Research

Nomadism and seasonal range expansion in a large frugivorous bird

Johanna Lenz, Katrin Böhning-Gaese, Wolfgang Fiedler and Thomas Mueller

J. Lenz (lenzjoha@gmail.com), K. Böhning-Gaese and T. Mueller, Biodiversity and Climate Research Centre, Senckenberg Gesellschaft für Naturforschung, Senckenberganlage 25, DE-60325 Frankfurt (Main), Germany. KB-G and TM also at: Goethe Univ. Frankfurt, Inst. for Ecology, Evolution and Diversity, Biologicum, Max-von-Laue-Straße 13, DE-60439 Frankfurt (Main), Germany. – W. Fiedler, Max Plank Inst. for Ornithology, Am Obstberg 1, DE-78315 Radolfzell, Germany.

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 contrasted the daily ranging behaviour between the breeding and non-breeding season of a frugivorous bird and demonstrate how larger seasonal ranges in the non-breeding season emerge through switching from a stationary home range behaviour to nomadism. We tracked movements of 29 male trumpeter hornbills *Bycanistes bucinator* across a fragmented landscape of eastern South Africa during different breeding and non-breeding seasons using high temporal resolution GPS data-loggers. Birds in the breeding seasons showed a typical, stationary home range pattern. In the non-breeding seasons birds, rather than expanding their stationary daily ranges, switched to nomadic movements that were characterized by shifts of the general location of daily ranges to a different area every couple of days. We also found that during the breeding seasons hornbills were mostly located in large continuous forests; birds in the non-breeding seasons frequently used forest patches within the agricultural landscape and residential areas. These seasonal differences in the movement behaviour of trumpeter hornbills may have important consequences for seed dispersal of plant species. Our findings show how seasonal range expansion of frugivorous birds may be driven by fundamental behavioural changes that have important consequences for ecosystem processes.

Investigations of animal movement patterns provide knowledge of ranging behaviour and space use which is particularly important if movements deliver essential ecosystem functions (Howe 1989, Nathan et al. 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 and Miriti 2004, Nathan et al. 2006). Large bird species are critically important especially where forest habitats are fragmented or degraded because, in principle, 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, Spiegel and Nathan 2007, Lenz et al. 2011).

To date, spatially explicit studies on ranging behaviour of large frugivorous birds that provide the level of detail necessary to evaluate how movement behaviour may affect ecosystem functioning are rare. Most studies on bird movements related to seed dispersal function are either conducted on a rather small spatial extent or with a broad temporal resolution (Côrtes and Uriarte 2013). While previous studies demonstrate the general pattern that birds have relatively

smaller seasonal ranges when nesting and feeding young and increase their ranges during the non-breeding season (Rolando 1998, Suryadi et al. 1998, Grant and Lichtfield 2003, Novoa et al. 2006), surprisingly little is known about the actual movement behaviour in the non-breeding season.

An increase of range sizes in the non-breeding season compared to the breeding season could be due to two fundamentally different processes: either the birds could continue to follow a typical home range pattern and remain stationary simply by increasing the size of their daily ranges, or could switch from home ranging to nomadic behaviour (Leighton and Leighton 1983, Roshier and Reid 2003, Mueller and Fagan 2008). If birds exhibit a nomadic behaviour, they would change their space use from day to day and switch location of daily ranges. The daily range size could show relatively little or no increase at all, but the location of daily ranges would be different among days. Distinguishing between these strategies is important since they most likely result in important differences in seed dispersal and ecosystem functioning.

One reason we have little empirical evidence of how range expansion of frugivorous birds in the non-breeding season takes place is that data availability for such fine-scaled

analyses has so far been limited (Otis and White 1999, Horne et al. 2007, Tomkiewicz et al. 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 with high temporal and spatial resolution (Kie et al. 2010, Tomkiewicz et al. 2010, Lenz et al. 2011). We used GPS data loggers to track movements of trumpeter hornbills *Bycanistes bucinator* during different breeding and non-breeding seasons 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 and Smith 1998, Kinnaird and O'Brien 2007, Kitamura 2011). A number of studies report a range expansion for the non-breeding season for hornbill species (Poonswad and Tsuji 1994, Suryadi et al. 1998, Holbrook et al. 2002, Kinnaird and O'Brien 2007), generally assumed to be linked to changes in fruit availability (Poonswad and Tsuji 1994, Anggraini et al. 2000, Holbrook et al 2002, Datta and Rawat 2003). The extent of range expansion, however, appears to be very variable (Kemp 1995, Whitney and Smith 1998, Holbrook et al. 2002, Kinnaird and O'Brien 2007) and, unless animals completely emigrate to a different region, the underlying behavioural processes that lead to seasonal range expansion are largely unknown. Especially evidence on how seasonal changes in daily movements lead to range expansion in the non-breeding season, e.g. whether range expansion is due to simple expansion of daily ranges or to a switch to nomadic movements, is lacking.

To our knowledge, we provide the first study investigating processes of seasonal range expansion of frugivorous bird species. In our analysis, we compared the mean and variance in the size of the daily ranges in the breeding and non-breeding seasons. Further we calculated the cumulative area increase of daily-ranges across several days to compare range expansion across days during the breeding and non-breeding seasons. We also performed seasonal comparisons of clustering and dispersion of locations among daily ranges to examine whether daily ranges were differently distributed in the breeding and non-breeding seasons within a bird's seasonal range. Finally, 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.

Methods

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 (central coordinates S30.71667; E30.23333), 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. 1999). 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. The next closest large forest is Umtamvuna Nature Reserve in the south west of Oribi Gorge (Fig. 1a). Forests are embedded in an intensively used agricultural matrix, mostly consisting of sugarcane and nut plantations, interspersed by residential areas (cf. Fig. 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 containing indigenous and exotic fruit-bearing trees.

We evaluated habitat cover in ArcGIS 10.0 (Environmental Systems Research Inst. 1999–2010) using the latest KwaZulu-Natal land-cover dataset derived from equivalent SPOT 2 and SPOT 4 satellite imagery captured in 2005–2006 at 20 m resolution (Geoterraimage, <www.geoterraimage.com>). We merged the habitat classes of the KZN land-cover dataset and determined two different categories, i.e. 'continuous forest' and 'non-forested habitat'. We defined 'continuous forest' as forested area (KZN land-cover: trees and bush cover >70%) larger than 156 ha, the largest forest patch within the agricultural matrix (Lenz et al. 2011). Thus, we classified as 'continuous forests' the three above-mentioned nature reserves and the densely wooded parts of the Mzimkhulu River valley. All other habitat types (for example all types of farming, rural and residential areas, gardens of farmsteads) and small forest patches within the agricultural matrix were grouped into 'non-forested habitat' (Fig. 1a, Lenz et al. 2011). In addition, the edges of the nature reserves were refined using Quickbird satellite imagery at 0.60 m resolution (GISCOE 2005; <www.giscoe.com>).

Study species

The trumpeter hornbill is one of the most abundant frugivorous species in Oribi Gorge (Bleher et al. 2003). With an average body weight of 565 g for females and 720 g for males (Kemp 1995) it is the largest obligate frugivorous bird species in South Africa. 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 small to large sized fruits. The breeding period of trumpeter hornbills in Natal in South Africa is from October to January and nesting lasts for at least 94 d (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 with their parents for about 6 months (Kemp 1995). 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 juveniles and adults (Kemp 1995).

Trapping and tracking

We caught trumpeter hornbills during breeding and non-breeding seasons between 2008 and 2011. We did not track females because data loggers might interfere with
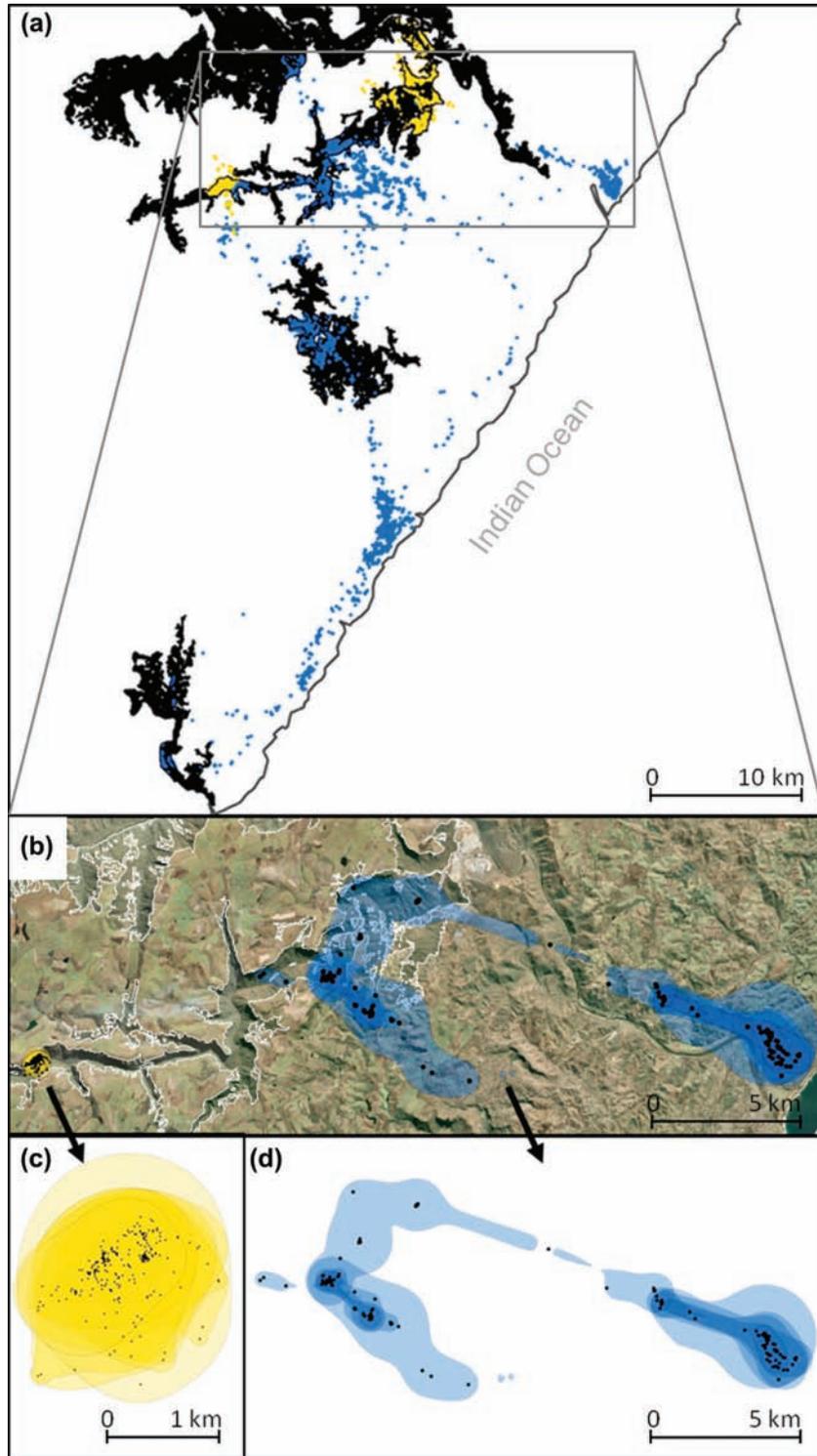
Figure 1. (a) Study area with all bird position data. Black areas are forest, white area is the fragmented landscape, blue points represent bird locations in the non-breeding seasons, yellow points represent bird locations in the breeding seasons. (b) Location of daily ranges of two different trumpeter hornbills within the study area and (c and d) in more detail the accumulation of the daily ranges per bird. Transparent polygons depict ranges of a single bird in the breeding season (c, yellow) and in the non-breeding season (d, blue). The underlying satellite image (b) shows the fragmented landscape of the northern part of the study area with white markings bordering the continuous forests, e.g. the Nature Reserve Oribi Gorge almost in the centre. Daily ranges in the breeding season were located almost only in the continuous forest and overlapped in large part (c). In contrast, daily ranges in the non-breeding season included wide areas of the fragmented landscape and shifted among several locations in the large seasonal ranges of the non-breeding season (d).

their breeding behaviour. We conducted trapping sessions during the breeding seasons in 2010 and 2011 (October–December), and during the non-breeding seasons of 2008, 2009 and 2010. Only two individuals were re-caught in two different seasons (the first in two different breeding seasons and the second in two different non-breeding seasons) and equipped with new data loggers. We used freestanding 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 (GPS-RF-tags, E-Obs GmbH; Munich, Germany; <www.e-obs.de>). For each bird, the weight of the data loggers was below the threshold of 3–5% of the birds' body weight (Kenward 2001, bird weight 600–880 g, data logger weight 27 to 39 g). 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 daylight. 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 d. To insure that we included only non-biased movement data we did not use the first three days of tracking (Lenz et al. 2011). We also considered only those days with at least 30 locations and used only data form birds that had a minimum of two days of tracking data.

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 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 ver. 2.13.0 (R development core team). 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 et al. 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 individuals and within individuals between days, 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 et al. 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 seasons. 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 (breeding/non-breeding season), incorporating random effects for both the logger ID 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 bird and season and again used linear mixed models with a fixed effect of season (breeding/non-breeding 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 2011).

Range expansion and stationarity of daily range locations

To estimate the degree of range expansion over several days in the non-breeding seasons compared to the breeding seasons, we calculated the cumulative area of multi-day ranges for birds in the breeding and in the non-breeding seasons. The size of multi-day ranges was calculated by overlaying daily ranges and calculating the size from the outer edge of the resulting multi-day range, thus overlapping areas were counted only once. We expected that cumulative multi-day range sizes increased faster from day to day in the non-breeding than in the breeding seasons. 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 non-consecutive days. We chose nine days because 22 of the 29 movement tracks consisted of at least nine days of bird movement data. We randomly drew nine daily ranges out of all daily ranges (without replacement) per bird and season and calculated cumulative areas by overlaying up to nine of these daily ranges. We repeated the procedure 1000 times and obtained

average cumulative multi-day range sizes from one to nine days per bird and season. 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 (breeding/non-breeding season) had a significant effect on cumulative multi-day range size. A significant interaction term indicates a different range expansion among the breeding and the non-breeding seasons. We calculated a random intercept and random slope model and included logger ID and tracking year as random effects for intercept and slope.

Characterizing patterns of locations among tracking days
To compare seasonal differences in ranging behaviour we examined for birds in each season the spatial clustering or dispersion of locations among days. Again we used only movement tracks containing at least nine days of movement data but used all days of each movement track for point pattern analysis. We analyzed for each bird and season 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 movement track. 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 seasonal range of the bird, thus birds use each site within its seasonal range with the same intensity. A clustering among days indicates that birds use different areas in their individual seasonal range with different intensity, i.e. that daily ranges are concentrated at certain sites within the seasonal range. We calculated for each bird and season the mean and the range of estimates for the bivariate K function at different spatial lags (s). The maximum spatial lag from which K values were calculated was smaller than half of the minimum extent in the x and y dimensions of the focal point pattern. We note that clustering or dispersion between point patterns may depend on the spatial distribution of the original point patterns themselves. However, with this analysis we aimed to achieve a comparison between seasons and because we were rather interested in the relative differences than in absolute K values, we used the simple bivariate k function assuming complete spatial randomness (CSR).

Results

After refinement of data (Methods) our analyses were based on 29 movement tracks of trumpeter hornbills ($n_{breeding\ seasons} = 9$; $n_{non-breeding\ seasons} = 20$) with movement data of on average 14 d per movement track (range 2–52) and 43 locations (range 30–54) d^{-1}. 22 of the 29 movement

tracks consisted of at least nine days of bird movement data. In total we had data from 457 tracking days ($n_{breeding\ seasons} = 165$; $n_{non-breeding\ seasons} = 292$) and 19 781 locations ($n_{breeding\ seasons} = 7645$; $n_{non-breeding\ seasons} = 12\,136$). Averaged measurement error as retrieved trough the GPS modules over all data loggers was 17 m (breeding seasons = 18 m, non-breeding seasons = 16 m). Median size of the 95% kernel of the daily ranges for birds tracked in the breeding seasons was 41.9 ha (range 1.8–418.8 ha) and for those tracked during the non-breeding seasons 164.4 ha (range 1.5–3520.67 ha; Fig. 2a). Daily range sizes in the breeding seasons ranged about three orders of magnitude and those in the non-breeding seasons about four orders of magnitude. When log-transforming daily range sizes and accounting for the random effects of logger ID and years, mean daily ranges were not significantly different between the breeding and the non-breeding seasons ($mean(log_{10})_{breeding\ seasons} = 36.0$ ha, $mean(log_{10})_{non-breeding\ seasons} = 129.4$ ha, $P_{MCMC} = 0.452$). Median of variances of daily range sizes of birds in the breeding seasons was 1.25 (range 1.07–1.95), of birds in the non-breeding seasons 1.68 (range 1.10–6.99, Fig. 2b). With log-transformed daily range sizes and incorporating the random effect of logger ID, variances of daily range sizes were significantly different between the breeding and the non-breeding seasons ($mean(log_{10})_{breeding\ seasons} = 1.32$, $mean(log_{10})_{non-breeding\ seasons} = 2.00$, $P_{MCMC} = 0.025$; Fig. 2b) with daily range sizes being more variable in the non-breeding seasons.

Cumulative area of multi-day ranges of up to nine days resulted in no significant increase in range size for birds in the breeding seasons, whereas hornbills in the non-breeding seasons significantly increased their cumulative ranges with
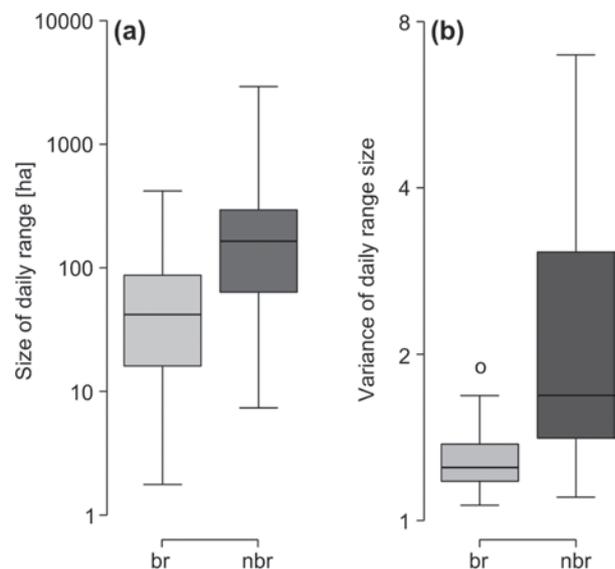

Figure 2. Differences (median, interquartile range and range) in (a) size of daily ranges and (b) of variances in daily range size for birds in the breeding seasons (br, light grey, n = 9 tracks) and birds in the non-breeding seasons (nbr, dark grey, n = 20 tracks). The daily ranges size did not differ significantly between the breeding and the non-breeding seasons (a) but the variances of daily range sizes was significantly greater for daily ranges in the non-breeding seasons compared to those from the breeding seasons.

Table 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 logger ID as random factors for intercept and slope. $n_{breeding\ seasons} = 8$ tracks, $n_{non-breeding\ seasons} = 14$ tracks; 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

days (Table 1, Fig. 3). Consequently, spatial variation in the location of daily ranges was significantly greater in the non-breeding seasons than in the breeding seasons (e.g. Fig. 1). During the non-breeding seasons we often observed nomadic movement behaviour of hornbills: the birds distributed their daily ranges in a wide area and built daily range aggregations within their seasonal ranges.

Results of the bivariate K function showed that trumpeter hornbills in the non-breeding seasons created a more spatially clustered pattern among daily ranges across their seasonal ranges than birds in the breeding seasons (except one individual that showed a pattern similar to the breeding seasons; Fig. 4). Birds did not randomly distribute their daily ranges across their total seasonal ranges; they rather clustered their daily ranges in specific regions of the large seasonal ranges in the non-breeding seasons. Hornbills in the breeding seasons however, distributed their daily

Figure 4. Comparison of spatial distribution of locations among daily ranges estimated with the bivariate K function. Shown is the linearized form of K ($^\wedge L_{12}$). Breeding seasons (dashed lines, light grey, n = 8 tracks), non-breeding seasons (solid lines, dark grey, n = 14 tracks). The bivariate K function estimates randomness, clustering, or dispersion between each day's locations and locations of all other days of a particular movement track as a function of spatial lag. Lines show the mean and shaded areas the range of all estimates. Values above zero indicate spatial dispersion and negative values indicate spatial clustering between locations of different days. Birds in the non-breeding seasons showed lower values of the bivariate K function, i.e. greater clustering than in the breeding seasons. This means, that within the large seasonal ranges of the non-breeding seasons daily ranges were more clustered than the seasonal ranges of the breeding seasons.

ranges in one location and relocations among daily ranges were thus more evenly distributed within the relatively small seasonal ranges of the breeding seasons. Birds in the breeding seasons spent most of their time within the continuous forest, as 94% of locations in the breeding seasons were located within continuous forest and only 6% were found in other habitats (for a typical example see Fig. 1). In contrast, only 32% of locations in the non-breeding seasons were within closed forests and 68% were located in other habitats.
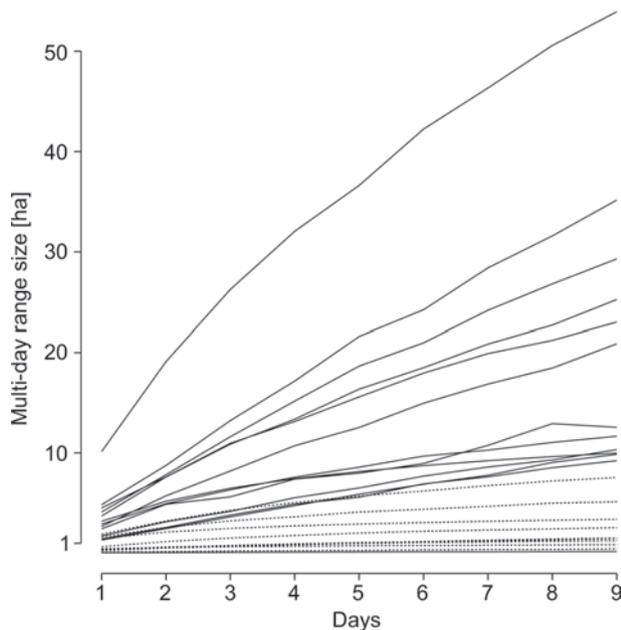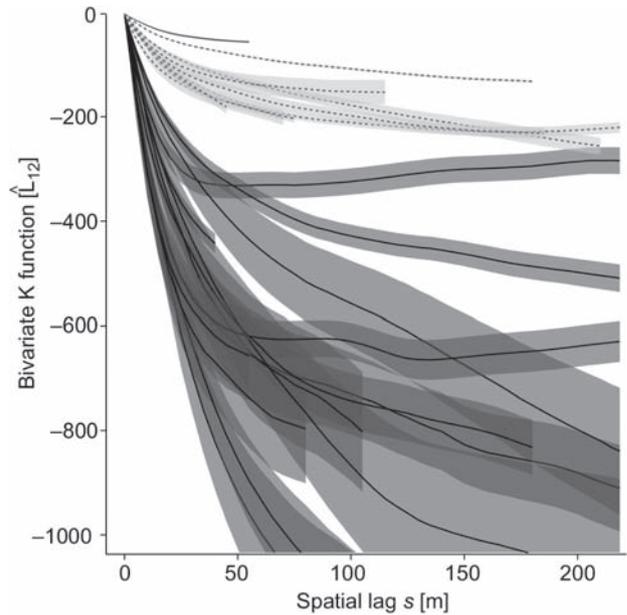

Figure 3. Mean of 1000 bootstrap estimates of cumulative area of multi-day ranges from one to nine randomly chosen days. Breeding seasons (dashed lines, n = 8 tracks), non-breeding seasons (solid lines, n = 14 tracks). Whereas multi-day ranges size increased with increasing number of included daily ranges for birds in the non-breeding seasons, for birds in the breeding seasons multi-day range size remained almost constant. Thus, birds in the non-breeding seasons regularly shifted their daily range site, whereas birds in the breeding seasons remained stationary at the same location.

Discussion

Our approach to investigate changes in ranging behaviour on a daily basis provided new insights into the underlying process of seasonal range expansion in large frugivorous birds. Range expansion during the non-breeding seasons happened due to a shift from typical stationary home range behaviour to a nomadic ranging behaviour where hornbills moved their daily ranges between different locations and not because of greater daily range sizes. In the non-breeding seasons daily ranges of trumpeter hornbills were more variable in size and location compared to the breeding seasons.

Breeding seasons

In the breeding seasons, hornbills had small daily ranges that were similar in size among days and cumulative multi-day range sizes did not increase significantly over time, demonstrating that daily ranges did not change their spatial location among days. In addition, we observed that in the breeding seasons 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, the very small ranges in combination with a 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 seasons: 1) ranging behaviour might be constrained due to central place foraging (Rosenberg and McKelvey 1999). A feeding hornbill has to visit the nest at least once every 1–2 h (Kemp 1995, Roberts et al. 2005, Kinnaird and O'Brien 2007). Thus, foraging within farmland to reach widely scattered food resources would result in higher energetic costs in the breeding seasons (Graham 2001). 2) Birds might find sufficient food resources within these small ranges during the breeding seasons. Within the forest, many trees of different species could occur within a small area; thus birds may reach different food resources easily. 3) Trumpeter hornbills might reach their food requirements by adding other food resources than fruits to their diet, such as insects and small reptiles (Kemp 1995). 4) Since there is evidence of cooperative breeding for hornbill species (Kemp 1995, Kinnaird and O'Brien 2007), it is possible that helpers, non-breeding trumpeter hornbills that carry supplementary food to a specific nest, contribute to cover the food demand of the female and offspring. Consequently, the food amount one bird has to gather would be reduced and small stationary daily ranges could be sufficient as foraging ground for one bird. 5) Agricultural areas might not provide any appropriate nesting trees, or these 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 breeding habitat that provides suitable nest sites and sufficient food resources during the breeding season.

Range expansion in the non-breeding seasons

Our findings support the general notion that seasonal range sizes of frugivorous birds increase during the non-breeding seasons (Suryadi et al. 1998, Grant and Lichtfield 2003, Novoa et al. 2006). While mean daily range sizes were not significantly larger in the non-breeding than in the breeding seasons, we found an increase of overall range size with cumulating daily ranges over time. This demonstrates that, for trumpeter hornbills, the process of range expansion during the non-breeding seasons emerges from a shift to a nomadic movement pattern.

In contrast to both home range movements where individuals range in rather small ranges and migratory movements with regular, seasonal movement from and to disjunct areas, nomadic movements are non-directed and unpredictable in space and time (Mueller and Fagan 2008). These types of movements have often been associated with unpredictable and ephemeral food resources that vary across broad scales beyond the size of a normal home range (Mueller et al. 2011). In the case of frugivorous birds, this applies to the density and the distribution of fruiting trees (Leighton and Leighton 1983). Since seasonal fluctuations in resource availability occur also in evergreen tropical forests, e.g. in fruit abundance, birds in general tend to exhibit a seasonal pattern in their phenology (Levey 1988, Poulin et al. 1992). This is also true for trumpeter hornbills in the study, which start breeding in October at a time of high fruit availability within the forests (Bleher et al. 2003). Consequently, with less fruit availability in the forests in the non-breeding seasons, different trees fruiting randomly at distant sites within the fragmented landscape may lead to nomadism in hornbills beyond the continuous forests.

We found that small daily ranges in the non-breeding seasons were usually located within the same general area for several days; whereas large daily ranges resulted from movements to a different general area (e.g. Fig. 1b), explaining the large variance in daily range sizes within these seasons. 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 switching of locations that hornbills exhibited in the non-breeding seasons. This switching behaviour is possible across large scales during the non-breeding seasons, because birds are not bound to a nest site and do not need to follow a central place foraging strategy. 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 (Rainey and Zuberbühler 2007, Kemp et al. 2011). In contrast to our findings, those shifts persisted for longer than only a few days and indicated a general and broader seasonal shift in foraging ground and tracking of fruit resources via seasonal migrations (Whitney and Smith 1998).

However, it is likely that there are additional advantages associated with the range expansion and dispersion during the non-breeding seasons. Hornbills may explore new areas to find new fruit resources and since birds form large communal flocks in the non-breeding season they may benefit from each other's knowledge of resource distributions (Krebs 1974, Giraldeau 1984). In addition, unmated and young hornbills may search for mating partners across a wider range and may find new suitable nest sites (Kinnaird and O'Brien 2007). Overall, social interaction may play an important role in range expansion of trumpeter hornbills during the non-breeding seasons.

Potential consequences for seed dispersal

The strong differences in ranging behaviour between the breeding and the non-breeding seasons likely have ecological consequences for plant species dispersed by trumpeter hornbills. In the breeding seasons, the small daily ranges of trumpeter hornbills would cause short-distance seed dispersal limited to the close neighbourhoods of the parental trees and seed transport by breeding birds would

concentrate seed deposition at the nesting tree (Howe 1989, Kitamura et al. 2004, Kitamura 2011). In addition, seed dispersal by hornbills during the breeding season may be largely limited to large, continuous forests and may not reach the smaller patches in the agricultural matrix.

In the non-breeding season, seed dispersal may reach further and into the agricultural landscape, since movement behaviour followed a nomadic pattern. 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. In addition, the long-distance flights exhibited to shift their daily range locations may allow for important long-distance seed dispersal by trumpeter hornbills during this time of the year.

Our day-based resolution of ranging behaviour revealed that range expansions of trumpeter hornbills in the non-breeding season were due to a nomadic shift of locations among daily ranges and not due to larger daily ranges per se. Seasonal changes in ranging behaviour of animals could cause important alterations in ecosystem functions and understanding the processes of range variation helps to determine the ecological consequences of those seasonal differences.

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