Rainfall predicts seasonal home range size variation in nyala

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1 INTRODUCTION

Optimal foraging theory posits that animals should minimize the size of their home range—the area used to meet their requirements (Burt, 1943)—around limiting resources (Ford, 1983). Hence individuals ranging in less productive habitats or exploiting patchy resources have larger home ranges (Ford, 1983), and spatio-temporal variations in resource availability can lead to changes in home range size (Fattebert, Baubet, Slotow, & Fischer, 2017; van Beest, Rivrud, Loë, Milner, & Mysterud, 2011). In nyala (Tragelaphus angasii), a mixed-feeder antelope, the effects of habitat variability on ranging and space use patterns are poorly understood (Kirby, Shannon, Page, & Slotow, 2008; Labão-Tello & van Gelder, 1975). A better understanding of the drivers affecting ranging patterns in nyala would help the design of evidence-based habitat management strategies.

In this highly dimorphic, polygynous species, males are expected to have larger home ranges than the females because of size-dependant metabolic rates (McNab, 1963). In polygynous species, females are expected to secure access to limiting resources through optimal foraging to successfully raise offspring, while males are expected to range more widely in order to increase mating opportunities with numerous females (Clutton-Brock, 1989; Fattebert et al., 2016). In the rain season, vegetation becomes more palatable with higher protein contents (Duncan & Poppi, 2008), and together with abundance of surface water, this should lead to a reduction of home range size (Bowers, Welch, & Carr, 1990). Alternatively, in the dry season, although food resources are more dispersed, scarcity of surface water could constrain ranging patterns around permanent surface water (Smit, Grant, & Whyte, 2007). We investigated seasonal variations of space use patterns in nyala, and tested the effects of sex, and rainfall as a metric of seasonal variability on home range size.

2 MATERIALS AND METHODS

2.1 Study area

The study area was the northern section of the Mun-Ya-Wana Private Game Reserve (27°92′–27°68S, 32°44′–32°20′E, 265 km²), South Africa. Climate is sub-tropical, with a hot, wet summer from mid-September to March (mean 31.5°C) and a mild, dry winter from April to mid-September (mean 23.5°C), with mean annual rainfall of 788 mm. Approximately 95% of the reserve lies below 100 m a. s. l. In the north, terrain is mostly flat with few gentle slopes, and vegetation consists mainly of open red sand bushveld, closed red sand bushveld and a small portion of sand forest (Mucina & Rutherford, 2006). The reserve has an extensive network of dirt roads for game viewing and management purposes (Figure 1).

2.2 Data collection

We immobilized nyala using Euthorphine hydrochlorine (M99). We fitted darts with a radio-transmitter for recovery. We outfitted nyala with VHF transmitters (Sirtrack®, New Zealand; 250 g; <1% body mass). We released all individuals at the capture site upon antagonization with diprenorphine (M5050). We radio-tracked nyala from September 2013 to December 2014. We relocated nyala by homing-in from a vehicle or on foot (Kernohan, Gitzen, & Millspaugh, 2001). Once the tracked animal was in sight, we recorded its relocation to the nearest 50 m using a hand-held GPS receiver (Garmin, USA). We collected rainfall data using rain gauges in the reserve (Table 1).
2.3 | Data analysis

We used the package adehabitatHR (Calenge, 2006) in R version 3.3.2 (R Core Team, 2016) to compute total (all data included for a given individual), and seasonal (2-month periods) home ranges and core ranges. We used the 95% and 50% minimum convex polygon (MCP; Hayne, 1949), and the 95% and 50% isopleths of the fixed kernel density estimator (FK; Worton, 1989) with a smoothing bandwidth of 100 m consistent with our tracking accuracy.

We tested for the effect of sex on total home range size, statistically controlling for the number of relocations using a multivariable linear model. We tested for the additive and interactive effects of sex and rainfall on bi-monthly home range, and core range size, controlling for the number of relocations, in an information-theoretic framework using generalized linear mixed-models (GLMM) fitted in the lme4 R package (Bates, Maechler, Bolker, & Walker, 2014). We fitted the individuals as random intercepts to account for pseudo-replication. To test for lag response, we tested for the effect of rainfall cumulated over (i) the 2 months concurrent to range calculation, (ii) the 1 month preceding and the first month concurrent to range calculation, and (iii) the 2 months preceding range calculation. We used the Akaike’s Information Criterion corrected for small sample size (AICc) to select for the most parsimonious model fitting the data (Burnham & Anderson, 2002).

3 | RESULTS

We captured and radio-tracked six adult nyala (three males, three females), and obtained 37 seasonal bi-monthly home range estimates. Overall, we obtained an average of 233 ± 107 (SD; range: 77–320) relocations per individual over 328 ± 157 (71–446) days of tracking. Bi-monthly, we obtained 38 ± 11 (13–52) relocations per individual (Table 2). Mean 95% MCP total home range size

![Figure 1: Total 95% minimum convex polygon home ranges of three male and three female nyala, in the northern section of the Mun-Ya-Wana Game Reserve, South Africa, 2013–2014. Inset represents the location of the study area in South Africa. Dirt road network used for game viewing and management purposes is shown.](image)
was 2.18 ± 1.28 km² (0.64–3.92; Table 2), and mean 95% FK total home range size was 2.42 ± 0.97 km² (1.18–3.30; Table 2). Mean 50% MCP total core range size was 0.53 ± 0.28 km² (0.14–0.78; Table 2), and mean 50% FK total core range size was 0.46 ± 0.20 km² (0.23–0.66; Table 2). There was no significant effect of sex or the number of relocations on home range size (MCP: \( F_{2,3} = 0.395, p = 0.704 \); FK: \( F_{2,3} = 0.130, p = 0.883 \)) or core range size (MCP: \( F_{2,3} = 0.328, p = 0.743 \); FK: \( F_{2,3} = 0.178, p = 0.845 \)). We acknowledge that one male (M2) was tracked over 2 months only before he shed his collar, and this was the smallest total home range size recorded (MCP: 0.64 km², FK: 1.18 km²).

Bi-monthly home range size (\( n = 37; \) MCP: 0.99 ± 0.71 km², range 0.31–2.75; FK: 1.41 ± 0.54 km², 0.70–2.55) was negatively related to rainfall cumulated over the 1 month preceding and the first month concurrent to range calculation (MCP: \( \beta = -0.0028 \) [95% CI: -0.0049, -0.0008]; FK: \( \beta = -0.0017; [-0.0037, -0.0007] \); Figure 2) with no effect of sex or the number of relocations (Tables S1 and S2). There was no relationship between sex, rainfall or the number of relocations and bi-monthly MCP core range size (0.29 ± 0.20 km², 0.04–0.75) with null model ranking first (Table S3) or FK core range size (0.32 ± 0.14 km², 0.16–0.68) with null model ranking within 2 ΔAICc of the top model (Table S4).

### 4 | DISCUSSION

Nyala home range sizes were in the same order of magnitude as previous studies in comparable environment (Hluhluwe Game Reserve) (Hluhluwe Game Reserve, South Africa, 2013–2014).
Reserve, South Africa: 0.65–0.83 km²; Anderson, 1980; Zinave National Park, Mozambique 0.4–3.90 km²; Labão-Tello & van Gelder, 1975). Contrary to our expectation, we did not detect significant sexual differences in total or seasonal range sizes. Noteworth-y, total home range size in male nyala appeared even smaller than in females (Table 2). In sexually dimorphic species with a promiscuous or polygynous mating system, female home ranges are expected to depend mostly on food availability and distribution (Clutton-Brock, 1989). Contrastingly, male ranging behaviour should be mostly driven by female distribution, and home range size is expected to be larger in males (Clutton-Brock, 1989; Fattebert et al., 2016). Given high dimorphism in nyala, with male averaging 108 kg and females 62 kg (Labão-Tello & van Gelder, 1975; Vincent, Hitchins, Bigalke, & Bass, 1968), size-dependant metabolic rates also predict larger home ranges in males (McNab, 1963). However, it is worth noting that two of the three females tracked were accompanied by a dependent offspring for at least part of the study. Female F3 lambed in late early October 2013, while female F5 lambed in late April 2014 (J. Janse van Rensburg pers. obs.). After a period of home range reduction during the first eighteen days, when female nyala return periodically to lambs concealed in thickets (Anderson, 1980), lactating females might have elevated energetic needs, and therefore range more widely (McNab, 1963). While reproduction appears to be aseasonal in nyala (Anderson, 1979, 1984; Labão-Tello & van Gelder, 1975; Vincent et al., 1968), including in our study area (J. Janse van Rensburg & J. Fattebert pers. obs.), data on more individuals would enable to rigorously test for possible difference in ranging patterns among females with or without dependent offspring.

A seminal study of ranging behaviour in nyala had failed to detect seasonal variation in home range size, although the limited sampling of an average 14 observations (range: 4–34) per individual somewhat limits ecological insights (Labão-Tello & van Gelder, 1975). Herein, we show that over shorter time periods, home range size in nyala correlated with rainfall. Rainfall is seasonal in our study system, and therefore is expected to be an important driver of plant phenology, thereby of food, and of surface water availability. We further demonstrate that level of precipitation up to 1 month before home range size measurement seems to affect home range size (Tables S1 and S2). Such a lag in response in ranging patterns to changes in the environment is expected, and most likely reflects vegetation phenology following rainfall (Bischof et al., 2012; Bohrer, Beck, Ngene, Skidmore, & Douglas-Hamilton, 2014; Mishra, Crews, Neeti, Meyer, & Young, 2015). Contrastingly, core range size was stable throughout the study with no informative effect of rainfall (Tables S3 and S4), consistent with most limiting resources being used and secured at the core level (Fattebert et al., 2016; Kernohan et al., 2001). Results using either the MCP or the kernel home range estimates were consistent, and both estimators proved adequate to compare relative range size over time (Signer, Balkenhol, Ditmer, & Fieberg, 2015).

5 | CONCLUSION

Rainfall appears to be a predictor of seasonal home range size in nyala with an 1-month lag and with no clear difference between males and females. However, we acknowledge that our dataset is too limited to draw any conclusive inference, and further studies are needed. Nyala body size allows for heavier GPS-collars to be used for tracking them. More frequent, regular sampling would enable to address cutting-edge research questions in spatial and movement ecology (Allen & Singh, 2016; Morelle et al., 2015), while documenting basic species natural history. In particular, investigating habitat selection patterns and accounting for predation risk and avoidance behaviour of risky area would dramatically improve our
understanding of nyala ecology (Burkepile et al., 2013; Thaker et al., 2011). In this regard, dispersal and landscape connectivity in heterogeneous landscapes should also be the focus of future research on the species (Fattebert, Robinson, Balme, Slotow, & Hunter, 2015; Pitman et al., 2017). A more comprehensive understanding of factors driving nyala spatial requirements would be valuable to design of evidence-based nyala population and nyala habitat management strategies, while helping with the design of predator-friendly game farming practices (Pitman et al., 2016).

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REFERENCES


**SUPPORTING INFORMATION**

Additional Supporting Information may be found online in the supporting information tab for this article.

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