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Response of wildlife to bush thinning on the north central freehold farmlands of Namibia

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ABSTRACT

Agriculture is considered the backbone of the Namibian economy. However, bush encroachment affects approximately 45 million hectares of Namibian farmland and in the absence of appropriate restoration measures, negatively affects local biodiversity and the national economy. Bush thinning operations on three freehold farms were assessed to examine the response of local ungulates (small, medium, large) and predators (meso, large).

Camera traps were used to capture wildlife in bush encroached and previously thinned habitats. We hypothesized that thinning would increase the activity of small, medium, and large ungulates, meso and large predators, and that the magnitude of the increase in activity at thinned sites would differ among animal types. Our results revealed that the expected animal captures were not equal – small, medium, and large ungulates were common, large predators were least common; thinned areas had more expected animal captures and overall animal-treatment interactions were almost significant ($p = 0.051$). The post-hoc tests of treatment by animal types showed significant differences between treatments for large predators ($p = 0.016$), with a positive response to the thinning treatment. The response to thinning was also positive for all other animal types, but insignificant.

Our results suggest that activity patterns of large predators could be substantially shifted by thinning operations in the Namibian farmland ecosystem. Consequentially, large predators may impact other animal types severely, especially if thinning is done on a small scale. Thinning at a larger scale might spread the predatory risk over a wider landscape, thus reducing the predatory risk effects. This would provide more options for animals to escape or avoid habitat edges that are highly frequented by predators.

This study demonstrated that bush thinning had overall positive to neutral effects and can be used as a method to restore wildlife habitats. To maintain a sparse vegetation structure and improved carrying capacity in previously restored areas, post-thinning management is required to control the re-established saplings.

1. Introduction

Bush encroachment - the increase in density and biomass of woody vegetation - has been widely reported globally (de Klerk, 2004; Van Auken, 2009; Gil-Romera et al., 2010; Khosikoma et al., 2012; Belay et al., 2013). Causes of bush encroachment include climate change, elevated atmospheric carbon dioxide concentrations, nitrogen pollution, drought, fire suppression, soil nutrients, increase in livestock vs decline in wildlife populations, grazing and poor rangeland management practices (de Klerk, 2004; Dando and Hansen, 1990; Archer, 1994; Bachelet et al., 2000; Bartolome et al., 2000; and Asner et al., 2004 cited in Sankey, 2012).

Bush encroachment is also known to have negative impacts in relation to livestock, wildlife and underground water recharge (Muroua et al., 2002; Meik et al., 2002; Gray and Bond, 2013; Buyer et al., 2016; Groengroeft et al., 2018). In Namibia, bush encroachment affects an estimated 45 million hectares of the total surface area (SAIEA, 2016). This has resulted in a decline in grazing capacity and economic losses of N$ 2.7 billion per annum in the livestock industry since 2015 (SAIEA, 2016).

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Controlling bush encroachment through thinning - a type of harvest that involve the selective reduction of vegetation densities on a cyclical basis has potential to promote greater herbaceous production, species richness, underground water recharge and soil moisture conditions (Birch and Middleton, 2017; Groengroeft et al., 2018; Haussmann et al., 2016; Honsbein et al., 2017; MITSMED, 2017; Richter et al., 2001; SAIEA, 2016; Smit, 2001; Stafford et al., 2017). These assumptions were relevant to this study, as restoring bush balance increases the overall rangeland productivity and potential to influence the presence or activity patterns of the local wildlife (MAWF, 2012; Muntifering et al., 2006; Nghikembua et al., 2016). The reduction of tree/shrub densities would stimulate grass growth due to release from competition between the herbaceous and woody components, consequentially this would increase forage capacity (Smit, 2004).

Bush harvesting – the process of felling trees/shrubs in the field has the potential to show varied impacts on wildlife according to the harvest intensity or methods reported in studies in southern Africa (Ben-Shahar, 1992; Isaacs et al., 2013; Muroua et al., 2002; Schwarz et al., 2018). These aforementioned studies showed that grazers (e.g. oryx *Oryx gazella*, red hartebeest *Alcelaphus buselaphus* ssp. *caama*, warthog *Phacochoerus africanus*, zebra *Equus burchelli*, and wildebeest *Connochaetes taurinus*) would benefit due to improved carrying capacity and habitat visibility; browsers (e.g. kudu *Tragelaphus strepsiceros*) may not benefit due to the reduction in cover and browsing vegetation. This underscores the importance of creating open patches for grazing, and retaining some tree/shrub clumps for browse, shelter, and breeding sites. The increase in herbaceous/ground cover also restores reptile diversity and small mammal abundance (Azor et al., 2015; Lee et al., 2018; Meik et al., 2002). Springhare (*Pedetes capensis)* and cape hare (*Lepus capensis*) are known to consume grass and browse on fresh green shoots, which are abundant in restored areas (Skinner et al., 2005; Zimmerman, 2009). This would also boost the prey availability for predators.

Excessive bush thinning denudes landscapes from vegetation; thus, ungulate abundances may decline (Isaacs et al., 2013). Bush thinning, if done in moderation, may not disrupt the stability of the ecosystem (Smit, 2004). Wild herbivores influence the structure of the vegetation through nutrient mediation and cycling, suppressing seed predators such as small mammals, influencing fires and fuel loads, and physically breaking soil caps and organic material through hoof action (Goheen et al., 2009; Tainton, 1999; van Langevelde et al., 2003; Savory and Butterfield, 2016). Predators are critical for the maintenance of ecosystems through reduction of herbivore populations. Moreover, the chase of prey or fear of predators results in ungulate aggregations and hoof action that churns the soil surface (Beschta, 2003; Ripple and Beschta, 2008; Ripple and Larsen, 2000; Savory and Butterfield, 2016).

Knowledge of species population density and the response of specific species to management actions are prerequisites for effective management (Sinclair et al., 2006; Witmer, 2005). Therefore, monitoring the impacts of bush thinning would reveal how wildlife respond to the process of reversing bush encroachment, and what management actions can be taken.

Here, we report the results of a study conducted on the north central freehold farmlands of Namibia where bush thinning operations were carried out with the purpose of restoring encroached habitat. The study aimed to examine the responses of local ungulates (small, medium, large) and predators (meso, large) to the thinning strategy. Effects on ungulates and predators that utilize the thinned treatment habitat have not been adequately researched, hence the need for this study.

We hypothesized that thinning would significantly increase the activity of small, medium, and large ungulates, meso and large predators; and that the magnitude of the increase in activity at thinned sites would differ among animal types. We sought to provide stakeholders with credible information detailing how thinning influences predators and their prey, and what management actions should be taken to ensure that negative impacts are avoided in the bush thinning process.

Studies in southern Africa explored the effects of bush clearing, primarily on wild herbivores. Our study utilized a different approach in examining effects associated with bush thinning: both predators and ungulates were monitored, treated plots had different post-thinning ages, trees/shrubs had been manually thinned as opposed to mechanically thinned or clearing. Also, survey methods were suited for detecting rare and elusive species (see methods), and restoration was done in a farmland matrix with integrated livestock and wildlife management. The Namibian farmland supports free-ranging wildlife, including a globally significant cheetah (*Acinonyx jubatus*) population. Due to loss of habitat, habitat fragmentation and human-wildlife conflict, the viability of the species is under threat (Johnson et al., 2013; Jeo et al., 2018; Marker et al., 2018).

2. Methods and materials

2.1. Study area

Camera trap surveys were conducted on three freehold farms; Cheetah View (#317), Boskop (#324) and Elandsvreugde (#367) in north central Namibia (mean farm size: 5735.2 ha (± 737.29 se); location: 20.477299 S, 17.024623 E) (Fig. 1). The farm perimeters were cattle proofed, bounded by a 1.5-m high fence that restricted cattle to grazing camps yet allowed wildlife movement. The most common land use type is livestock farming mixed with free-range wildlife, ecotourism and harvesting of native bush biomass. Several semi-permanent water resources are present and provide year-round drinking water to livestock and wildlife. Mean annual rainfall in the study area is 444 mm (43.7 var.); mean annual temperature is 19.2 °C (5.9 var.); mean daily maxima are 22.7 °C (0.5 var.) in January and 13.4 °C (0.5 var.) in July (Fick and Hijmans, 2017). Three distinct seasons define the climate of the area: hot and dry (Sept–Dec), hot and wet (Jan–Apr), and cold and dry (May–Aug). Thornbush savannah is the characteristic vegetation of the area (Geiss, 1971, cited in Erkkilä and Siiskonen, 1992). Topographically, the terrain is generally flat, with slight undulations; consequently, this allows slow rainfall runoff on the farms. Since 2005, all three farms acquired the Forest Stewardship Council certification for sustainable forestry (certificate: FSC-C004580).

2.2. Study design

The study utilized a block design consisting of a previously thinned and a non-thinned plot located in proximity: mean distance 692 m, 153 standard deviation (sd) (Fig. 2). Two camera stations were established within each plot. During the period 2002–2013, manual thinning had been applied to woody vegetation only. A single thinning cycle was conducted, and bush densities were reduced by approximately 50%. During the thinning, some tree/shrub clumps were retained to provide shade and nesting habitat for wildlife. Plots differed in post-thinning age, sizes (min: 2.4 ha., max: 29.7 ha.) and location; these decisions were made prior to the start of our study. In our study, only plots where the post-thinning age was ≥ 3 years were selected (Table 1). Nevertheless, this experimental design provides a first step towards evaluating the thinning operations conducted since 2002. After 2005, aftercare treatment (application of Picloram active arboricide, commercially known as Access®) was carried out to prevent stump regrowth on freshly cut stumps. In our study, eleven previously thinned plots had been treated with Access®, and only two previously thinned plots were not treated. The study design involved 13 blocks with a total of 26 plots and 52 camera trap stations. Only one thinned treatment type was used which consisted of plots with varying post-thinning ages (Table 1).

Camera traps are widely used to assess the impacts of different management regimes on wildlife (Kauffman et al., 2007); population abundance and density estimation (Marker et al., 2008; Rowcliffe et al., 2008; Stein et al., 2011); effects of logging on wildlife (Brodie et al., 2015; Granados et al., 2016; Jati et al., 2018) and the monitoring of

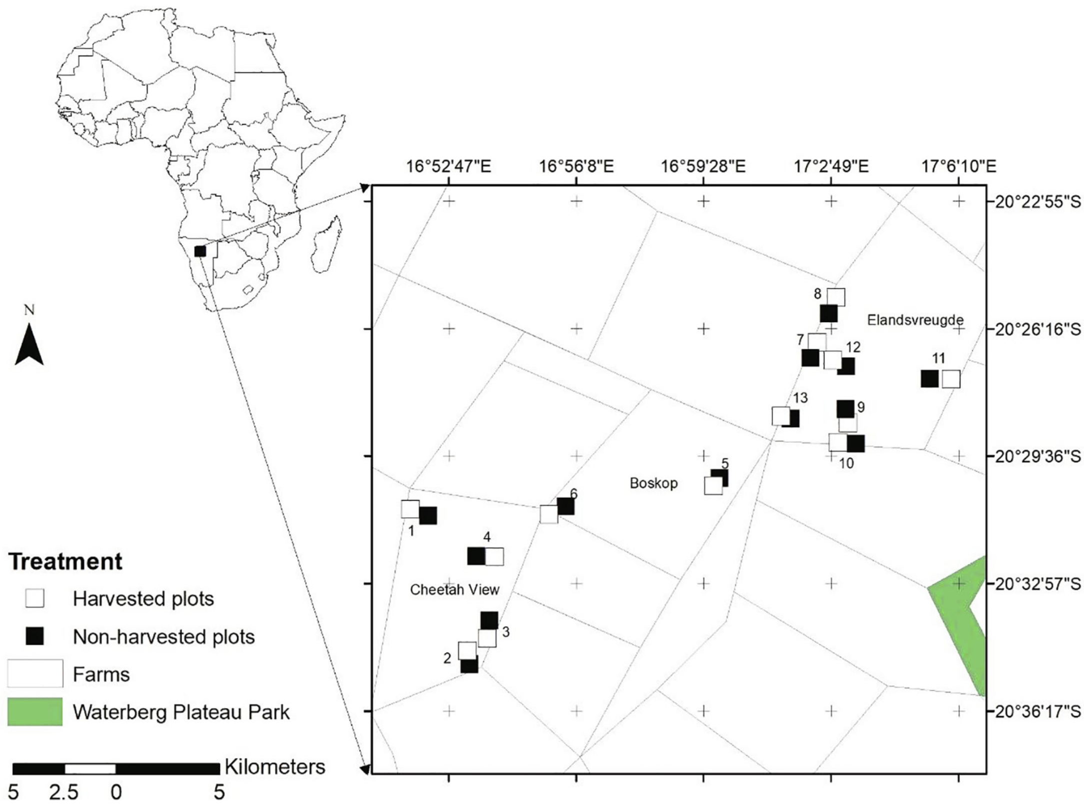

Fig 1. Map of the study area showing the location of the surveyed farms in north central Namibia. White and black squares represents blocks (plot pairs) with a thinned (open square) and non-thinned (black square) plot.

mammalia distribution across landscapes (Anderson et al., 2016; Cusack et al., 2015; Hedwig et al., 2018; Rich et al., 2016). Camera traps are non-intrusive and can detect elusive species or those present at low population densities (Fabiano et al., 2018).

2.3. Sampling design

Systematic random sampling methods were employed for the selection of survey locations. A regular grid of 100 m^2 was overlaid on each study plot. Thereafter, two random survey locations per study plot were selected on the grid, thus, a block pair consisted of four survey locations (2 thinned, 2 non-thinned). All selected areas were assigned geographic coordinates and then uploaded onto a handheld GPS (Garmin Etrex 30, Garmin international, Inc., Olathe, Kansas, USA) for location in the field. The software program ArcGIS 9.3 (ESRI, 2008) was used in the grid design, randomization and assigning of geographic coordinates. Randomization was carried out with Hawths Sampling Tools (Beyer, 2004) within ArcGIS 9.3. In general, we followed the same criteria for camera placement as described in Cusack et al. (2015): survey locations were placed either at the randomized spot or at any suitable area within a 50 m radius that incorporated game trails and off-trails placements.

This approach was employed as other studies (e.g. Cusack et al., 2015; Mann et al., 2015) have found that detection probabilities of some species were greater at trails or off-trails, and that slight differences occur in some species. Large predators, especially cheetah and leopard (*Panthera pardus*), tend to have high detection probabilities on trails or at scent marking posts (Cusack et al., 2015; Fabiano et al., 2018; Walker et al., 2016), whereas, meso predators, such as caracal (*Caracal caracal*), jackal (*Canis mesomelas*), honey badger (*Mellivora capensis*), African wild cat (*Felis silvestris lybica*) and herbivores kudu, eland *Tragelaphus oryx* and warthog use both trails and random locations that may differ in intensity depending on the season (Cusack et al., 2015; Mann et al., 2015). An equal number of stations were placed in

Fig 2. Representation of non-thinned (left) and previously thinned (right) plots demonstrating differences in vegetation structure. Non-thinned plots have higher tree/shrub density, limited habitat visibility and less grass cover than thinned plots.

Table 1
List of study plots, indicating dates of thinning treatment, post-thinning ages, tree/shrub densities and canopy cover at the survey period 2016 – 2017.

Block	Thinning completed	Thinned plot					Non-thinned plot			
		Post-thinning age at survey	Tree/shrub density ha^{-1}		Canopy cover %		Tree/shrub density ha^{-1}		Canopy cover %	
			Mean	Stdev	Mean	Stdev.	Mean	Stdev.	Mean	Stdev.
1	31/05/2005	11.7	1061.0	335.9	30.3	22.2	866.5	357.1	17.3	15.0
2	26/09/2012	4.4	1635.8	681.6	28.3	5.5	1713.1	486.5	67.2	27.9
3	01/06/2013	3.7	693.8	391.9	15.1	13.4	1432.4	629.0	65.1	27.6
4	28/02/2013	4	1515.8	936.3	24.7	39.1	1288.4	491.9	29.5	25.7
5	30/09/2010	6.4	641.0	232.5	12.5	23.4	2069.0	536.4	35.9	25.9
6	14/04/2012	4.9	778.1	362.9	4.2	3.4	1002.1	507.9	35.5	23.5
7	31/03/2007	9.9	2216.4	1975.0	41.6	24.1	1338.1	473.6	35.0	19.8
8	31/03/2003	13.9	1489.9	683.9	29.1	29.1	1149.5	592.2	30.0	19.3
9	14/02/2008	9	1102.3	467.7	17.0	16.6	1096.4	660.7	33.6	25.0
10	23/02/2009	7	1010.5	359.9	17.8	21.3	909.5	408.0	64.6	41.6
11	16/02/2010	7	1781.0	1563.3	8.3	14.1	1117.9	384.0	57.1	45.1
12	15/05/2013	3.8	939.5	298.7	6.7	8.2	1757.3	364.4	37.8	28.4
13	14/02/2014	3	840.0	463.7	11.7	13.4	1753.7	881.4	94.3	38.4
	Mean (sd.)	6.8 (3.4)	1276.44	996.14	20.95	22.72	1255.43	593.69	44.93	33.78

each treatment area – 26 camera trap stations in the thinned and non-thinned treatments, respectively (total = 52). Placement of camera trap stations was balanced between treatments: off-trail (n = 12 in thinned and n = 12 non-thinned), and on-trail (n = 14 thinned, n = 14 non-thinned). At each station, clearing of small bushes (≤ 1 m) and grasses within 5 m of the camera was carried out to create a line of sight with no obstructions, such as tall grass, or branches that may trigger the camera to capture non-target images.

At each survey location, the camera traps were placed under shade as much as possible to prevent overheating and were positioned to face the direction that the animals were likely to approach. Tree trunks or metal poles were used to mount the camera traps at approximately 60 cm aboveground. Camera traps were angled to face away from the northeast and southwest to avoid sun exposure and over exposure of images.

Surveys were carried out from September 2016 – July 2017 over two rotations at the same locations, separated by 190.83 (± 42.1 sd.) days. The Bushnell Trophy Cam camera trap model was used for 91.4% of the trapping period. Spypoint BF10 HD cameras traps were used in 8.65% of the trapping period from September until December 2016 due to camera shortages. Camera trap sensitivity was set to low with a single shot taken at 10 s intervals once the camera was triggered. This prevented battery wastage from moving vegetation and from animals that may tend to remain longer at the station. All cameras were set to capture images in a 24H period and each image had a date, time, temperature, and moon phase stamp. Camera traps were active at the station for a minimum of 21 and maximum 36 days (Mean (± sd): 25.2 (± 4.28).

Camera traps in the thinned treatment area could potentially detect wildlife from a greater distance due to reduced tree/shrub densities and better habitat visibility. In the non-thinned treatment area, visibility was limited due to bush encroachment and only animals close to the camera trap were likely to be captured. This may present a weakness in terms of the analysis conducted, since our results may be affected by lower detectability of animals, especially in the non-thinned areas. Nevertheless, we attempted to control for equal camera coverage and increasing detection probability by deploying an equal number of camera traps at trails, off-trails and treatment areas. Also, clearing around the camera traps was done to ensure that an immediate visibility zone was created at each station, cameras were angled to face the direction in which animals were likely to approach and line of sight had no obstructions. This was done to maximize the capture of animals passing by, regardless of treatment.

2.4. Species of interest

The study focused on three large predators: cheetah, leopard, and brown hyena (*Parachyaena brunnea*); four meso predators: African wildcat, caracal, honey badger and jackal; four large ungulates: eland, oryx, kudu, red hartebeest; a medium ungulate: warthog; and two small ungulates: steenbok (*Raphicerus campestris*) and duiker (*Sylvicapra grimmia*). We selected these species due to their economic and conservation importance, and because they represent different body sizes and habitat requirements. The species selected also ranged in their conservation status from huntable to protected (Durant et al., 2015; NAPHA, 2015; Stein et al., 2016; SWA, 1975ab; Wiesel, 2015).

2.5. Data analysis

Images were identified to species level; metadata (date, time, species, camera trap stations) were extracted using CamtrapR (Niedballa et al., 2016). Images were considered independent by deleting duplicates. Image records obtained in this case were separated from each other by a minimum of 31:03 min for the predators and 39:35 min for all ungulates.

A generalized linear mixed-effects model with Poisson distribution and log link function (GLMM) (Bates et al., 2015) was used for the modelling task. The number of images captured were used as a response variable, covariates were animal type (meso and large predators; small, medium and large ungulates), treatment (thinned, non-thinned) and the animal type-treatment interactions, survey length, camera trap start time, post-thinning age and camera trap locations (ontrail, off trail). In the analysis, large predators were used as the reference level in the animal type variable. Random factors were block (plot pair), plot, camera trap stations and observations. The expected number of animals within the 3-week survey period h at camera station i of plot j in block k was expressed as:

$$E(y_{kij}) = exp(\boldsymbol{x}_{kji}\boldsymbol{\beta} + b_k + c_{kj} + d_{kji} + e_{kjih},)$$

where E (y_{kji}) = mean image captures; $\acute{\boldsymbol{x}}_{kji}\boldsymbol{\beta}$ includes the effects of fixed factors; animal type, treatment, the animal type-treatment interactions, camera trap start time (expressed as weeks since first camera was active in the study area), centered survey length (expressed as survey length − 21), centered post-thinning age (expressed as post-thinning ages – 6.82, where 6.82 is the mean post-thinning age over all treated plots) and camera trap locations (ontrail, off trail); $b_k + c_{kj} + d_{kji} + e_{kjih}$ includes the nested random effects for block (plot pair), plot, camera station, and observation respectively. The observation level random effect was included to model the overdispersion observed in the initial model. Observations were the number of independent image records for each animal type, per camera trap stations. The data were checked for overdispersion by exploring the ratio between the Pearson statistic *P* (sum of squared Pearson residuals) and the residuals degrees of freedom (n - p), the value > 1 indicating overdispersion. The systematic part of the final model was examined graphically by evaluating the trends and homoscedasticity of the Pearson and deviance residuals; normal q-q plots of random effects were used to evaluate the assumption of the normality of random effects (Mehtatalo and Lappi, 2020). All analyses were performed within R (version 3.5.2; R Core Team, 2017). Hypothesis test about the GLMM model coefficients were based on Wald $\chi 2$ tests of the fitted final model using R functions Anova and lht of package car (Fox and Weisberg, 2011).

3. Results

3.1. Number of images captured

Cameras were operational for 2624 camera trap station days: 1311 in the thinned area, 1313 in the non-thinned area. The total number of images recorded was 14,044. We selected 1992 separate occasion images for analysis: 1159 from the thinned area, 833 from the non-thinned area, following the exclusion of duplicates and species of no interest. Fourteen different species were recorded (Table 2, Appendix 1). Days to first detection were longer amongst large predators than for any other species. Overall, warthog and oryx were detected more frequently than any other species in the study area. Almost all camera stations captured the species of interest; however, five stations in the thinned area and two in the non-thinned area did not detect any species of interest in one of the survey periods. Cheetahs were very rare with only a single male detected on one occasion. Caracal, red hartebeest, and eland were also rarely sighted.

3.2. Number of images captured and animal type-treatment interactions

The baseline category (β_0) of the GLMM model (Tables 3 and 4) shows that the mean number of large predators captured in the thinned area would be 0.24 per 21-day period, at the start time of the camera traps, also in reference to off-trail camera traps. The positive values for the effects of other animal types show that they were more abundant than the baseline category (β_0). In the same treatment, all other animal types were more abundant than the baseline (β_0) with the mean captures of large ungulates being 8.12, medium ungulates 5.86, meso predators 2.31 and small ungulates 8.4 times more frequent than the large predators (Tables 3 and 4).

The parameter estimate β_5 refers to mean captures of large predators in the non-thinned treatment (Tables 3 and 4). The number of large predators was only 25% of the expected amount in the thinned treatment (non-thinned = 0.06, thinned = 0.24) (Tables 3 and 4). For the other animal types, less animals were also recorded in the non-thinned area than in the thinned area. In relation to the thinned area, mean captures in the non-thinned area were only 80.2% for large ungulates, 58.5% for medium ungulates, 71.4% for meso predators and 98.5% for small ungulates. This shows that the mean captures of the non-thinned were less by 75% for large predators, 19.9% for large ungulates, 41.6% for medium ungulates, 28.8% for meso predators and 1.2% for small ungulates (Tables 3 and 4).

Wald chi-square tests revealed statistically significant differences in the mean captures among the animal types (Table 5). Differences in the mean captures between treatments was almost significant (p = 0.051);

Table 3
Generalized linear mixed-effects model (GLMM) showing effects of covariates on the capture of different animal types.

Variable	Parameter (β)	Estimate	Std. error	exp(β)
Fixed effects				
(Intercept)	β_0	−1.417	0.329	0.242
Large ungulate	β_1	2.095	0.289	8.124
Medium ungulate	β_2	1.769	0.292	5.863
Meso predator	β_3	0.838	0.306	2.311
Small ungulate	β_4	2.129	0.288	8.404
Treatment Non-thinned	β_5	−1.402	0.477	0.246
Camera trapping start time	β_6	0.015	0.007	1.015
Survey length	β_7	0.058	0.024	1.060
Post-thinning age	β_8	−0.077	0.052	0.926
Station location (trail)	β_9	−0.033	0.229	0.967
Large ungulate: Non-thinned	β_{10}	1.180	0.488	3.255
Medium ungulate: Non-thinned	β_{11}	0.865	0.496	2.375
Meso predator: Non-thinned	β_{12}	1.063	0.514	2.894
Small ungulate: Non-thinned	β_{13}	1.390	0.486	4.016
Random effects				
		Variance	Stdev.	
Observation	e_{kji}	1.034	1.017	
Camera station	d_{kji}	0.462	0.680	
Plot	c_{kj}	0.050	0.223	
Block	b_k	0.000	0.000	

Table 2
Detection of species showing delay in days to first image capture, total number of independent image records and animal group sizes.

Animal type/common name (species)	Median Days to first capture	Percentage of study sites with captures		Detections overall		Group size overall	
		Thinned	Non-thinned	Thinned	Non-thinned	Thinned	Non-thinned
Large predator							
Brown hyena (*Parachyaena brunnea*)	11	38.5	30.8	31	4	31	4
Cheetah (*Acinonyx jubatus*)	21	7.7		1	0	1	0
Leopard (*Panthera parous*)	12	61.5	53.8	27	7	27	7
Large ungulate							
Eland (*Tragelaphus oryx*)	9.5	30.8	15.4	17	3	18	3
Kudu (*Tragelaphus strepsiceros*)	8	92.3	100	89	71	133	89
Oryx (*Oryx gazella*)	6.5	92.3	100	214	174	236	194
Red hartebeest (*Alcelaphus buselaphus* ssp. *caama*)	6.5	23.1	15.4	5	6	15	9
Medium ungulate							
Warthog (*Phacochoerus africanus*)	4	92.3	100	322	185	415	226
Meso predators							
African wild cat (*Felis silvestris lybica*)	11	76.9	53.8	30	14	30	14
Caracal (*Caracal caracal*)	13.5	15.4	15.4	3	3	3	3
Honey badger (*Mellivora capensis*)	10	30.8	53.8	7	11	8	11
Jackal (*Canis mesomelas*)	5	61.5	61.5	72	60	72	61
Small ungulates							
Duiker (*Sylvicapra grimmia*)	5	92.3	100	149	182	150	183
Steenbok (*Raphicerus campestris*)	6.5	100	100	192	113	197	120
Total	8	58.2	61.5	1159	833	1336	924

Table 4
Expected number of captures in the thinned and non-thinned treatment estimated from the GLMM model coefficients.

Treatment/animal type	Model coefficients (β)	Sum(β)	Expected capture (exp(sum(β))	± 95% Confidence level
Thinned				
Large predator	β0 + β5 (0)	−1.417	0.242	0.525
Large ungulate	β0 + β1(1) + β5(0) + β11(0)	0.678	1.969	0.925
Medium ungulate	β0 + β2(1) + β5(0) + β12(0)	0.352	1.421	0.931
Meso predator	β0 + β3(1) + β5(0) + β13(0)	−0.58	0.56	0.956
Small ungulate	β0 + β4(1) + β5(0) + β14(0)	0.712	2.037	0.924
Non-thinned				
Large predator	β0 + β5(1)	−2.82	0.06	0.206
Large ungulate	β0 + β1(1) + β5(1) + β11(1)	0.455	1.577	0.945
Medium ungulate	β0 + β2(1) + β5(1) + β12(1)	−0.186	0.83	0.967
Meso predator	β0 + β3(1) + β5(1) + β13(1)	−0.919	0.399	1.028
Small ungulate	β0 + β4(1) + β5(1) + β14(1)	0.699	2.012	0.942

Table 5
Hypothesis tests of the estimated GLMM model coefficients.

	χ^2	Df	Pr(> Chisq)
(Intercept)	18.607	1	2E-05
Animal type	80.111	4	< 2E-16
Camera trapping starting time	4.717	1	0.030
Survey length	5.748	1	0.017
Centered age post-thinning age	2.186	1	0.139
Camera station location	0.02	1	0.884
Effect of treatment by animal type			
Overall	11.042	5	0.051
Large predators	8.657	1	0.016
Large ungulates	0.499	1	1
Medium ungulates	2.66	1	0.515
Meso predators	0.909	1	1
Small ungulates	0.002	1	1

Note: The p-values for the effect of treatment by animal type were adjusted for multiple testing using the Bonferroni method.

the post-hoc tests of treatments by animal types showed significant differences between treatments for large predators ($p = 0.016$), with a positive response to the thinning treatment. The response to thinning was also positive for all other animal types, but insignificant (Table 5).

The small values of the parameter estimates for camera trap start time (β_6), centered post-thinning age (β_8), survey length (β_7) and camera placement on-trail (β_9) can be directly interpreted as approximate relative changes in the expected number of animal captures. The numbers of animal captures were significantly positively related with a unit increase in the camera trap start time (β_6) (Table 5). Thus, mean captures obtained with every unit (1 week) increase in camera trap start time would increase by approximately 1.5% (Fig. 3). Increasing survey length (β_7) beyond 21 days by a unit (1 day) has a significant positive effect on the expected animal captures (Table 5). Thus, captures obtained with every unit (1 day) increase beyond 21 days would increase by approximately 5.8% (Fig. 4). Post-thinning age and camera placement did not have any significant effects on the mean captures (Tables 3 and 5).

4. Discussion

The results indicate that ungulates (small, medium, large) had highest expected captures and predators (meso and large) had the lowest, thinned plots had the highest expected captures; and that overall animal-treatment interactions were almost significant ($p = 0.051$). Regarding large predators, a positive and significant response to the thinning treatment was observed with substantial differences between the treatments ($p = 0.016$). This result indicates that large predators are sensitive to changes in vegetation structure. The response to thinning was also positive for all other animal types, but insignificant. Thinning caused a slight increase by 19.9% and 41.6% amongst large and medium ungulates, respectively. This provides one possible explanation for the considerable occurrence of large predators. Leopards prefer areas with adequate prey abundance, whereas brown hyena would frequent kill sites of other apex predators for scavenging opportunities (Marker and Dickman, 2005; Stein et al., 2011; Stein et al., 2013; Wiesel, 2015). Another possible explanation is the enhanced hunting efficiency due to the ecotones (habitat edges) created by thinning that allows concealment while stalking, high sighting visibility to detect prey, and ease of chasing due to reduced tree/shrub densities (de Klerk, 2004; Muntifering et al., 2006; Nghikembua et al., 2016).

Contrary to our expectations, expected captures of small, medium, and large ungulates and meso predators were not significantly different between treatments. One possible explanation for these occurrences is the significant presence of large predators at the thinned plots that likely cause a phenomenon known as the landscape of fear (LOF) (Kohl et al., 2018; Suraci et al., 2016). As a result, other animal types would reduce their activity or presence in thinned plots due to a perceived predation risk. Also, since tree/shrub cover (Table1), relied upon by prey when evading predators was reduced by thinning, the landscape of fear factor may be further amplified. Our inability to detect significant results may also be due to random variability in the data, not a lack of treatment effect. The difference in expected captures may indicate a true treatment effects due to thinning, which is just too small to become significant with our sample size. Because some species can utilize both treatments equally; a mixture of open and dense thorn bush savannah would be optimal. Stratifying thinning at different intensities has potential to yield different responses: thinning moderately causes minimal effects, whereas intensively thinning causes significant positive or negative responses as preferred habitat conditions are modified (Ben-Shahar, 1992; Isaacs et al., 2013; Schwarz et al., 2018; Seung-Hun et al., 2017).

The increase of animal captures over the follow up period (April–July) may be due to seasonal conditions. This period coincided with the end of the growing season, where surface water was abundant and vegetation productivity improved, and could cause animal numbers to fluctuate. The effect of survey length on captures was significant. This suggest that increasing survey length for rarely sighted individuals (e.g. cheetahs, caracal), increases chance of capture (Brassine and Parker, 2015). This leads to over-counting among common species, which may present a problem in analysis. The survey length examined (21–36 days) may not be optimum for some species, but a compromise for recording activity patterns of both common and elusive resident wildlife.

Expected image captures were slightly higher off-trail than on-trail. Wildlife, especially large predators, are known to frequent trails more than random locations (Cusack et al., 2015; Fabiano et al., 2018; Mann et al., 2015) and this was expected to occur in both treatment areas. Increased presence of animals on trails was anticipated specifically in the dense non-thinned area where movement is impeded by

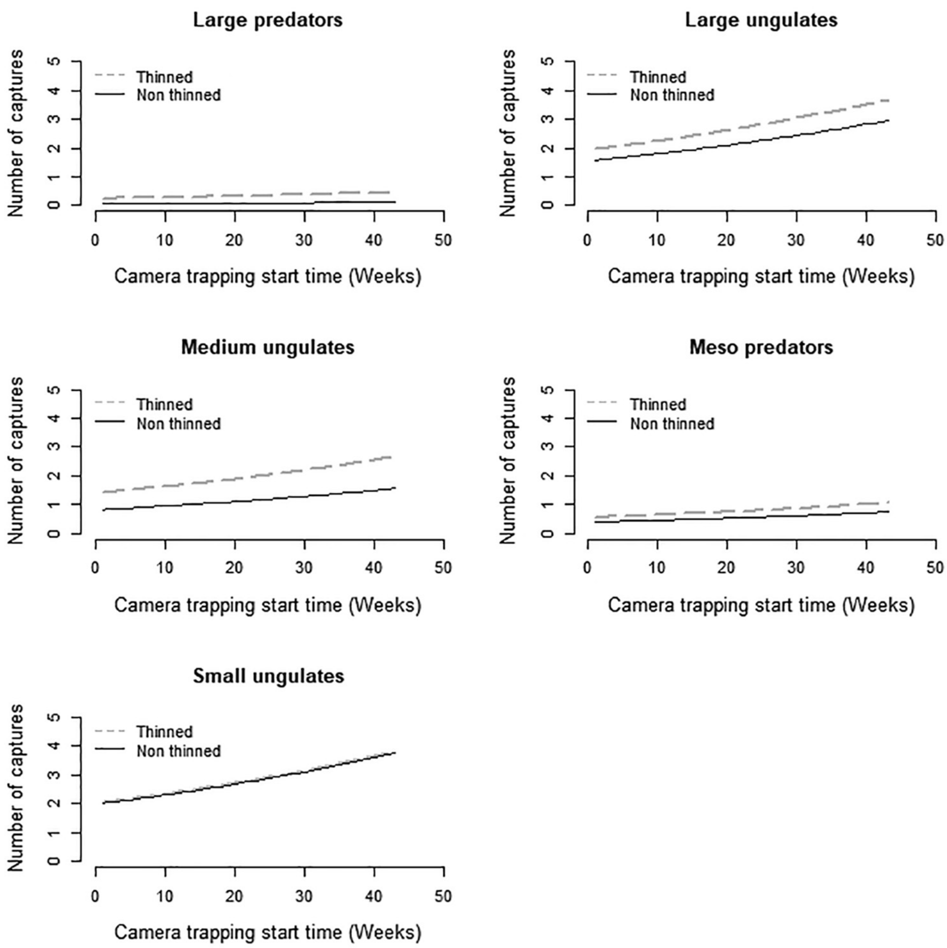

Fig. 3. Effect camera trapping start time on animal captures in the follow up period (weeks since first camera operation date) shows a 1.5% increase in expected captures with a 1-unit increase (weeks) since the first camera traps were active.

impenetrable thickets (de Klerk, 2004; Muntifering et al., 2006).

Bush thinning was applied to promote carrying capacity and restore wildlife habitat. With thinning, remaining tree/shrubs may respond by increasing their reproductive output and growth rates (Brown et al., 2019; Smit, 2014). This was apparent in the study area since tree/shrub densities in previously thinned plots (54%, n = 7) exceeded their non-thinned plot pairs (Table 1). It was apparent that through natural regeneration, saplings established at higher densities especially in previously thinned plots (see Table 1; blocks 1, 4, 7, 8, 9, 10, 11) and, with time, could develop a dense vegetation structure. Without post-thinning management, eventual loss of carrying capacity and sparsely vegetated wildlife habitat may occur.

5. Conclusions and management recommendations

Our results indicate that bush thinning had an overall positive to neutral effect on the wildlife within the study area. We found that large predators were the most responsive to thinning than any other animal type. This suggest that activity patterns of large predators could be substantially shifted by thinning operations. Contrary to our expectations, thinning did not cause a significant response amongst the ungulates (small, medium, large) and meso predators, even though the estimated effect was positive. This is despite the fact this method increases the grazing and browsing capacity that benefit these animal types. The missing or lower effect for ungulates may result from that the ungulates (small, medium, large) and meso predators did not increase their activity in thinned areas significantly due to the fear resulting from increased presence of large predators. This fear could be amplified further especially by the reduction of tree/shrub cover used for safety. Thus, if thinning is done on a smaller scale, then large predators may impact other animal types severely. However, if thinning is done over larger areas, then the predatory risk could potentially be reduced by spreading it over larger areas. This is because larger thinned areas could provide more options for animals to escape or avoid habitat edges that are highly frequented by predators.

The higher frequencies of large predator captures is a potential risk of livestock predation if farmers do not protect their animals in thinned areas. Alternatively, by not thinning tree/shrubs, farmers risk further economic losses due to poor carrying capacity. Thus, thinning tree/shrubs to increase rangeland productivity is inevitable.

Our study provides baseline information for incorporation into the area's management plans. Future studies should consider monitoring wildlife in relation to different tree/shrubs thinning levels since only one thinning treatment type was used in this study. We recommend (i) long term monitoring of wildlife to reveal trends in activity patterns spanning multiple seasons; (ii) post thinning management by reducing regenerating tree/shrub cohorts in restored areas to prevent re-encroachment and loss of wildlife habitats.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

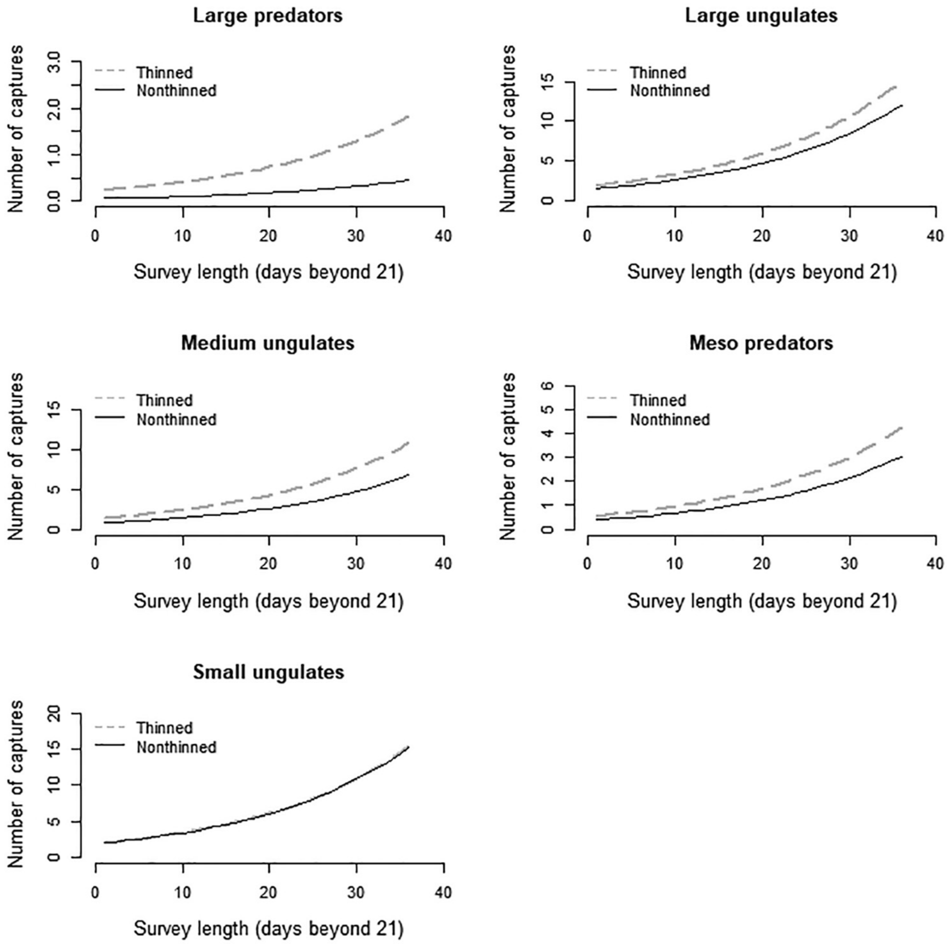

Fig 4. Effect of increasing survey length beyond 21 days on the mean capture of animals using camera traps shows a 5.8% increase in expected captures with a 1-unit increase (days) beyond 21 days.

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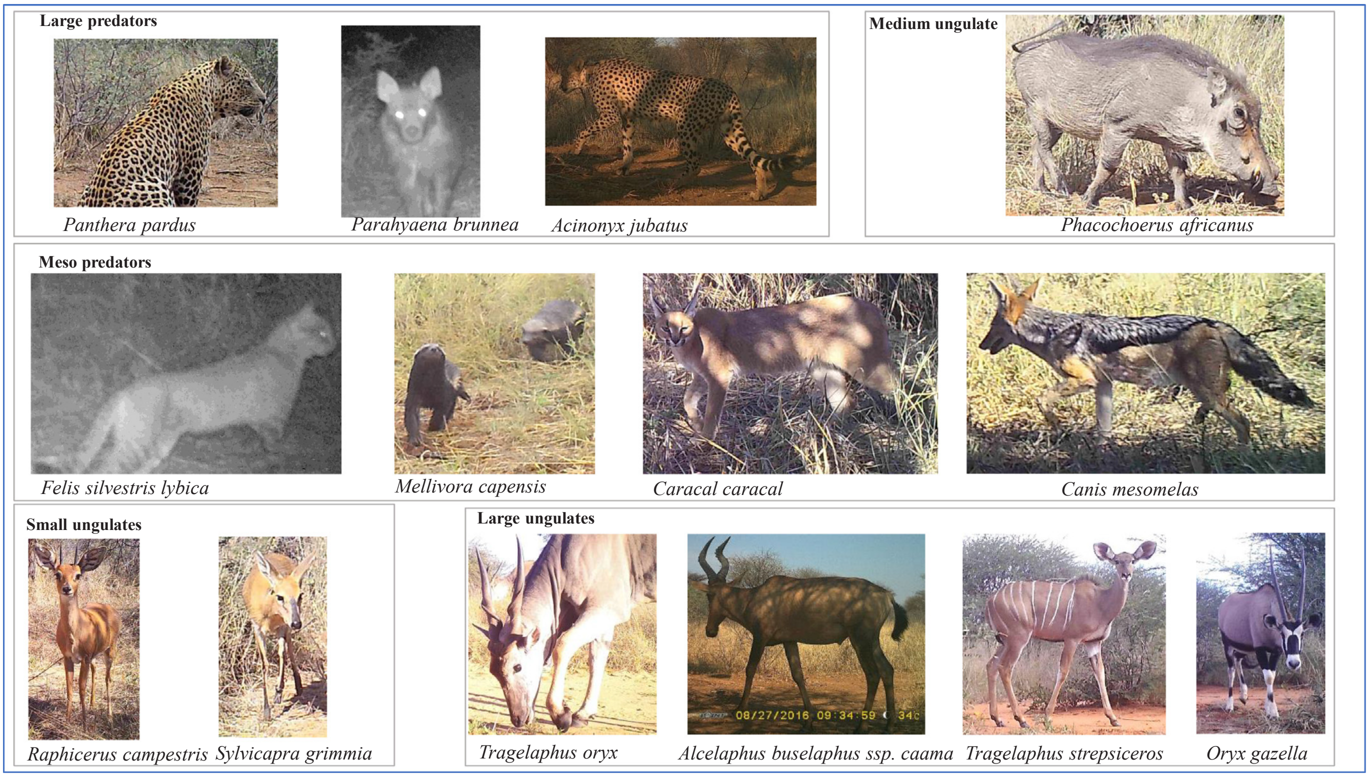
Appendix 1. Predator and ungulate captures in the study area.



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