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Natal dispersal in the Southern Ground Hornbill *Bucorvus leadbeateri*

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Dispersal is of ecological and evolutionary importance for population biology because it affects a species' ability to expand its range, to colonise new favourable habitats and to increase the likelihood of population persistence. Male birds are mostly philopatric, delaying dispersal or dispersing closer to their natal territories than females. Females tend to disperse further than their male siblings to reduce the chance of inbreeding. Dispersal in the cooperative breeding Southern Ground Hornbill *Bucorvus leadbeateri* is poorly understood. It is not known how far individuals disperse, or what the difference in dispersal age and distance is between males and females. We investigated dispersal events using field observations of ringed individuals within groups in a study population and resightings in surrounding areas. A total of 113 individuals from 19 groups were ringed during 2005–2015. Of these, 14 were breeding adults who never dispersed. Of the remaining 99, 27 were still present in their natal groups at the end of the study, four deaths were confirmed, 50 disappeared from their group and were never seen again (excluded from further analysis), and 18 were confirmed to have dispersed by direct observations in secondary groups. Median dispersal distance was similar for females and males (22 km and 25 km, respectively). Females dispersed younger than males (eight months post-fledging and 44 months post-fledging, respectively). One male delayed dispersal beyond nine years and all females dispersed before three years post-fledging. These data provide insights into the dispersal dynamics and dispersal propensity of this endangered species. Ways to improve data collection and the study of dispersal in this species are discussed.

La dispersion du Bucorve du Sud *Bucorvus leadbeateri*

Les phénomènes de dispersion ont une importance tant écologique qu'en termes de processus évolutifs pour mieux comprendre la biologie des populations. La dispersion influence directement la capacité des espèces à accroître leur distribution spatiale et coloniser de nouveaux habitats favorables pour augmenter les chances de survie de ses populations. Les oiseaux mâles sont pour la plupart philopatrics, reportant dans le temps leur dispersion ou assurant une dispersion plus proche de leur territoire natal que les femelles. Les femelles ont tendance à se disperser plus loin que les mâles d'une même couvée pour réduire les probabilités de consanguinité. Le phénomène de dispersion chez les Bucorves du Sud *Bucorvus leadbeateri*, espèce ayant pour trait comportemental la reproduction communautaire, est très peu connu. On ne connaît pas à quelle distance les individus se dispersent ou la différence de dispersion entre les mâles et les femelles en termes d'âge et de distance de dispersion. Nous avons recherché des événements spontanés de dispersion via des observations de terrain sur des individus bagués au sein de groupes d'une population à l'étude ainsi que de nouvelles observations dans les zones alentours. Un total de 113 individus, émanant de 19 groupes, ont été bagués entre 2005 et 2015. Parmi ceux-ci, 14 étaient des adultes reproducteurs qui n'ont jamais effectué de dispersion. Parmi les 99 restant, 27 étaient toujours présents dans leur groupe familial initial à la fin de l'étude, 4 morts ont été avérés, 50 ont disparus de leur groupe et n'ont jamais été revus (excluant des données pour de futures analyses) et 18 ont assuré une dispersion vers des groupes secondaires, confirmé par observations directes. Les médianes de distances de dispersion se sont révélées similaires entre individus mâles et femelles (25 et 22 km respectivement). Les femelles ont effectué la dispersion à plus jeune âge que les mâles (8 mois et 44 mois après le premier envol, respectivement). Cas particulier, un mâle a retardé sa dispersion au-delà de 9 ans alors que toutes les femelles ont effectué leur dispersion dans les trois années après leur sortie du nid. Ces données fournissent de nouvelles connaissances sur les dynamiques de dispersion et la propension à effectuer ce trait comportemental chez cette espèce en danger. Des pistes de réflexion concernant l'amélioration de la collecte de données et l'étude des phénomènes de dispersion sont présentées pour conclure.

Keywords: cooperative breeding, dispersal, ground hornbills, philopatry, resightings

Introduction

Natal dispersal in animals is the movement of individuals away from their place of birth to the first site where they attempt to breed (Greenwood and Harvey 1982). The

movement of individual birds away from their place of hatching to new areas affects the potential for colonisation of new favourable habitats (Brotons et al. 2005), range

expansion (Walters et al. 2002; Duckworth and Badyaev 2007; Armstrong et al. 2015) and gene flow (Double et al. 2005; Woxvold et al. 2006; Kurvers et al. 2014).

Several ultimate and proximate factors drive the decision to disperse. Ultimate factors include kin interactions, inbreeding avoidance and habitat variability (Bowler and Benton 2005). Dispersal can act to reduce the level of competition between close relatives for a breeding opportunity at the natal site, because dispersing individuals will compete with non-kin (Hamilton and May 1977) and lower the chance of breeding with close relatives (Howard 1960; Woxvold et al. 2006; Nelson-Flower et al. 2012). The costs of breeding between close relatives are widely recognised, such as reduced hatch rate, brood size and survival (Keller and Waller 2002). Proximate factors that trigger dispersal decisions may be influenced by the need to avoid crowded areas or areas lacking in food supply (Howard 1960). Understanding a species ability to disperse and what conditions favour or limit dispersal is important to understanding the species' ability to track environmental shifts and thus the likelihood of a species persistence (Ferriere et al. 2000).

Birds mostly exhibit male philopatry and female-biased dispersal (Greenwood and Harvey 1982; Williams and Rabenold 2005; Temple et al. 2006). In most bird species, males display 'resource defence' where they defend resources to attract females (Greenwood 1980). The resources that individuals defend may include access to a nest site or high-quality foraging, or both. Therefore, securing access to these resources is important for future breeding opportunities and overall individual fitness. This type of mating system is linked to male philopatry on the assumption that a male will have greater ease of acquiring a territory closer to home than further away (Greenwood 1980). This may occur either by greater familiarity with the surrounding habitat or knowledge of potential breeding gaps (Greenwood and Harvey 1982; Zack and Stutchbury 1992). In addition, it may occur through benefits associated with nepotism, whereby increased survival or securing a resource could be enhanced by the presence of relatives (Greenwood 1980; Koenig and Dickinson 2004). Under these scenarios, it may benefit a male to delay dispersal rather than to disperse (Koenig et al. 1992).

If male offspring delay dispersal, then any female siblings remaining and hoping to breed near the natal site would run the risk of pairing with close relatives. Dispersing further than male relatives can assist in reducing inbreeding if inbreeding is costly, and thus helps individuals to escape the negative effects associated with inbreeding depression. But not all species show this difference in dispersal distances between the sexes (Blackmore et al. 2011; Nelson-Flower et al. 2012; Engler et al. 2014). In some cases, the dispersal distances are similar because of a distance limitation, such as on relatively small islands (Engler et al. 2014). In another cases, females may not have to disperse far to avoid pairing with close relatives, due to their ability to recognise and avoid familiar group members as mates (Nelson-Flower et al. 2012).

The Southern Ground Hornbill *Bucorvus leadbeateri* (hereafter ground hornbill) is the largest cooperative breeding bird in the world. The species is listed as

Vulnerable globally (BirdLife International 2016) and Endangered in South Africa where declines have been caused chiefly by habitat loss and secondary poisoning (Taylor and Kemp 2015). Ground hornbill groups typically comprise a breeding pair and a variable number of mostly male non-breeding helpers (Kemp 1988). A study that used observations of unringed but individually identifiable individuals in the Kruger National Park suggested that males and females had different dispersal strategies (Kemp 1988). In that study, Kemp (1988) found that young females were indistinguishable from young males until females develop a blue throat colour when mature (~age 5–6 years; Theron et al. 2013). Young females were thought to disperse once mature and non-breeding females 'floated' between home ranges (sometimes for years) alone, or in all-female groups of up to three individuals (Kemp 1988). Female subadults seldom undertook any helper roles and presumably gained greater protection from being in a group than floating alone (Kemp 1988). Males delayed dispersal and assisted with territory defence, predator detection and rearing the next generation (Kemp 1988). They remained in their natal territories for at least six years, after which they presumably inherited the natal or a neighbouring territory (Kemp 1988). We test the generality of Kemp's (1988) inference of male philopatry and female dispersal using dispersal events of ringed individuals and investigate the relationship between dispersal distance and the number of months post-fledging that an individual was estimated to have dispersed (hereafter age at dispersal). Arthropods are an important food source for ground hornbills (Kemp 1976) and invertebrate abundance is closely linked to rainfall (Kemp 1976; Sinclair 1978; Cumming and Bernard 1997). Given that dispersal in birds is costly (Kingma et al. 2016), we predicted that individual ground hornbills should disperse further in a year when rainfall, as a proxy for food availability, is high.

Methods

The core study area was the Associated Private Nature Reserves (APNR; 1 800 km², centred on 24.16° S, 31.18° E) in north-eastern South Africa and data were collected during 2005–2015. The study area has distinct wet (October–March) and dry (April–September) seasons with a 2000–2015 mean annual precipitation of 472 ± 152 mm (range 214–948 mm), which is patchily distributed. Daily mean minimum and maximum temperatures range seasonally from 10 to 20 °C and from 20 to 33 °C, respectively. The geomorphology is undulating, with rocky outcrops in the north and flat, grassy plains in the south. The vegetation varies from open savanna to closed woodland.

The focus of the Southern Ground Hornbill research programme in north-eastern South Africa was to compare breeding attempts and breeding success between groups using natural nests and nest boxes. Group observations were not the primary focus and, as such, there was no standardisation of group observations to record the presence/absence of ringed individuals. Although every attempt was made to make regular contact with groups,

resightings of ringed individuals were irregular and infrequent due to the large territory sizes (~60 km²), the wary nature of individuals and the dense habitat in the study area. It is within this context that we present the basics of dispersal data analysed after 11 years of infrequent sightings in the first attempt to describe dispersal using ringing-resightings data for the first time in this species.

For the purpose of investigating dispersal tendencies we used ringing data and direct observations of ground hornbills accumulated during 2005–2007 and again during 2011–2015 (no group sightings were recorded during 2008–2010), and data were analysed during 2016–2017. Monthly rainfall data were obtained from reserve records of rainfall collected at 14 rain gauges checked daily throughout the study area. Monthly rainfall data were obtained for the period 2004–2015 and annual totals were averaged to get a long-term mean annual precipitation for the study period, including the year prior to 2005. Group home ranges were determined by the use of a minimum convex polygon, which included all locations of group sightings taken during 2000–2015.

Individual ground hornbills were ringed with a unique combination of three plastic colour rings and one metal numbered ring. Most individuals were ringed as chicks a few days before fledging. Subadult and adult birds were captured using walk-in traps at dawn, making use of call-up recordings and life-size, fibreglass ground hornbill decoys in the trap to attract groups to the capture site. The age of immature individuals was estimated using plumage, bill size and throat patch colour (Kemp and Kemp 1980): 0–1 years: off-white throat colour, blackish-brown plumage, white primaries flecked with brown, bill markedly smaller than that of adult; 1–2 years: black feathers growing in from first moult, particularly on the upper-wing coverts; 2–3 years: plumage mainly black and there is a touch of orange on the throat skin; 3–4 years: throat skin inflated and is orange, eye-skin is also orange, plumage entirely black except for pure white primaries; 4–6 years: throat colour deepens toward the red of the adult, bill grows to full size, female violet-blue patch appears only at the very end of this stage. Individuals were sexed using the colour of the facial skin or by using genetic markers (Theron et al. 2013) where possible. Not all individuals could be sexed due to some individuals without DNA samples dispersing before their sex could be determined using throat colour.

Groups with ringed individuals were encountered opportunistically or, where possible, located by their duet calls at dawn. The location was recorded using a Garmin 76CSx Map GPS, as well as the group size and demographic composition. Sightings of ringed individuals in neighbouring Kruger National Park were provided by South African National Parks and Endangered Wildlife Trust field staff. These sightings, typically with photographs to confirm ring combinations, were largely provided by tourists who submitted them to Kruger field staff as part of a ground hornbill sighting programme.

Dispersal date was recorded as the midway point between the date the individual was last observed in its natal group and the first date it was observed in a secondary group. Estimates of age at dispersal were excluded from the analysis for birds where the interval

between relevant sightings was greater than six months. Dispersal distance was calculated as the straight-line between the nest site of the natal group and the secondary group. If the location of the new nest site was not known, the distance from the natal nest to where the individual was seen with the secondary group was used.

Statistical analyses

The program R version 3.0.3 (R Core Team 2014) was used for all statistical analyses. A Wilcoxon rank-sum test was used to analyse differences in dispersal age between females and males. All average values reported are accompanied by measured standard deviations (SDs).

A linear mixed model (package 'nlme'; Pinheiro et al. 2017) was fitted to the observational data, using R, to investigate factors related to natal dispersal distances. Data were considered for 16 individuals from eight groups for which both gender and dispersal distances were known. Data exploration followed the protocols described in Zuur and Ieno (2016). We modelled the log (base 10) of *dispersal distance* (continuous; the distance in kilometres between the natal nest site and the nest site of the new group) as a function of *age* (discrete; age at dispersal in months as calculated from fledging), *gender* (binary; male or female) and *rainfall of the previous year* (continuous; total rainfall in millimetres during July–June).

The response variable, dispersal distance, was log-transformed to bring in the outlier dispersal distance that was greater than 100 km. Where the new nest site was not known, dispersal distance was calculated to where the individual was last seen with the new group. Dispersal age was taken as the midway between the date it was last seen in the group, and the day it was reported as absent. *Group identity* (categorical) was initially included as a random intercept to allow for group-specific tendencies, but the variability of this random effect was estimated to be zero; it was therefore removed and a simpler linear model adopted.

Model fit was verified using plots of residuals against fitted values as well as residuals versus each explanatory variable used in the full model. A histogram of residuals was created to confirm a normal distribution. The diagnostics confirmed that model assumptions hold. Variables were checked for collinearity by calculating variance inflation factors (VIF) in the 'car' package (Fox and Weisberg 2011), and all variables had a VIF < 3. Confidence intervals (95%) for each parameter were obtained using Wald's approximation (Wald 1947).

The overall *p*-value for the model was > 0.1 and the model is discussed in light of this. It is also noted that the sample size for the analysis is relatively small (*n* = 16), and only dispersals with resightings are included. The reason we do not have resighting data for all ringed individuals could be due to several factors including, but not limited to, individuals dying without being found or, more likely, dispersing further than what was detectable.

Results

A total of 113 individuals were ringed from 19 groups during 2005–2015 in the core study area. Groups were observed an average of 10 ± 12 times a year (range 1–71 times a

year, $n = 1\ 363$ group observations; Table 1). In each group contact, 75% of the individuals on average could be checked for rings. There were cases when a group was not sited for an entire year (Table 1). During 2005–2015, the average density of breeding and non-breeding groups in the study site was one group per $72 \pm 7\ \text{km}^2$ (range of one group per 60–72 km^2). Metal rings had a life-span of >10 years (KFC pers. obs.). A few single plastic coloured rings were known to be removed/lost, but individuals could still be identified using photographs of the metal ring and/or the remaining colour combination together with group identity and individual age.

A total of 15 individuals were ringed as adults, 12 as subadults (age 1–6 years) and 86 as nestlings. Of these ringed birds, 35 were females, 48 were males and 30 were of unknown sex. Of the 83 sexed individuals, 56 were sexed by using molecular markers and 27 by observations of their throat skin colour. A total of 14 individuals were ringed as breeders from 10 groups (10 females and four males), and no breeders were observed to switch groups. The 99 individuals ringed during 2005–2015 (Table 2) that were classified as non-breeders were analysed for the natal dispersal, dispersal distance and age at dispersal results.

Natal dispersal

Of the 99 non-breeding individuals, 50 disappeared from their natal groups and it could not be confirmed whether these individuals dispersed or died (51%). These 50 individuals were excluded from further analysis. A total of 27 ringed individuals were still present in the study site at the end of the study and four confirmed deaths were recorded. Eighteen of the 99 non-breeding individuals (seven females, nine males and two unknown sex) were resighted in secondary groups after dispersing from their natal group (Figure 1, Table 3). These 18 individuals were used for the analysis of dispersal distance.

Dispersal distance

Of the 18 individuals that were observed again after leaving their natal groups, 10 dispersed into secondary groups within the core study area and eight dispersed into secondary groups in the neighbouring Kruger National Park (Figure 1). Individuals dispersed on average $35 \pm 31\ \text{km}$ from their natal home range (range 5–118 km , $n = 18$). Females dispersed on average $41 \pm 40\ \text{km}$ (range 5–118 km , median 22 km , $n = 7$) and males dispersed on average $34 \pm 27\ \text{km}$ (range 8–79 km , median 25 km , $n = 9$). All but one female dispersed at least four home ranges away from their natal groups, whereas most males dispersed into groups 1–2 home ranges from the natal group (Figure 2).

A linear model identified a non-significant negative relationship between rainfall and dispersal distance (Table 4). Average rainfall of $443 \pm 129\ \text{mm}$ (range 249–651 mm) was recorded over the previous year for each group during 2005–2015. For every 50 mm increase in rainfall over the previous year, dispersal distance decreased by 18% (multiplicative effect: 0.816; 95% CI: 0.681, 0.977; $p = 0.03$; Table 4). However, the high overall p -value for the model (0.16), compared with that for a model with no predictors, suggested that there was little evidence that rainfall, gender or age were related to dispersal distance (Table 4). Therefore, the reproducibility of this finding should be tested using a larger sample size.

Age at dispersal

Age at dispersal was accurately known for 12 of the 18 individuals that were seen again after dispersing (46%; Table 3), of which six were female, four were male and the sexes of two were unconfirmed. Females dispersed an average of 12 ± 9 months post-fledging (range 2–24 months, median 8 months) and males at 48 ± 42 months post-fledging (range 8–96 months, median

Table 1: Sighting frequency of 19 ringed Southern Ground Hornbills *Bucorvus leadbeateri* groups. No group sightings occurred during 2008–2010. Dashed lines reflect years when a group had not yet been discovered

Group	2005	2006	2007	2011	2012	2013	2014	2015	Group total
Addger	4	5	1	0	3	2	10	9	34
Caroline	4	1	4	0	1	5	23	18	56
Copenhagen	1	1	11	2	4	17	16	7	59
DeLuca	7	2	3	0	1	2	15	2	32
Giraffe	4	6	4	0	0	0	1	0	15
Goedehoop	1	0	6	1	0	3	0	0	11
Hermansburg	10	4	20	1	1	2	6	6	50
Janovsky	2	5	26	2	7	22	12	4	80
Java	–	–	–	1	2	12	58	8	81
Johnniesdale	5	6	5	0	2	6	11	71	106
Karan Khaya	15	10	13	1	3	7	66	10	125
Keer Keer	15	5	9	2	13	33	47	19	143
Lornay	1	1	3	1	2	12	13	6	39
Ntoma	2	6	18	0	0	2	1	3	32
Ntsiri	31	17	11	23	12	13	37	23	167
Pitlochry	21	7	25	1	9	6	9	9	87
RhinoRoad	18	8	6	3	12	12	8	20	87
Senalala	19	10	34	8	6	22	17	8	124
Strydom	1	3	7	5	0	4	10	5	35
Annual total	161	97	206	51	78	182	360	228	1 363

Table 2: Timeline of the ringing of 99 non-breeding Southern Ground Hornbills *Bucorvus leadbeateri* in 19 groups

Group	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	Group total
Addger	1	2	0	1	0	1	0	1	0	1	1	8
Caroline	1	0	0	0	0	1	0	1	0	1	1	5
Copenhagen	0	0	4	0	1	1	1	0	1	1	1	10
DeLuca	1	0	1	1	1	0	0	0	0	0	0	4
Giraffe	0	0	0	1	0	0	0	0	0	0	0	1
Goedehoop	0	0	0	0	0	1	1	0	1	0	0	3
Hermansburg	1	0	1	0	1	0	0	0	0	0	0	3
Janovsky	0	1	0	1	1	0	1	0	1	1	0	6
Java	0	0	0	0	0	0	0	0	0	1	1	2
Johnniesdale	1	1	1	1	1	1	1	0	0	1	0	8
Karan Khaya	1	1	1	1	1	3	1	0	1	1	1	12
Keer Keer	1	0	1	0	1	1	1	1	0	1	0	7
Lornay	0	0	0	0	0	0	1	0	1	0	0	2
Ntoma	0	2	0	0	0	0	0	0	0	0	0	2
Ntsiri	0	0	1	0	1	0	1	0	0	0	0	3
Pitlochry	2	0	1	1	1	0	1	0	0	0	0	6
RhinoRoad	1	0	1	1	1	1	1	0	0	1	1	8
Senalala	1	1	1	1	1	1	0	1	0	0	0	7
Strydom	0	0	0	0	0	0	1	1	0	0	0	2
Annual total	11	8	13	9	11	11	11	5	5	9	6	99

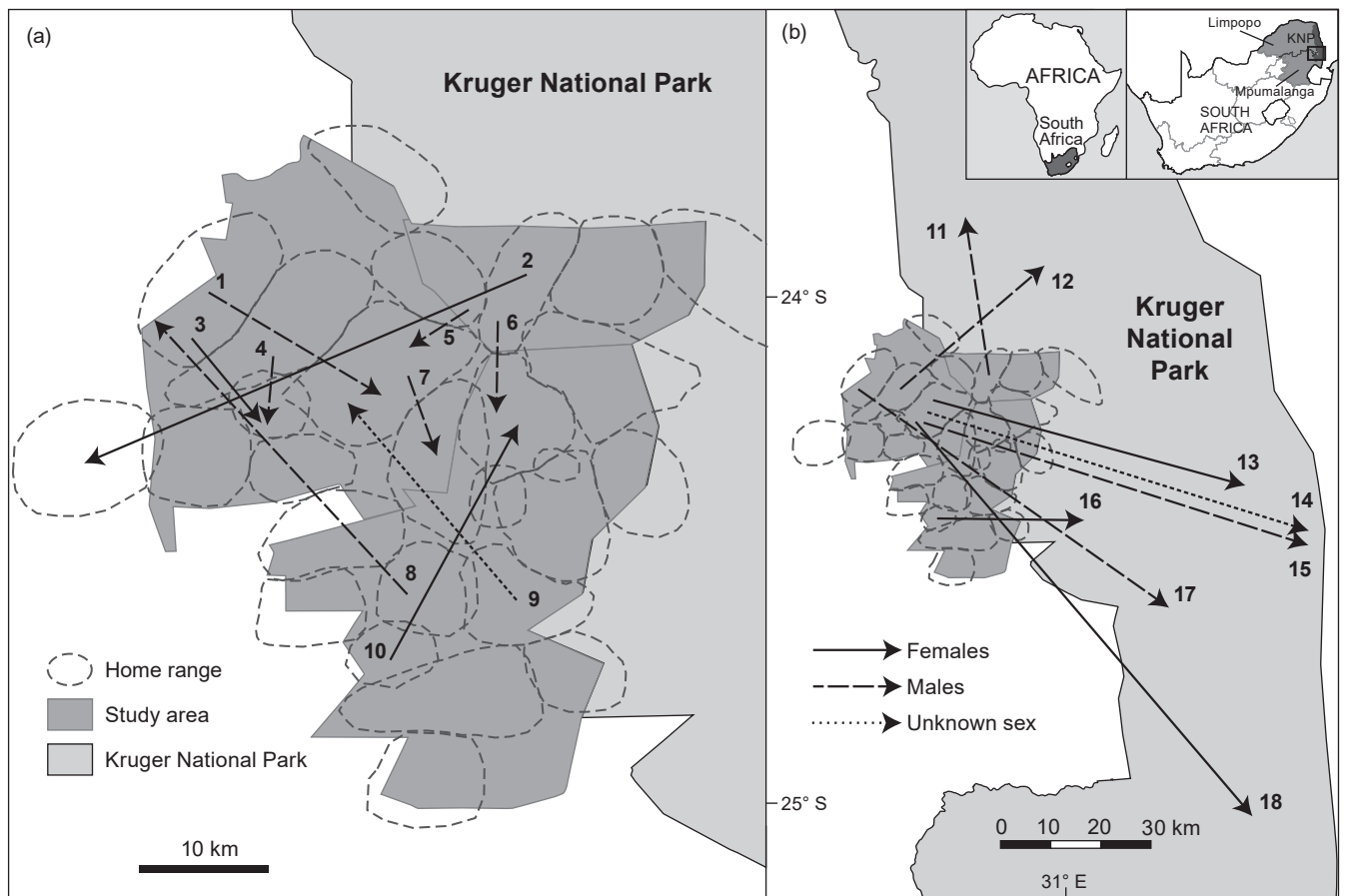


Figure 1: Natal dispersal of 18 Southern Ground Hornbill *Bucorvus leadbeateri* individuals within (a) and outside (b) the core study area in north-eastern South Africa. Polygons are home ranges of Ground Hornbill groups. Solid line = females; dashed line = males; points = unknown sex. Numbers adjacent to each line correspond to individual attributes in Table 3

Table 3: Southern Ground Hornbill *Bucorvus leadbeateri* individuals that dispersed from their natal groups and were subsequently seen in secondary groups either within the core study area (Figure 1A) or in the neighbouring Kruger National Park (Figure 1B) in north-eastern South Africa. DNA = molecular markers used to sex individuals, TC = relying on the colour of the throat to sex individuals as per Kemp and Kemp (1980)

ID	Year fledged	Sex	Sexing method	Year ringed	Age ringed	Natal group	Year last seen in natal group	Year dispersed	Natal group size	Group density (group km ⁻²)	Rainfall in previous year (mm) ^a	Estimated dispersal age (months)	Dispersal accuracy ^b	Dispersal distance (km)	Secondary group	Secondary group size	No. times seen ^c
1	2011	M	DNA	2011	Chick	Janovsky	2013	2013	5	0.015	605	31	9.2	16	Senalala	5	4
2	2007	F	DNA	2007	Chick	Ntsiri	2007	2007	4	0.013	343	9	0.4	40	Jejane	3	2
3	2009	F	DNA	2009	Chick	Janovsky	2009	2009	4	0.013	504	2	2.5	16	Nhamp.	6	4
4	2009	M	DNA	2009	Chick	Pitlochry	2009	2010	4	0.014	476	19	19.1	8	Nhamp.	6	5
5	2012	F	DNA	2012	Chick	Strydom	2013	2013	3	0.015	645	22	0.5	5	Senalala	4	5
6	2009	M	TC	2009	Chick	Ntsiri	2009	2010	3	0.013	398	9	9.1	12	Java	5	8
7 ^d	2006	M	DNA	2006	Chick	Senalala	2011	2011	6	0.014	317	69	1.0	13	Keer Keer	5	9
8	2010	M	TC	2010	Chick	Caroline	2010	2012	6	0.014	633	26	26.4	29	Janovsky	5	3
9	2005	na	-	2005	Chick	Adder	2006	2006	3	0.013	249	22	2.5	20	Senalala	6	2
10	2007	F	DNA	2007	Chick	Hburg	2007	2007	3	0.013	469	8	0.1	22	Java	6	2
11	2011	M	DNA	2011	Chick	Ntsiri	2012	2012	3	0.014	455	19	1.8	35	Nandzane	5	4
12	2000	M	DNA	2005	Subadult	Pitlochry	2007	2008	5	0.013	447	96	5.4	39	Phal. Gate	5	3
13	2010	F	DNA	2010	Chick	Senalala	2011	2012	6	0.014	317	24	5.2	65	S100	5	2
14	2012	na	-	2012	Chick	Senalala	2012	2012	5	0.014	447	9	0.3	79	Singita Leb.	4	2
15	2009	M	DNA	2009	Chick	Senalala	2009	2011	4	0.013	299	22	22.7	79	Singita Leb.	5	3
16	2009	F	DNA	2009	Chick	Hburg	2009	2009	3	0.013	651	8	8.6	19	Orpen Gate	4	4
17	2007	M	TC	2007	Chick	Janovsky	2007	2007	4	0.013	447	8	0.4	76	Hamilton's	2	2
18	2007	F	DNA	2007	Chick	Senalala	2007	2007	5	0.013	278	7	1.4	118	Lower Sabie	5	4

^a July–June rainfall

^b Bold values indicate those individuals for which dispersal age was not accurately known (>6 months). These five individuals were excluded from the age at dispersal analysis

^c Number of times the individual was seen in the secondary group after dispersing

^d Acquired breeding status in the secondary group

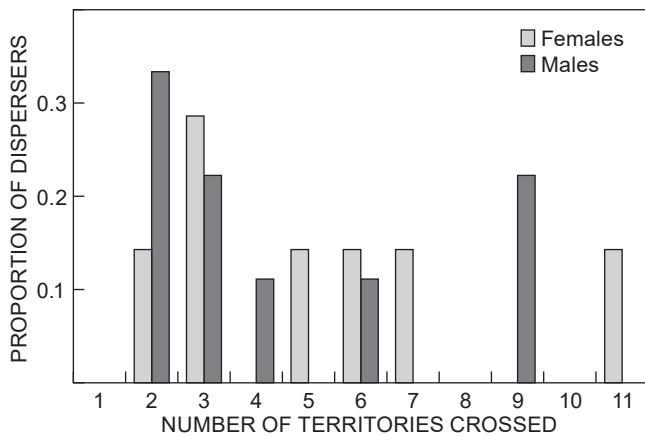


Figure 2: Number of home ranges that dispersing Southern Ground Hornbills *Bucorvus leadbeateri* females ($n = 7$) and males ($n = 9$) crossed when dispersing to a new group

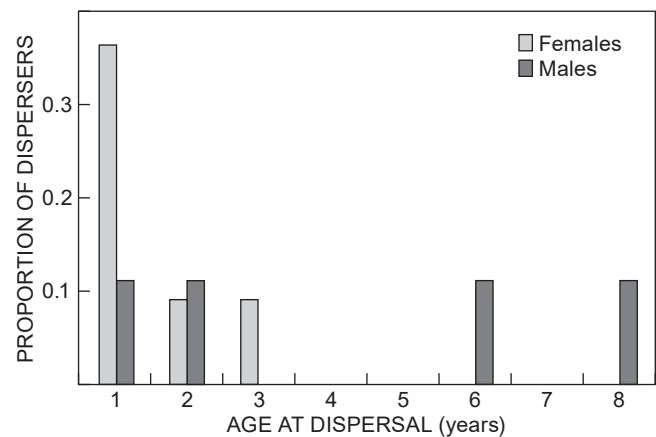


Figure 3: Age at dispersal for Southern Ground Hornbills *Bucorvus leadbeateri* for six females and four males

Table 4: Linear model relationships of rainfall over the previous year, gender and age with dispersal distance of 18 Southern Ground Hornbills *Bucorvus leadbeateri* individuals ($R^2 = 0.34$). Model compared with a null: $p = 0.16$

Variable	Coefficient (95% CI) ^a	Ratio change (95% CI) ^b	<i>P</i>
Rainfall (units of 50 mm)	-0.088 (-0.167, -0.010)	0.816 (0.681, 0.977)	0.03
Gender (Ref: Female)	0.0008 (-0.432, 0.434)	1.002 (0.370, 2.714)	0.99
Age (months)	-0.002 (-0.011, 0.007)	0.996 (0.976, 1.017)	0.70

^a Linear model parameters when modelling log (base 10) of dispersal distance

^b The implied ratio or multiplicative change in average dispersal distance (untransformed) associated with a change in the predictor

44 months). However, possibly due to the limited sample size, the analysis of dispersal age by sex was not significant ($W = 5.5, p = 0.20$). A single male delayed dispersal up to eight years, but all females dispersed before the age of three years (Figure 3). One male remained as a helper with the natal group for at least nine years. One male dispersed into a neighbouring group and became the breeding male (Table 3).

Discussion

This is the first time that resighting data have been presented for the Southern Ground Hornbill. Although the dispersal distances for 18 individuals indicated that females dispersed further and younger than males as predicted, these findings were not significant, possibly due to the limited sample size ($n = 18$). Furthermore, for ground hornbills that occupy large home ranges and could potentially travel large distances outside of the core study area, direct observations likely represent an underestimate of dispersal abilities. Even though ringing of ground hornbill individuals has been ongoing since 2005, the resighting data are not yet appropriate for robust modelling of factors

influencing dispersal distances or age, indicating the importance of long-term studies continuing for several decades for this species, if direct observations are to boost indirect observations of dispersal in the future (see below). If, however, it is the case that males and females disperse equally far from their natal group, this raises questions on how ground hornbills avoid inbreeding. Most other studies of dispersal in birds found that females disperse further than males, largely to reduce the risk of inbreeding. However, some studies have found that males and females disperse equally far (Nelson-Flower et al. 2012; Engler et al. 2014; van Dijk et al. 2015). In the cooperative breeding Southern Pied Babbler *Turdoides bicolor*, inbreeding avoidance was facilitated by females moving beyond the range of genetically similar individuals, and by recognising and avoiding familiar group members as mates (Nelson-Flower et al. 2012).

Field studies investigating dispersal in animals are typically limited both spatially and temporally, which could lead to underestimates of dispersal distances and abilities (Koenig et al. 1996). It is therefore possible that ground hornbill individuals dispersed beyond the range of detection. The extended period that individuals may float between groups (sometimes as long as three years; KFC pers. obs.) coupled with their long life-span (± 65 years; A Kemp, pers. comm., 2014) means obtaining direct observational data over a sufficient time-scale is difficult in this species. In addition, the high proportion of individuals that were not resighted (51%) suggests that either mortality is high, which is unlikely, or that individuals are dispersing beyond the range of detectability.

The difference in median dispersal age between males and females was marked, although limited by the small sample size and thus non-significant (8 months for females, 44 months for males; $p = 0.20$). Males delayed dispersal up to eight years, whereas all females dispersed before three years of age. This suggests that females are not inclined to wait until they are mature before dispersing, as suggested by Kemp (1988), but appear to do so long before they attain maturity.





These data were gathered from opportunistic sightings of a large number of groups. Future studies with more rigorous and standardised group searching efforts could

contribute further to our understanding of dispersal in this species. Especially useful would be targeting fewer groups more intensively to make data collection more feasible. A worthwhile future study would combine direct observations of ringed individuals with fine-scale genetic structure of study groups, as seen in other species (Double et al. 2005; Temple et al. 2006; Woxvold et al. 2006; Nelson-Flower et al. 2012; Vangestel et al. 2013), to gain a more accurate understanding of dispersal in ground hornbills.

Finally, the presence of male ground hornbills with blue throat patches (L Kemp, pers. comm.; none identified in our study area as of 2015) is an important factor to consider when using throat colour to sex individuals in the absence of a DNA sample. Studies where individuals are ringed, sampled and monitored over a longitudinal study such as the research programme in the APNR, would benefit from using individuals sexed using DNA samples only, to ensure that no errors of sexual misidentification cloud our understanding of dispersal in this species if blue-throated males are found to occur in reasonable numbers in the wild, and are therefore at risk of being misidentified as female.

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