal, i.e., patches in the upper 5% of betweenness centrality. Red lines: potential seed dispersal paths. Red dots: Nodes of network, scaled by betweenness centrality, i.e. number of geodesics (shortest paths) from all nodes to all others that pass through that node.*

5.5. Discussion

We showed that 32 hornbills tracked over 543 days provided potential functional connectivity to link a network of 100 forest patches ranging 50 km from north to south and 30 km east to west. While potential between-patch seed dispersal was relatively rare it occurred across distances sufficiently large to connect almost all patches visited by hornbills in this highly fragmented landscape. Overall landscape connectivity measured as *IIC* increased from about 10% to about 24% and we identified critical stepping-stones that were instrumental for network integrity.

The size of the network connected via between-patch dispersal and the maximum between-patch dispersal distance of about 15 km were comparable to scales of predicted climate-change induced spatial shifts in broad leaf tropical and subtropical forests (3.3 km per decade, Loarie *et al.* 2009). This means that hornbills – under current levels of fragmentation – could potentially provide the broad scale movements trees will need to adjust to expected shifts in their preferred climatic conditions. It is important to consider though that the network diameter was 9 links: If a tree species were to travel through the entire network it would require several iterations of seedling establishment, regrowth, fruiting and new seed dispersal. Tree species, that generally have a long generation time, would thus need centuries to travel from one end of the network to the farthest topological other end. Furthermore, to date there is generally little evidence for latitudinal range shifts in trees: A recent comprehensive review estimated rapid latitudinal species' range shifts of 16.9 kilometres per decade (Chen *et al.* 2011) but did not include any plant species in this estimate. Zuh *et al.* (2012) found a general lack of response of trees to climate change across eastern North America, which may be due to the low establishment success of newly colonizing trees species compared to established species (Ibanez *et al.* 2009).

Coastal scarp forests in KwaZulu-Natal are not only predicted to be affected by climate change, but will likely face even greater levels of fragmentation in the future (Eeley *et al.* 1999, 2001). Under the current levels of fragmentation, of all visited forest patches only three were not connected to the main network. The other 100 patches had at least one connection to the network that connected all these patches with each other. However, many forest patches in the study area were not visited by hornbills at all (Fig. 5.4, lightly grey shaded patches). This may be because we did not track all hornbills in the area, because we tracked birds only for a limited time, or it may be that some of the unvisited forest patches did not constitute adequate habitat. Disentangling selection of forest patches was beyond the scope of this study, but it is important to note that it is a possibility that some of the forest patches in the study area may never be visited by hornbills. We also found that patch-to-nearest-patch distances were slightly shorter than potential between-patch dispersal distances, which means that dispersal events were not always limited to the nearest neighbour but that between-patch dispersal to other than the nearest neighbour was also likely. This was confirmed by the graph analysis, which showed that - on average - 4.5 potential connections to other neighbouring patches existed. Importantly, the maximum predicted between-patch dispersal distance (14,790 m) was greater than the greatest nearest-neighbour distance of patches (5,413 m), which means that, hornbill movements could, in theory, connect all patches in the landscape with each other. That being said, in our large sample of 23,794 relocations, we did not find all patches being connected since three patches had no potential connection to the main network. Overall our study finds that movements of hornbills are at scales sufficient to providing connectivity in this highly fragmented landscape.

Nevertheless, we also found evidence that fragmentation already at present day levels had significant effects on the dispersal ability of hornbills: Failed dispersal had smaller distances than successful between-patch dispersal indicating that many seeds may have been deposited before a bird was reaching suitable forest habitat and that large stretches of matrix habitat may impose problems for successful between-patch dispersal. Likewise the average patch-to-all-other-patches distances were significantly greater than between-patch dispersal distances which demonstrates that seeds would need to move through the landscape from patch to patch rather than being able to cross the entire study area within a single move.

We also point out that rates of between-patch dispersal were substantially lower in the breeding season (4% versus 8%, see Fig. 5.1) and that all between-patch dispersal across distances greater than 3 km happened in the non-breeding season (January-October). That implies that in the breeding season of hornbills landscape connectivity for fruiting trees may be greatly reduced and especially for tree species that are fruiting exclusively in November – December seed dispersal among patches may be extremely rare.

Another critical issue for network connectivity are stepping-stones: We identified all patches in the upper five percentile of betweenness centrality (Fig. Fig. 5.4). These patches were instrumental for network integrity since without them the network would likely disintegrate into separated components. Two of those stepping-stones were the large nature reserves in the area, Oribi Gorge and Mbumbasi Nature Reserves. These reserves were critical for providing dispersal links to neighbouring patches in their surrounding and linking them to the overall network, which demonstrates that the importance of these reserves for plant populations goes well beyond their borders and extends to the entire region. Two other stepping-stones were small forest patches at the coast. They were linking the two reserves and their neighbouring patches to larger stretches of forest in the south. Based on our movement data that connection would have been lost without these rather small patches and the network would disintegrate into separate components. While the importance of the large nature reserves for conservation may be apparent independent of this study, these smaller patches at the coastline have been revealed by our tracking data to be key components for plant dispersal in the study area. Protecting and maintaining these small forest patches will be important for future conservation of hornbills and plant diversity in the area.

While combining high resolution movement and landscape data does offer new opportunities in understanding seed dispersal, it is also important to consider the assumptions that have to be made. Generally, (1) there will be always a limited number of birds tracked over a limited time. In addition, (2) our study considers only seed dispersal by hornbills, and (3) investigates potential connectivity only. That means on the one hand that if more birds had been tracked or if other frugivorous bird species had been considered the network of connected patches may increase in size and connectedness. However, the number of tracked hornbills (32 individuals) and the number of tracking days (543) is to our knowledge by far the highest ever reported in the literature for frugivorous birds and should constitute a significant portion of hornbills in the area. In addition, trumpeter hornbills are the largest obligate frugivorous birds in South Africa and large birds have on average larger home ranges than smaller birds (Jetz *et al.* 2002). Thus, our data shed light rather on the maximum scale at which frugivorous bird species may facilitate functional connectivity of landscapes. Focusing on potential functional connectivity does not consider whether seeds were actually moved nor on their establishment and colonization success. For our study we made the assumptions that every relocation of a bird in a forest patch had the same probability of being a starting point for seed dispersal, that seeds get deposited throughout the flight, and that establishment was equally likely for all forest patches. There is evidence from other regions and hornbill species that some of these assumptions may not always be met (reviewed in Kitamura 2011). For example, in India, seeds deposited at hornbill nest sites had a higher predation rate than at the parent fruiting tree (Velho *et al.* 2009). Nevertheless, it will be extremely difficult to obtain data on establishment success of the about 600 tree species located in this hotspot of biodiversity (Mittermeier *et al.* 2004) and it is unlikely that considering establishment success will change the overall spatial patterns in seed dispersal paths and connectivity in the landscape. To date, studies that have attempted to estimate actual versus potential connectivity and linking dispersal mechanisms with reproduction success (Rico *et al.* 2012), have not used spatially explicit models for dispersal – and thus do not touch on one of the key aspects of functional connectivity covered in this study.

We demonstrate that linking high-resolution movement data and GPTs with high-resolution landscape data provides new insights into landscape connectivity. Novel bird tracking data provide unbiased estimates of long-distance movements that not only reveal how often potential between-patch dispersal occurs but also where in the landscape connections among forest patches exist. The identification of stepping-stones in fragmented landscapes via spatially explicit mapping of dispersal pathways constitutes a new quality of information on landscape connectivity that will be key to future conservation management.

5.5 Acknowledgements

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6 GENERAL DISCUSSION

Seed dispersal is a crucial process (in ecosystem functioning) counteracting biodiversity loss. It is a key determinant of dispersal ability and recruitment success of plant species and affects their spatial distribution and thus the species composition of plant communities (Nathan & Muller-Landau 2000). Additionally, seed dispersal induces gene-flow and facilitates genetic diversity in plant populations enhancing the adaptability of plant species to changing environmental conditions (Hamrick *et al.* 1993). Altogether, seed dispersal function is an essential element for sustainment of local plant diversity, restoration of forests and maintenance of biodiversity.

Given the increasing global environmental change, research on seed dispersal function is a central issue in recent plant community ecology (Schupp *et al.* 2010). Thereby, increasing emphasis needs to be placed on long-distance seed dispersal as this process facilitates the exchange of individuals among spatially separated populations and the colonisation of new sites (Clark *et al.* 2005, Nathan 2006), enhancing the sustainability of plant species threatened by habitat alteration and climate change. However, since long-distance seed dispersal events are difficult to measure, our current understanding of seed dispersal function is very limited for long-distance seed dispersal (Cain *et al.* 2000*,* Nathan & Muller-Landau 2000, Nathan 2006). Filling that research gap and improving the ability to measure and map long-distance seed dispersal is a major challenge to better understanding ecosystem functioning in the face of changing environmental conditions (Cain *et al.* 2000, Trakhtenbrot *et al.* 2005, Nathan 2006).

With my thesis I narrowed that gap through analysing factors influencing long-distance seed dispersal by using new approaches to determine movement behaviour and potential seed dispersal patterns of trumpeter hornbills. Estimating detailed habitat-specific seed dispersal kernels, I could show that the landscape structure strongly influenced the seed dispersal potential of trumpeter hornbills, with larger dispersal distances in fragmented landscapes than in continuous forests. By calculating daily ranges of trumpeter hornbills, I could show that seasonal changes of ranging behaviour across fragmented landscapes can follow a shift from local movements to nomadic movement behaviour rather than daily range expansions. Finally, modelling a spatially explicit map of potential seed dispersal pathways into the landscape revealed the high ability of trumpeter hornbills to enhance functional connectivity of the fragmented landscape. My work is based upon a large amount of high resolution movement data of trumpeter hornbills which I collected in several field seasons (total of 13 months) in South Africa. I obtained a sample size enabling fine-scaled analyses distinguishing movement data between habitats, seasons and days.

Meet the challenge of measuring long-distance seed dispersal

Recent technological improvements enable researches to collect a new generation of movement data (Cagnacci *et al.* 2010) which provide a basis for detailed and thorough seed dispersal measurements (Holland *et al.* 2009). When following seeds in real time, detectability of animal-mediated seed dispersal generally decreases with increasing speed and distance of animal movements. This problem is typical for many avian frugivores (Jordano 2007). The difficulty of tracking seed dispersal carried out by rapidly moving animals increases when the species themselves are inconspicuous, move in complex terrain, or both. Even though trumpeter hornbills are less inconspicuous, direct observations of long-distance movements in their entirety are virtually impossible. Trumpeter hornbills are highly mobile and movements encompass habitats such as closed tropical forests which are often hard for observers to access. For this reason, it was sensible to use a different strategy to overcome the difficulty of collecting direct movement observations in order to estimate seed dispersal patterns of trumpeter hornbills.

While seed dispersal by smaller bird species has been successfully directly observed (Gómez 2003, Sun *et al.* 2007), most studies on seed dispersal by large birds so far made use of terrestrial VHF-radiotracking (Holbrook & Smith 2000, Graham 2001, Holbrook 2011, Breitbach *et al.* 2012). However, detectability of long-distance movements depends on the ability of the observer to stay within the signal of the tracking device (e.g. Holbrook & Smith 2002). Another challenge is that the accuracy of VHF-radio triangulation declines with distance to the observer (Tucker 1979, Millspaugh & Marzluff 2001). Consequently, there is a bias against frequency and precision of long-distance movements. Argos satellite tracking can be successfully applied to follow migration routes of animals independently of direct observation. However, the sampling intervals here are mostly irregular and the temporal and spatial resolution of the data is too limited for studying movement behaviour at scales relevant for seed dispersal (Soutullo 2007, Tomkiewicz *et al.* 2010).

I recorded movement data of trumpeter hornbills with GPS (global positioning system) tracking technology. GPS tracking was first suitable only for large vertebrates able to carry large batteries and/or solar chargers. Recent technological developments now offer the opportunity to use GPS equipment to track the movements of smaller animals (Cagnacci *et al.* 2010), like frugivorous birds (Holland *et al.* 2009, Kays *et al.* 2011). GPS tracking has several advantages over other tracking methods; it allows one to record animal positions without the problem of altered animal behaviour due to the proximity of the researcher, in areas that are remote or difficult to access, at higher rates and shorter intervals and typically with high spatial accuracy (Frair *et al.* 2010, Recio *et al.* 2011). The usage of novel GPS data loggers enabled me to record movement data of trumpeter hornbills in high temporal and spatial resolution, with high accuracy and unbiased for long-distance movements.

Variability of seed dispersal function in space and time

The dispersal ability of plant species mainly depends on the scale and the shape of the initial seed shadow (Wenny & Levey 1998). Seed shadows of plant species with fleshy fruits are mainly determined by the foraging and movement behaviour of frugivores (Schupp *et al.* 2002, Westcott *et al.* 2005). Consequently, factors influencing the movement behaviour of frugivores indirectly influence plant dispersal. Changes in the movement behaviour of birds can follow spatial and temporal patterns and may induce variability of seed dispersal function in space and time (Rolando 1989, Rosenberg & McKelvey 1999, Graham 2001, Levey *et al.* 2002). However, studies on seed dispersal by large bird species either focus on one habitat type and/or one season (e.g. Wesctott *et al.* 2005, Holbrook 2011) or are of rather coarse resolution (e.g. Holbrook *et al.* 2002). Obtaining movement data of hornbills encompassing different habitat types and seasons allowed me to show in detail that both landscape structure and seasonality noticeably influenced the ranging behaviour of trumpeter hornbills, leading to high variation in seed dispersal potential.

Spatial variability (between habitat types)

The effect of habitat type on seed dispersal at long distances has remained largely unexplored (Carlo *et al.* 2013), although long-distance seed dispersal has stirred large interest during the last decades (Nathan 2005). Long-distance seed dispersal events are typically rather rare (Willson 1993a). Within continuous forest, seed dispersal kernels were suggested to be leptokurtic, with high seed-deposition rates close to the parental tree and rare long-distance seed dispersal (Howe & Smallwood 1982, Willson 1993a, Westcott & Graham 2000, but see Murray 1988, Sun *et al.* 1997). Forest fragmentation is assumed to further reduce seed dispersal function (Cordeiro & Howe 2003, McConkey & Drake 2006, Uriarte *et al.* 2011). There is evidence that particularly larger bird species have high potential for long-distance seed dispersal also in heterogeneous landscapes (Graham 2001, Holbrook & Smith 2002, Kinnaird & O'Brien, Sun *et al.* 2007, Kitamura 2011). However, so far no study has quantified in detail the spatial variability in the seed dispersal pattern between landscape types for large bird species like hornbills.

Chapter 2 of my thesis shows GPS-based seed dispersal kernels of trumpeter hornbills derived from non-fragmented and fragmented landscapes. My results show for the first time a direct comparison between seed dispersal kernels from different habitat types. Seed dispersal kernels differed considerably between landscape types (Fig. 3.4). Nevertheless, dispersal distance was much larger in fragmented landscapes than in continuous forests with modelled dispersal distances of 512 m compared to 160 m and a threefold higher maximum of potential dispersal distance. This outcome is important in several ways: first, it reveals the high potential of trumpeter hornbills for long-distance seed transport across fragmented landscapes; second, it points out that landscape structure considerably influences seed dispersal patterns of hornbills; and third, it shows that long-distance seed dispersal potential was higher and not lower in the fragmented landscape.

The increase of dispersal distances in the fragmented landscape probably resulted from a scattered distribution of resources across distant habitat patches. This could have forced trumpeter hornbills to travel longer distances between resources. Birds may adopt faster and straighter movements during flights between patches than they would exhibit e.g. in continuous forests (Baguette & Van Dyck 2007). Reasons for this could be intrinsic factors like attempting to reduce a higher predation risk in the open landscape (Bélisele 2005), lowering the energy demand for long-distance movements (Graham 2001), or memorizing the spatial distribution of resource availability (Fagot & Cook 2006). Straight movements may increase maximum flight distance within the seed retention time and thus may result in larger dispersal distances. Additionally, extrinsic factors may enhance long-distance seed dispersal, such as connecting structures like corridors (Levey *et al.* 2005) and single trees (Graham 2001). Unfortunately, since recording the distribution of resources and connectivity structures in the study area was impractical, I was not able to address these factors in detail in this analysis. Nonetheless, the increasing potential for long-distance seed transport across fragmented landscapes highlights the importance of fine-scaled analyses differentiating movement data between habitat types and points out the potentially eminent functional role of certain seed-dispersing species.

Temporal variability (between seasons)

Temporal variations are a common phenomenon in plant-frugivore interactions (e.g. Loisell & Blake 1991, Levey 1988, Jordano *et al.* 1995). Differences in the phenology of either the plant species, e.g. fruit ripening, abundance and distribution, or of the frugivore species, e.g. reproductive phase are assumed to lead to seasonal shifts in movement behaviour of frugivores (Herrera 1984, Leighton & Leighton 1983).

Seasonal fluctuations in occurrence and density of individuals have been previously detected for several hornbill species (Kemp 1995, Kinnaird *et al.* 1996, Whitney & Smith 1998, Kinnaird & O'Brien 2007, Rainey & Zuberbühler 2007, Kitamura 2011). For instance, Holbrook and colleagues (2002) found large-scale movements of a hornbill species in Africa. Thereby, these studies indicate a general seasonal shift in foraging ground and tracking of fruit resources via seasonal migrations (Whitney & Smith 1998). However, much information is anecdotal and the differences in methodology, accuracy and duration of observations impede comparison between studies and species (e.g. Kinnaird *et al.* 1996, Kinnaird & O'Brien 2007). So far, detailed quantitative knowledge on how large frugivorous birds accomplish different ranges in different seasons remains elusive.

I calculated daily ranges of trumpeter hornbills from the breeding and the non-breeding season to study ranging patterns and the process of seasonal range shifts (chapter 4). My results showed for the first time that range expansion during the non-breeding season can follow complex patterns of daily range aggregation. The ranging behaviour changed from an overall almost stationary daily range aggregation in the breeding season to a widely scattered distribution of daily range aggregations in the non-breeding season. Whereas birds did not perform strict short-distance migrations, nomadic movements occurred on a small spatial scale. This pattern indicates that birds shift from local movements to nomadic movement behaviour rather than performing daily range expansions. This information denotes important ecological consequences for seed dispersal function, since plant species benefit differently from seed dispersal agents depending on their fruiting period. The subsequent investigation of seasonality in habitat use indicated that landscape fragmentation played a large part in the pattern of daily range aggregation. Whereas daily range aggregations in the breeding season were located mainly in the continuous forests, daily movements in the non-breeding season areas also made use of the fragmented landscape. Consequently, the nomadic movement pattern could also have been a result of the scattered spatial distribution of habitat patches and resources.

Social behaviour

Seasonal differences in ranging behaviour could be influenced by changes in social behaviour of hornbills. Something I could not quantify but did observe, were strong differences in the foraging group size of trumpeter hornbills in the study area. During the breeding season, trumpeter hornbills foraged mainly solitarily or in small family groups, whereas during the non-breeding season birds were often observed in large groups (own observation, see Kemp 1995). Group foraging may benefit individuals, e.g. through an increase of foraging efficiency of patchily distributed food resources and a decrease of an individuals' predation pressure and consequently need for vigilance (Weatherhead 1983). A group of hornbills would need to explore more food resources and thus possibly fly larger distances to satisfy each individual's food demand than a single foraging bird would (Karubian & Duãres 2009). This could be one of the reasons why hornbills expand their ranges in the non-breeding season and make several long-distance flights between distant forest patches. During the breeding season, hornbills in the study area foraged mostly solitarily and within the continuous forest, rarely crossing the open fragmented landscape. Breeding activities would constrain hornbills spatially and temporally to the location of the nest site. Since females stay in the nest during breeding, male hornbills would have to gather food for all family members, thus energy demands may particularly affect their movements during the breeding season (Stearns 1992).

These seasonal differences in social organisation could also influence the characteristics of the seed shadow (Karubian & Durães 2009). However, inclusion of social behaviour in seed dispersal research is challenging, since it is difficult to quantify social behaviour and the influencing factors (Dennins & Westcott 2006, Russo *et al.* 2006). Detailed analyses of ranging behaviour in a daily resolution may help us to understand the factors influencing the movement behaviour of frugivorous birds, e.g. to a better understanding of the influence of landscape structure on the range expansion process. Finally, I was able to point out the importance of continuous forest as breeding habitat for trumpeter hornbills, thereby providing important information regarding the landscape structure necessary for the long-term persistence of an important disperser species within the study area.

From seed dispersal kernel to spatially explicit connectivity measures

High potential for long-distance seed dispersal in fragmented landscapes does not necessarily enhance functional connectivity of fragmented landscapes. Functional connectivity is given through the possibility of gene flow between occupied habitats and of colonization of unoccupied habitat patches (Tischendorf & Fahrig 2000). Only seed dispersal resulting in movements of seeds between forest patches would facilitate functional landscape connectivity. However, between-patch seed movements are difficult to monitor. The seed dispersal kernels for trumpeter hornbills were calculated applying simple mechanistic models. These models are based on movement and seed retention data but do not incorporate spatial information (Cousens *et al.* 2008). Indeed, birds cover large distances during the seed retention time, but whether seed dispersal connects distant forest patches remains unknown. Consequently, simple seed dispersal kernels display the probability distribution of dispersal distances but do not allow for estimation of the spatial distribution of seeds (Westcott *et al.* 2005, Russo *et al.* 2006). Direct measurement of a bird species' contribution to functional connectivity is so far only feasible on rather small scales. Direct observations of bird movements, relocation of marked seeds and molecular methods rarely cover dispersal distances and study areas of more than a few hectares (e.g. Levey & Sargent 2000, Gómez 2003, Magrach *et al.* 2012). This is a rather small scale compared to the seed dispersal potential of trumpeter hornbills. Trumpeter hornbills showed seed dispersal potential for distances of several kilometres and up to 9 km (Fig. 3.4) and recorded location data covered an area of about 500 km^2, making direct measurements of seed transport among patches impractical (see above). When between-patch seed movements cannot be monitored directly, more spatial information needs to be included in movement data to obtain more spatially-explicit seed dispersal distributions. A combination of an evaluation of landscape structure with biological information on organism dispersal can be used to achieve realistic models of potential functional connectivity (Calabrese & Fagan 2004). Detailed knowledge of the underlying habitat allows valuing habitat remnants according to their likelihood of being possible seed sources and suitable seed recruitment environments. Together with the data on movement and seed retention time of birds, seed movement can be modelled into the landscape by choosing start points of seed dispersal events only from within suitable habitat and determining thereafter the location of the endpoint of seed dispersal events.

Chapter 5 of my thesis shows for the first time a fusion of fine-scaled movement data and seed-retention times with exact landscape data. This allowed me to map spatially explicit seed dispersal pathways of trumpeter hornbills on the landscape and to display possible between-patch dispersal-events. Trumpeter hornbills showed the potential to enhance functional connectivity of the landscape more than twofold and thus may facilitate seed transport to and from forest patches. Overall dispersal networks of hornbills contained almost 100 patches in an area of 50 km south-north and 30 km east-west direction. This finding adds important evidence showing the value of long-distance seed dispersal within fragmented landscapes. Additionally, visualizing potential seed dispersal pathways provides further information on landscape elements likely improving bird movements and thus enhancing long-distance seed dispersal. For trumpeter hornbills, six forest patches were identified as critical stepping-stones for seed dispersal distribution, which is important knowledge for conservation management in the study area. Nevertheless, long-distance seed dispersal and increased landscape connectivity are no guaranty for successful plant recruitment within fragmented landscapes.

Seed deposition-site and plant recruitment success

An important limitation in studying long-distance seed dispersal function is to determine the subsequent success of plant dispersal (Cain *et al.* 2000). My analyses are based on virtually tracked seeds, thus bear limitations in showing only the potential seed dispersal pattern of trumpeter hornbills. Seed deposition site is only an estimate from modelled seed dispersal distribution and resulting plant recruitment success remains elusive. Plant establishment follows from successful seed dispersal, not from the seed dispersal process per se. Successful seed dispersal results in seed survival, seedling establishment and plant development into an individual able to produce its own offspring (Wang & Smith 2002). This process starts with seed removal from the parental tree, followed by propagule treatment in the intestines of frugivores during dispersal. Fruit digestion through birds is generally assumed to either have neutral effects or to enhance seed germination through pulp-removal (Wenny 2001, Barnea & Friedman 1991, Whitney *et al.* 1998). At the seed-deposition site, factors like the microhabitat, seed-predation and herbivory are crucial determinants of the success rate of seed dispersal (Schupp 1993, Nathan & Muller-Landau 2000). Seed dispersal by animals could lead to disproportional seed deposition in areas suitable for plant establishment, e.g. into another forest patch rather than into the matrix. Even though trumpeter hornbills enhanced functional landscape connectivity twofold during the non-breeding season, potential between-patch dispersal events were rather rare. One reason for this could be that trumpeter hornbills include in their foraging ground many gardens of farmstead. These gardens may provide fruit sources for hornbills, but seed survival and seedling establishment there are rather unlikely.

Directed seed dispersal by animals could also result in clumped seed deposition at sites favoured by the disperser species, like perches, nests or resting sites (Daniel & Wenny 1998, Schupp *et al.* 2002). Seed dispersal during the breeding season was probably constrained to the forest. Seed clumping is assumed to have rather negative effects on seed dispersal success, due to density-dependent mortality, competition and an increase in the pathogen attacks and increased seed-predator attraction that typically occur below parent trees (Janzen 1971, Howe 1998). Depending on the degree of aggregation, repeated seed dispersal to certain sites does not necessarily result in only negative consequences for plant dispersal. Conversely, the number and frequency of dispersed propagules to one site could enhance the probability of successful plant recruitment, and/or overlapping seed shadows of conspecifics could increase genetic diversity of seedlings, presumably enhancing population establishment success (Simberloff 2009). Even though the connectivity measurement for trumpeter hornbill seed dispersal showed a connection of each patch to on average 4.5 other patches, a true dispersal rate is missing.

Whether seed dispersal results in plant establishment or not could be answered by applying genetic methods. Determining the genetic relationship between individuals of different populations could give evidence of long-distance seed dispersal and successful recruitment of seeds (Ouborg *et al.* 1999, Cain *et al.* 2000). However, genetic methods are limited in their spatial scale since they are complex and labour-intensive and thus would require an immense effort when studying long-distance seed dispersal (Nathan 2000). Additionally, pure population genetics lacks information about the seed-dispersing species and the seed dispersal process, e.g. about the contribution of secondary seed dispersal (Jordano *et al.* 2007). Trumpeter hornbills feed on a variety of fruits (see Kemp 1995) which in turn are consumed by many other fruivgores (Bleher *et al.* 2003). Consequently, genetic methods alone are unsuitable to estimate seed dispersal success of trumpeter hornbills if seed deposition cannot be directly related to hornbill dispersal.

Seed shadows are teamwork

Evaluation of the ultimate contribution and significance of trumpeter hornbills to seed shadows and thus to plant dispersal in the study area cannot be accomplished by measuring seed dispersal potential by trumpeter hornbills only. In general, seed-shadows of fleshy-fruiting plants are generated by several frugivorous species (Clark *et al.* 2005), contributing differentially to seed shadows (Howe 1989, Wenny & Levey 1998, Jordano & Schupp 2000). Estimation of a frugivore's significance in seed dispersal function in a certain area would require separation of its own generated seed shadow from the total seed shadow generated by all furgivores present. Moreover, to estimate a frugivorous species' contribution to a particular area of the seed shadow, e.g. long-distance dispersal, one would need to identify and quantify the dispersal kernel generated by each frugivore. The significance of a single species to seed dispersal function in a particular area can only be determined when all species with the same functional trait are known. However, since fragmentation of tropical forest results in frugivore loss, a decline in abundance or local extirpation of significant seed dispersers has potentially strong influences on seed dispersal distributions (Turner 1996, Markl *et al.* 2012).

Loss of long-distance seed dispersal

Some species are more severely affected by tropical forest fragmentation than others, and large vertebrates are of particular concern (Wright 2003, Corlett 2007, Peres & Palacios 2007). Since large frugivores are especially crucial for long-distance seed dispersal (Wright *et al.* 2007, Wotton & Kelly 2012), this function is particularly vulnerable to human activities. Additionally, large-seeded plant species depend on a few large animals for effective dispersal, since seed size limits the number of frugivores that can disperse the seeds (Leighton &

Leighton 1983, Cramer *et al.* 2007). Functional diversity among species could compensate for a species loss, since frugivore species are dissimilarly affected by human activities and respond differently to environmental changes (Dennis & Wescott 2006, Cramer *et al.* 2007, Jordano *et al.* 2007). For instance, in landscapes where large mammals are already missing, avian frugivores could persist and become the only remaining long-distance seed-dispersers (Holbrook *et al.* 2002). Birds and mammals usually feed on different sets of plant species (Poulsen *et al.* 2002, Flörchinger *et al.* 2010), however, and the abundance of large obligate avian frugivores is also assumed to decline when overall food resources decrease, e.g. due to increasing fragmentation (Howe 1984, Cordeiro & Howe 2001, Moran *et al.* 2004, Markl *et al.* 2012). Consequently, further species loss may ultimately result in degradation of a crucial ecosystem function which in turn will accelerate biodiversity loss in the tropical and subtropical forests worldwide.

Narrowing the gap in long-distance seed dispersal research

My thesis focused on the seed dispersal potential of one particular species, the trumpeter hornbill. In general, hornbill species are suggested to play a major role in ecosystem functioning as seed dispersers (Whitney *et al.* 1998, Whitney & Smith 1998, Holbrook & Smith 2000, Bleher & Böhning-Gaese 2001, Kemp 2001, Poulsen *et al.* 2002, Kinnaird & O'Brien 2007, Sethi & Howe 2009), but so far no study has investigated seed dispersal function and the factors influencing seed dispersal distribution in such detail for any large frugivorous bird species.

I have shown that landscape structure strongly influences seed dispersal patterns, which at the same time most likely undergo strong seasonal variations. During the non-breeding season, trumpeter hornbills frequently moved into the fragmented agricultural landscape and exhibited a high potential to facilitate long-distance seed dispersal and functional landscape connectivity. Indeed, the scale of habitat fragmentation is highly variable between landscapes and I studied hornbill movement behaviour and seed dispersal patterns in only two different habitat types. Nonetheless, I assume that, due to their body size, the variety of fruits they feed on and their high mobility, trumpeter hornbills are likely one of the most important seed-dispersers in the fragmented landscapes within their geographic range in Southern Africa.

Dispersal ability is one key process determining the migration capacity of plant species, plant species distribution and distribution of plant species communities (Cain *et al.* 2000, Nathan & Muller-Landau 2000). In my thesis I showed how novel applications of high-quality data can help to improve our understanding of seed dispersal function. Rapid progress in tracking technology promises a quick enhancement of ways to achieve highly detailed data on movement and feeding behaviour of animals (Holland *et al.* 2009, Cagnacci *et al.* 2010). As empirical data become more detailed, we gain possibilities to refine our knowledge of ecological processes. With my research, I have highlighted the importance of incorporating different landscape structures and seasonality on the way of moving closer to a comprehensive understanding of seed dispersal processes under changing environmental conditions.

7 ZUSAMMENFASSUNG

Samenausbreitung über lange Distanzen ist ein entscheidender Prozess um eine Ausbreitung von fleischig fruchtenden Baumarten zwischen Waldfragmenten zu ermöglichen. Besonders sind große frugivore Vogelarten in der Lage, Samen zwischen Waldfragmenten und über weite Distanzen zu transportieren. Beides ist wichtig, damit fundamentale genetische und demographische Prozesses von Pflanzenpopulationen aufrechterhalten werden können. In Anbetracht dessen, dass global zunehmend Wälder zerstört und fragmentiert werden, ist die Erforschung von Langstreckensamenausbreitung zu einem zentralen Thema der Ökologie geworden. In meiner Doktorarbeit untersuchte ich das Bewegungsverhalten und die Samenausbreitungsmuster von Trompeter Hornvögeln *(Bycanites bucinator),* einer großen obligaten frugivoren Vogelart, in KwaZulu-Natal, Südafrika. Ich analysierte (i) die Fähigkeit von Trompeter Hornvögeln Langstreckensamenausbreitung zu leisten, (ii) saisonale Unterschiede in dem Bewegungsverhalten dieser Art, und (iii) das Potential von Trompeter Hornvögeln eine funktionale Konnektivität zwischen räumlich voneinander getrennten Waldstücken in einer fragmentierten Landschaft zu ermöglichen. Unter Verwendung von hochauflösenden GPS (global positioning system)-Datenloggern zeichnete ich zeitlich und räumlich hoch detailliert die Bewegungen von Trompeter Hornvögeln auf. Ich bezog Bewegungsdaten sowohl aus geschlossenen Wäldern als auch aus fragmentierter Agrarlandschaft während und außerhalb der Brutzeit. Als erstes berechnete ich Wahrscheinlichkeitsverteilungen für die Ausbreitungsdistanzen (engl.: *seed dispersal kernel).* Ich konnte dabei zwischen Samenausbreitung in geschlossenen Wäldern und fragmentierter Agrarlandschaft unterscheiden. Die Verteilungen zeigten, dass Trompeter Hornvögel ein generell hohes Potential hatten, Samen über Distanzen von mehr als 100 m zu transportieren und Ausbreitungsdistanzen von bis zu 14,5 km bereitstellen konnten. Die *seed dispersal kernels* unterschieden sich deutlich zwischen den beiden Habitat-Typen. Ich fand ein bimodales Muster mit weiteren Ausbreitungsdistanzen für fragmentiertes Agrarland und ein unimodales Muster für geschlossene Wälder. Meine Ergebnisse zeigten, dass die Landschaftsstruktur einen starken Einfluss auf das Bewegungsverhalten von Trompeter Hornvögeln ausübte. Vermutlich spiegelte sich diese Variation im Verhalten der Tiere in der Form der *seed dispersal kernels* wider. Als Zweites kalkulierte ich für jeden individuellen

Vogel tägliche Streifgebiete, um Verschiedenheiten im Bewegungsverhalten der Tiere vergleichend zwischen der Brut- und der Nichtbrutzeit zu untersuchen. Ich analysierte die Unterschiede im täglichen Bewegungsverhalten sowie im Aufbau mehrtägiger Streifgebiete. Dabei betrachtete ich Unterschiede in der Habitatnutzung und evaluierte mögliche Konsequenzen für die Samenausbreitung während verschiedener Saisons. Meine Ergebnisse zeigten, dass mehrtägige Streifgebiete innerhalb der Brutzeit aus stark überlappenden, annähernd stationären täglichen Streifgebieten gebildet wurden, die fast ausschließlich auf den geschlossenen Wald begrenzt waren. Während der Nichtbrutzeitzeit dagegen formten die Vögel Streifgebiete über mehrere Tage, indem sie ihre Bewegungsräume in ein generell anderes Gebiet verschoben. Dabei fügten sich mehrere kleine und wenige große tägliche Streifgebiete zu generell größeren mehrtägigen Streifgebieten in der Nichtbrutzeitzeit als in der Brutzeit zusammen. Saisonale Variationen im Bewegungsverhalten und im Prozess der Streifgebietsausdehnung resultierten in bedeutenden Konsequenzen für die Samenausbreitung. Während in der Brutzeit eher nur kurze Ausbreitungsdistanzen und wenig räumliche Variation möglich war, bestand in der Nichtbrutzeit die Möglichkeit für mehr Ausbreitung zwischen Waldfragmenten und über weitere Stecken. Zuletzt machte ich mir eine Projektion von simulierter Samenausbreitung auf eine hoch aufgelöste Habitatkarte zu nutze, um zu bestimmen zu welchem Maß Trompeter Hornvögel eine funktionale Verbindung zwischen Pflanzenpopulationen aus isolierten Waldfragmenten herzustellen vermögen. Ungefähr 7% der simulierten Samenausbreitung waren potentiell Ausbreitungsereignisse zwischen Waldfragmenten und die Hornvögel verbanden eine Netzwerk von 100 Waldstücken mit einer Ausdehnung von ungefähr 50 km. Trompeter Hornvögel hatten die Fähigkeit die funktionale Konnektivität der Landschaft um mehr als das Zweifache zu erhöhen. Weiterhin stellte sich heraus, dass einige Waldfragmente besonders wichtige Verbindungsstücke für den Samentransport innerhalb des Netzwerks waren. Zusammenfassend hebt meine Arbeit die herausragende Rolle großer frugivorer Vögel, wie Trompeter Hornvögel, für die Samenausbreitung innerhalb fragmentierter Landschaften hervor. Weiterhin zeigt sie die Wichtigkeit der Verwendung von fein-skalierten Bewegungsdaten und hochauflösenden Habitatkarten, sowie die Einbeziehung von verschiedener Landschaftsstrukturen und Saisons für ein übergreifendes Verständnis der Funktion der Samenausbreitung.

7.1 Muster der Samenausbreitung durch Trompeter Hornvögel in einer fragmentierten Landschaft

Hinsichtlich der zunehmenden Fragmentierung und Zerstörung von Wäldern ist es von großer Bedeutung zu verstehen, welchen Einfluss die Landschaftsstruktur auf die Samenausbreitung durch frugivore Vögel hat. Generell geht man davon aus, dass der Samentransport durch Vögel vorherrschend nur über kurze Distanzen stattfindet. Es gibt jedoch derzeit ein großes Defizit an Studien, welche die Samenausbreitung speziell durch große frugivore Vögel innerhalb komplexer, fragmentierter Landschaften untersuchen. Mit Hilfe einer Kombination aus Bewegungsdaten und Verdauungszeiten simulierten wir die Verteilungen der potentiellen Samenausbreitungsdistanzen von Trompeter Hornvögeln innerhalb geschlossener Wälder und fragmentierter Landschaften, um die Auswirkungen von Fragmentierung sichtbar zu machen.

An der Ostküste Südafrikas haben wir mittels hochauflösender GPS Sender die Bewegungen von 10 Trompeter Hornvögeln aufgezeichnet. Für jedes Tier wurde in 15 min Intervallen über den Tag hinweg die Position erfasst. Zusätzlich führten wir mit Tieren in Gefangenschaft Fütterungsexperimente durch, um die Darmpassagezeiten verschiedener Samen zu ermitteln. Durch Kombination der Verteilung von Schrittlängen aus den Bewegungsdaten mit jener der Darmpassagezeiten konnten wir potentielle Samenausbreitungsdistanzen von Trompeter Hornvögeln simulieren. Eine vorhergehende Unterteilung Daten in Bewegungen aus geschlossenen Wäldern und aus der fragmentierten Landschaft, ermöglichte es uns, die Ausbreitungsdistanzen habitatspezifisch zu kalkulieren.

Wir fanden eine mittlere Darmpassagezeit von 57 min mit einem Maximum von 2,5 h. Innerhalb dieses Zeitfensters folgten die Samenausbreitungsdistanzen in geschlossenen Wäldern einer unimodalen Verteilung mit einem Gipfel bei 160 m, wohingegen sie für fragmentierte Agraralandschaften ein bimodales Muster aufwiesen, mit je einem Gipfel bei 25 und 512 m. Mit annähernd 9 km war die maximale Ausbreitungsdistanz hier fast dreimal so hoch wie in geschlossenen Wäldern.

Wir konnten damit zeigen, dass die Landschaftsstruktur einen großen Einfluss auf die Bewegungsmuster und das Samenausbreitungspotential von Trompeter Hornvögeln hat. Die große Mobilität der Tiere, ihre zahlreichen Langstreckenflüge, sowie ihre hohe Abundanz lassen vermuten, dass sie eine essentielle Rolle für die Ausbreitung von Samen in den fragmentierten Landschaften dieser Region spielen.

7.2 Saisonale Streifgebietserweiterung eines großen frugivoren Vogels

Jahreszeitliche Variationen in den Bewegungen frugivorer Vögel können zu saisonalen Schwankungen in ihrer Funktion als Samenausbreiter führen. Während der Brutzeit haben Vögel zumeist kleinere Streifgebiete, die sie außerhalb der Brutzeit zu wesentlich größeren Gebieten ausdehnen können. Bisher haben wir jedoch kein detailliertes Wissen darüber, wie das Bewegungsverhalten zu diesen Unterschieden führt. Um diesen Fragen nachzugehen, haben wir die Unterschiede in der Raumnutzung von großen frugivoren Vögeln zwischen der Brut- und der Nichtbrutzeit untersucht. Unsere Studie ist die erste, die auf der Basis von täglichen Bewegungsräumen analysiert, welche Prozesse dazu führen, dass außerhalb der Brutzeit insgesamt größere Streifgebiete geformt werden.

Wir nutzen die "Brownian bridge movement method" (BBMM) um aus den Bewegungsdaten von 31 Trompeter Hornvögeln individuelle tägliche Bewegungsräume zu berechnen. Wir untersuchten die Größe und Variabilität, sowie die räumliche und habitatspezifische Lage der täglichen Bewegungsräume aus der Brut- und der Nichtbrutzeit. Wir verglichen den Flächenzuwachs bei Überlagerung mehrerer täglicher Bewegungsräume und ermittelten durch Punktmusteranalyse deren räumliche Verteilung innerhalb eines mehrtägigen Streifgebiets, um den Prozess der Streifgebietsvergrößerung außerhalb der Brutzeit zu erkennen.

Wir zeigten, dass Trompeter Hornvögel ihr Streifgebiet außerhalb der Brutzeit nicht durch generell größere tägliche Bewegungsräume ausdehnten, sondern durch eine weiträumige Verschiebung von mehrtägigen Streifgebieten. Während tägliche Bewegungsräume in der Brutzeit nahezu stationär und auf den geschlossenen Wald beschränkt waren, schlossen die Vögel außerhalb der Brutzeit regelmäßig neue Gebiete in der fragmentierten Landschaft in ihr Streifgebiet mit ein. Daraus können große saisonale Unterschiede in der Distanz und der räumlichen Variation für eine Samenausbreitung durch Trompeter Hornvögel resultieren.

Mit dieser detaillierten Analysen des Bewegungsverhaltens von Trompeter Hornvögeln konnten wir zeigen, dass saisonale Variationen in dem Bewegungsmuster eines großen frugivoren Vogels komplexen Prozessen folgen können und bedeutende ökologische Konsequenzen für die Samenausbreitung innerhalb fragmentierter Landschaften hervorrufen können.

7.3 Große frugivore Vögel ermöglichen eine funktionale Konnektivität innerhalb fragmentierter Landschaften

Für eine erfolgreiche Samenausbreitung ist neben der Ausbreitungsdistanz vor allem der Ort, zu dem der Same transportiert wird, von größter Bedeutung. In einer fragmentierten Landschaft ist es besonders wichtig, dass Samen zwischen Waldinseln ausgebreitet werden, wodurch eine funktionale Verbindung zwischen isolierten Pflanzenpopulationen hergestellt wird. Es ist bisher kaum etwas darüber bekannt, ob und wie eine solche Verbindung durch frugivore Vogelarten geschaffen wird und welche strukturellen Voraussetzungen sie unterliegt. Mittels einer Projektion möglicher Samenausbreitungsereignisse auf eine detaillierte Habitatkarte haben wir die Häufigkeit sowie die Wege potentiellen Samentransports durch Trompeter Hornvögel zwischen Waldfragmenten bestimmt.

Für 31 Trompeter Hornvögel simulierten wir mittels einer Kombination von Bewegungsdaten und Darmpassagezeiten (s. Kapitel 1.2) potentielle Samenausbreitungsereignisse ausgehend von Wäldern und Waldfragmenten. Eine Verschneidung mit einer hochaufgelösten Habitatkarte ermöglichte es uns, den Ankunftsort der fiktiven Samen festzustellen, womit wir die Häufigkeit sowie die Wege eines potentiellen Samentransports zwischen Waldfragmenten bestimmen konnten.

Unsere Ergebnisse zeigten, dass zwar allgemein die Möglichkeit eines Samentransports zwischen Waldinseln relativ gering war (~7% der fiktiven Samen erreichten Wald), Trompeter Hornvögel aber eine Samenausbreitung zwischen Fragmenten von bis zu 15 km Entfernung zueinander bewirken können. Mehr als 100 Waldinseln wurden von den Tieren über eine Distanz von 50 km miteinander verbunden und wir konnten bestimmte Waldinseln identifizieren, die als Trittsteine eine zentrale Rolle für den Erhalt der Transportwege zu spielen scheinen.

Mit dieser Studie konnten wir zeigen, dass große frugivore Vögel in der Lage sind einen funktionale Verbindung zwischen räumlich isolierten Pflanzenpopulationen aufrechtzuerhalten. Die Kombination von hochauflösenden Bewegungs- und Landschaftsdaten ermöglichte es uns Vermutungen darüber anzustellen, welche Verbindungsdichte auf Landschaftsebene ausschlaggebend für den Erhalt von Ökosystemfunktionen in fragmentierten Landschaften ist.

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10 APPENDICES

Appendix 1: Seed dispersal kernel for 10 individuals

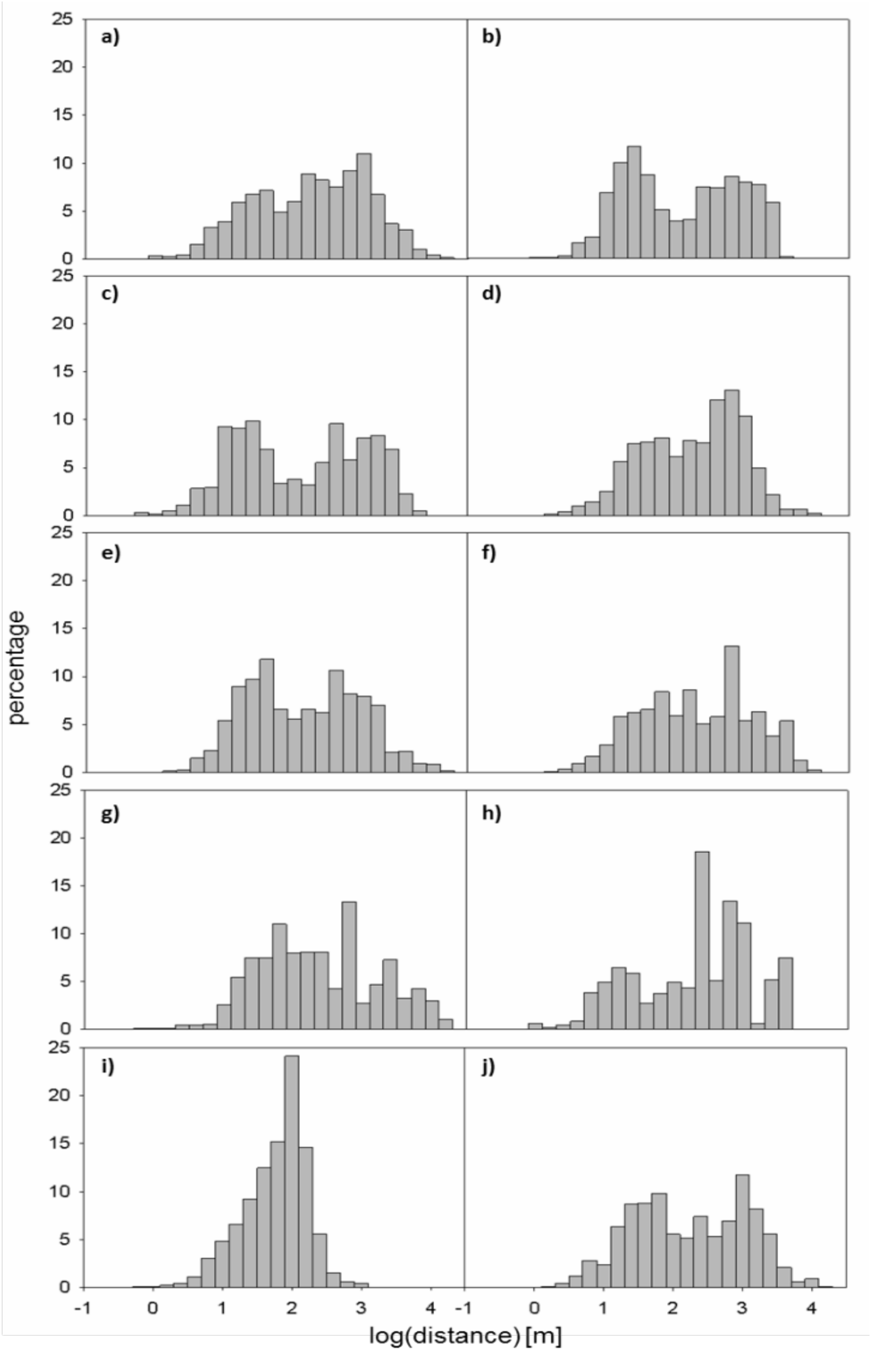

Figure A1*: Seed dispersal distributions of the 10 Trumpeter hornbills.*

Appendix 2: Measurement error for GPS data loggers.

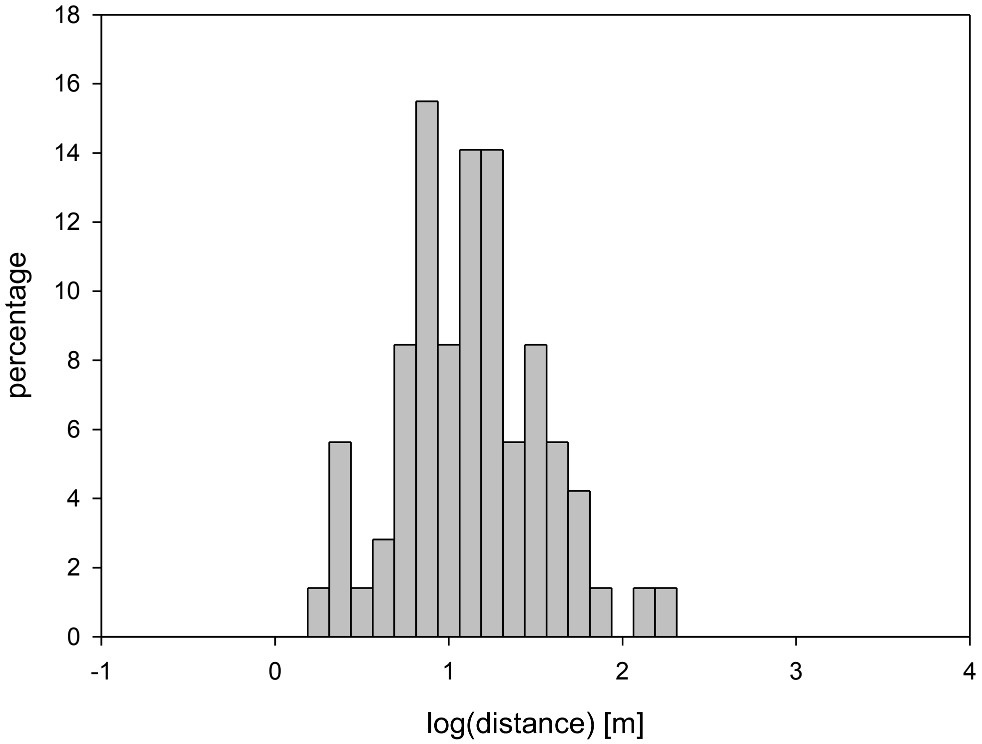

Figure A2: *Distribution of measurement error for GPS data loggers of tracking seasons in 2008 and 2009. Percentage of measurement error for each distance class (n = 142 locations, 71 in the open, 71 under tree canopies).*

11 CURRICULUM VITEA

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