# Spatio-temporal separation between lions and leopards in the Kruger National Park and the Timbavati Private Nature Reserve, South Africa

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Original research article

# Spatio-temporal separation between lions and leopards in the Kruger National Park and the Timbavati Private Nature Reserve, South Africa

Nakedi W. Maputla [a,b,*], Nkabeng T. Maruping [c], Christian T. Chimimba [b], Sam M. Ferreira [d]

[a] African Wildlife Foundation (AWF), AWF Conservation Centre, Ngong Road, Karen, P.O. Box 310, 00502, Nairobi, Kenya
[b] Mammal Research Institute (MRI) and DST-NRF Centre of Excellence for Invasion Biology (CIB), Department of Zoology & Entomology, University of Pretoria, Private Bag X20, Hatfield, 0028, South Africa
[c] Department of Nature Conservation, Tshwane University of Technology, Private Bag X680, Pretoria West, 0001, South Africa
[d] Scientific Services, South African National Parks (SANPARKS), Skukuza, 1350, South Africa

## ARTICLE INFO

## ABSTRACT

Understanding of the underlying processes that drive coexistence among apex predators is of great importance to landscape managers overseeing their persistence. Two pressing questions stand out. These questions relate to whether space use by subordinate carnivores is a function of resource distribution and shifts in resource availability or fine scale movement associations with sympatric top predators that dominate them. We hypothesized that leopard movements were primarily resource-driven and secondarily, competition driven. Using data from leopards and lions collared in the Kruger National Park (Kruger) and the neighboring Timbavati Private Nature Reserve (Timbavati), we investigated the associations between leopard GPS fixes and resource distribution. We built landscapes of movement activities of lions to investigate the relationships with leopard movements. Results suggested that leopard movements were strongly resource-driven. Lion influence did not come out strongly on leopards collared in the Kruger. In the Timbavati however, lion movements appeared to strongly influence the male leopard movements. We concluded that resources were the main driver of leopard movement behavior and that differences in observed behaviors between Kruger and Timbavati were as a result of different management regimes practiced in the two reserves.

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## 1. Introduction

Mechanisms that drive processes underlying the co-existence of large mammalian carnivores highlight the importance or a lack thereof of apex predators in suppressing population abundances of smaller predators (Ritchie and Johnson, 2009); altering space use by smaller predators (Harihar et al., 2011; Broekhuis et al., 2013; Du Preez et al., 2015); and altering feeding ecology of smaller predators through interference competition (Elmhagen et al., 2010; Cozzi et al., 2012; Du Preez et al., 2015). On the other hand, co-evolution of large carnivores that live sympatric may have resulted in the extant level of interaction among large carnivores (Owen-Smith and Mills, 2008b).

In African carnivore assemblages, resource acquisition by leopards (*Panthera pardus*), cheetah (*Acynonyx jubatus*) and wild dogs (*Lycaon pictus*) was inherent to intraguild competition avoidance of lions (*P. leo*) (Vanak et al., 2013; Du Preez et al., 2015). In addition, to avoid immediate risk, cheetahs positioned themselves far from proximity of lions or spotted hyaenas (*Crocuta crocuta*) (Broekhuis et al., 2013). This is however, not only confined to relationships between predators. At the ecosystem level, intraguild relationships are intertwined with interguild interactions; thus influencing ecosystem structure and functionality by changing population dynamics and foraging behavior, i.e., cascading effects (Johnson et al., 1992; Packer et al., 2005). For example, in Yellowstone National Park, USA, the elk (*Cervus canadensis*) changed their movement behavior in response to wolf (*Canis lupus*) presence, thus altering trophic cascades that led to reduction in the use of certain aspen patches (Fortin et al., 2005). Similarly, in South Africa, zebra (*Equus burchelli*) in Kruger National Park (*Kruger*) were reported to alter their step lengths immediately after contacting or sensing lions and the step length shortened with increasing distance between the zebra and the lions (Van Langevelde et al., 2013). In Hwange National Park, Zimbabwe, use of water sources by buffalo was during the day when it was warm and lions were not active (Valeix et al., 2009).

Besides demonstrating predator–prey and predator–predator relationships, these examples emphasize the importance of predation in regulating top-down processes in an ecosystem. In small reserves, which lack heterogeneity (Vanak et al., 2013), interactions between apex predators and smaller predators may be accentuated (Creel and Creel, 1996; Cristescu et al., 2013). In large reserves characterized by heterogeneous landscapes (Johnson et al., 1992); species-rich habitats with varying abundances of prey species (Gittleman, 1985); and varying climatic conditions along a spatio-temporal scale gradient (Owen-Smith and Mills, 2008a) may buffer and mask these intra-guild interactions. In addition, anthropogenic activities – such as the introduction of an invasive species – coupled with stochastic events, for example, the emergence of extrinsic disease, may affect interactions between species concerned resulting in altered processes in an ecosystem (Clout and Russell, 2007).

In Kruger, lions and leopards coexist throughout the park. At population level, it is unknown whether competition for space or resources influences coexistence (Owen-Smith and Mills, 2008b). Even so, the meso-predator release hypothesis predicts that lions as apex predators, should influence land use by leopards (Trewby et al., 2008).

The emergence of an extrinsic disease, caused by the pathogen *Mycobacterium bovis* that causes bovine tuberculosis (bTB), is a major concern for conservationists (see Ferreira and Funston, 2010). Introduced into the Kruger by human activities in the 1960s (Bengis et al., 2003), the disease has as a reservoir host, the Cape buffalo (*Syncerus caffer*). It spilled over into other species including greater kudu (*Tragelaphus strepsiceros*) and warthog (*Phacochoerus africanus*) (Caron et al., 2003; Keet et al., 1996). These affected species are important prey species for lions thus placing lions in direct contact with the disease where it is prevalent. Consequently, lions may be affected by the disease although population level effects are not detectable (Ferreira and Funston, 2010). In addition, the disease may spread readily through the lion populations facilitated by intra-specific behavioral patterns in lions (Maruping, 2015). Bovine tuberculosis may not affect the leopard population. Leopards are solitary, reducing intra-specific transmission mechanisms; and their diet is not dominated by reservoir hosts (Keet et al., 1996; Hayward et al., 2006; Renwick et al., 2007). Consequently, Van Helden and Uys (2009) predicted that bTB in lions could potentially lead to declines in lions; thus triggering meso-predator release in leopards. This prediction was however, weakened by the findings through numerical comparisons that meso-predator release may not materialize in Kruger's leopard population (Maputla, 2014). Numerical comparisons did not, however, answer questions relating to space use by leopards.

Smit (2011) noted that the distribution of ruminants associated with areas of high quality forage. In a separate study, Wessels et al. (2006) found a modest relationship between herbaceous biomass and the Normalized Difference Vegetation Index (NDVI). Notionally, predators that feed on those ruminants, should forage in areas highly visited by those ruminants. By extension, we hypothesized that leopard movement patterns should associate with highly productive sites since resource distribution is an important variable in the use of landscape by leopards (Bailey, 1993). We expected that thick herbaceous layer should provide enough cover for a hunting leopard, which relies on ambush to catch prey (Bailey, 1993, Hayward et al., 2006). During the dry season, we expect water distribution to be confined to a few permanent water points along the major rivers and smaller rivers in the study area; by extension, we expect to observe heightened leopard activity around those water points. In the rainy season however, we expect several temporary water points to be distributed patchily on the landscape as a result of the rain; thus water dependent herbivores would not be pressured to visit permanent water points, but use the water points that are in their close proximity.

Accordingly, we predicted that leopard space use should be primarily driven by resources that directly and indirectly affect food acquisition and secondarily, lion spatial use. Equally, lion abundances and space use are generally resource-driven (Owen-Smith and Mills, 2008a,b). That means in areas of territorial overlap, conflicts between leopards and lions should be expected. Leopards being smaller predators, should therefore use the landscape as a function of lion space use. Consequently, these observations lead to the prediction that in addition to resource distribution, leopard movements may be influenced by lion space use.

Using spatial data from leopards and lions in the Kruger and the neighboring Timbavati Private Nature Reserve (Timbavati), we hypothesized that a set of variables including habitat productivity as predicted by enhanced vegetation index models, water distribution, proximity to roads, proximity to streams, and the presence of lions influenced leopard movement behavior. Specifically we predicted that space use by leopards was primarily resource-driven and secondarily driven by lion space use. Conservation implications of this study may guide management decisions surrounding large carnivore management in large reserves.
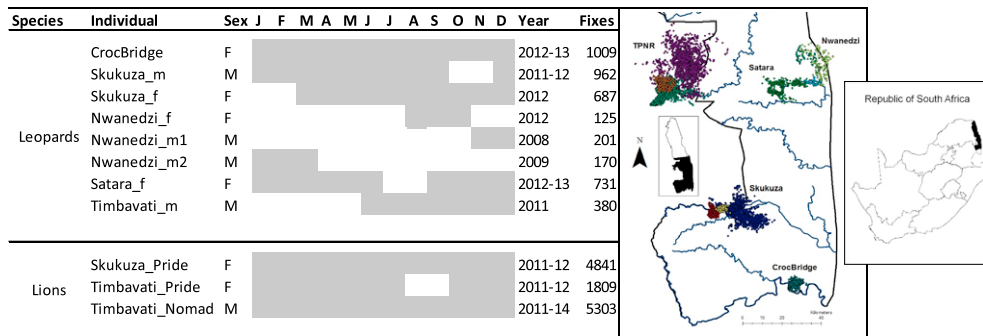
| Species | Individual | Sex | J F M A M J J A S O N D | Year | Fixes |
|---|---|---|---|---|---|
| Leopards | CrocBridge | F |  | 2012-13 | 1009 |
|  | Skukuza_m | M |  | 2011-12 | 962 |
|  | Skukuza_f | F |  | 2012 | 687 |
|  | Nwanedzi_f | F |  | 2012 | 125 |
|  | Nwanedzi_m1 | M |  | 2008 | 201 |
|  | Nwanedzi_m2 | M |  | 2009 | 170 |
|  | Satara_f | F |  | 2012-13 | 731 |
|  | Timbavati_m | M |  | 2011 | 380 |
| Lions | Skukuza_Pride | F |  | 2011-12 | 4841 |
|  | Timbavati_Pride | F |  | 2011-12 | 1809 |
|  | Timbavati_Nomad | M |  | 2011-14 | 5303 |



**Fig. 1.** A map showing southern Kruger National Park (Kruger) and the Timbavati Private Nature Reserve (Timbavati), South Africa, where the study was undertaken. Lion data are from the Skukuza and Timbavati study sites. Leopard data are from all the study sites. Shaded area represents the months that each collar was active.

## 2. Materials and methods

### 2.1. Study sites

The Kruger is located at the north-east corner of South Africa between 22°25′–25°32′S and 30°50′–32°02′E. It covers an area $\approx$ 19 495 km$^2$. In length, the park is $\approx$ 400 km in length while on average it is $\approx$ 65 km wide. The park borders Zimbabwe in the north and the entire length of the eastern boundary is shared with the Mozambican border. The topography of the park is variable and is reflected in the 35 landscapes that the park comprises. The landscapes also reflect an increasing north to south rainfall gradient (Joubert, 1986) and two major soil types (the basalt soils in the east and the granite soils in the west) that characterize the park (Venter, 1986). Two perennial rivers namely the Sabie River in the south and the Olifants River in the center, dissect the park into northern, central and southern regions.

For this study, we focused on the central and southern regions south of the Olifants River (Fig. 1). The two regions have variable terrain characterized by extremely irregular incised areas immediately south of the Olifants River; moderately undulating and southern basalt plains in the east; and low mountains and hills represented by the Lebombo Mountains in the far east on the border with Moçambique and Malelane Mountains on the south west corner of Kruger (Gertenbach, 1983, Venter et al., 2003). Notable large mammals that inhabit the area include buffalo, elephants (*Loxodonta africana*), zebra, kudu (*Tragelaphus strepsiceros*), large numbers of impala (*Aepyceros melampus*) and five large carnivore species including lions, spotted hyaenas, leopards, cheetahs, and wild dogs.

The Timbavati is situated between 24°24′S and 31°21′E, covers an area $\approx$ 550 km$^2$ and is located on the central west border of the Kruger (Fig. 1). The reserve comprises *Combretum apiculatum*, *A. nigrescens*, and *Colophospermum mopani* as the dominant vegetation types with mostly granite or basalt as the principal soil types (Hall-Martin et al., 1975). The reserve is dominated by large numbers of impala, elephants, and warthog (*Phacochoerus africanus*), which are believed to have altered field conditions of the reserve (Pietersen, 1992). Large carnivore species in the reserve include lions, spotted hyaenas, leopards, cheetahs and wild dogs.

### 2.2. Data collection

#### 2.2.1. Study animals

Three male and four female leopards were fitted with satellite ($n = 5$), and global system for mobile communications (GSM; $n = 2$) collars with global positioning system (GPS) capabilities between 2008 and 2013 in Kruger. One male leopard was fitted with a GSM collar in the Timbavati between June 2011 and December 2011 (African Wildlife Tracking; www.awt.co.za). Collars recorded between four and six GPS fixes per day from 16:00 when leopards became active, until 11:00 in the morning when leopard activities became minimal (Bailey, 1993). All leopards in Kruger were captured using baited steel cages. The cages where placed on tree branches to discourage capture of non-target species. Consequently, captured leopards were immobilized and collared following guidelines described in Bailey (1993). The procedures were performed by qualified veterinarians screened and trained to uphold and practice the strictest animal handling ethics. The male leopard (Timbavati male) from Timbavati was free-darted at a bait station by a qualified veterinarian overseen by an experienced official from Mpumalanga Tourism and Parks Agency to ensure that proper animal ethics were adhered to.

Standard procedures for lion captures were used (Smuts et al., 1977) and darting was performed by a qualified veterinary practitioner to ensure that animal handling ethics were not violated. A female lion was collared in the Skukuza area in the southern section of Kruger in 2011 (Maruping, 2015). Two lions, a female within a pride and a nomadic male were collared in Timbavati between in October 2011. The collars were programmed to yield four GPS fixes daily when the lions were active.

### 2.2.2. Landscape features

For the Kruger study area, we obtained landscape and landform data as well as landscape features from the SANParks data repository and viewed these in ArcMap for ArcGIS 10.1 (Environmental Systems Research Institute [ESRI], Redlands, California, 1969). These included woody cover percentage and water distribution raster datasets as well as roads and drainage lines. Land features and rasters were clipped according to the minimum convex polygon for each individual leopard using the Clipping Tool in Data Management Tools for ArcGIS 10.1 to avoid including landscape features that were outside the leopards' home ranges in the analyses. Wessels et al. (2006) noted that vegetation productivity can be associated with interpolated normalized difference vegetation index tree cover images captured by Moderate Resolution Imaging Spectroradiometer satellite and processed by the Council for Scientific and Industrial Research's Meraka Institute, Pretoria, South Africa. For this study, we used the enhanced vegetation index, an enhanced version of the normalized difference vegetation index. Similarly, Smit (2011) noted that ruminants in Kruger associated with the areas of high productivity. Accordingly, using the Spatial Analyst Tool in ArcTools for ArcGIS 10.1 (ESRI, Redlands, California 1969), we created mosaic raster datasets so that we had average EVI values throughout the park (CSIR Meraka). The mosaic raster datasets were arranged according to the duration that the collar was active during the dry and growing seasons. These were also clipped to the extent of the minimum convex polygon for each leopard collared.

### 2.2.3. Data extraction

We used the Near Tool within Proximity Tools (Analysis Tools; ArcTools) to measure the distance between GPS fixes and the nearest stream or road for each leopard from the Kruger study area. Data on landscape features for the Timbavati were not readily available, therefore the study area was excluded. Values from raster datasets including enhanced vegetation index model, woody cover, and water distribution were extracted for each GPS fix using the Extraction Tool in Data Management Tools (ArcTools; Spatial Analyst Tools).

### 2.2.4. Visitation rates and duration of visit

We used T-Locoh (Lyons et al., 2013) a program that takes into account time when local hulls are constructed within Statistical Program R 3.1.0 (R Core Team, 2014). We calculated visitation rates and duration of visit for every 15 nearest-neighbor points to create hulls that were time sensitive based on the dates and times of the geographical fixes. These were used to investigate how leopards associated with indices of resource distribution and lion landscape use. Preliminary data inspection revealed that movement patterns were not consistent between the males and females and between dry and wet seasons for the collared leopards. Dry season ran from April to the end of September while the wet season ran from October to March. Consequently, we analyzed data by subdividing them according to sex and season. For the Kruger study area, most of the males were collared in the wet season with only the Skukuza male's collar functioning during both seasons. As a result, for the male leopards in the Kruger study area ($n = 3$), we only assessed the wet season.

### 2.2.5. Landscapes of activity for lions

Using Kriging, an interpolation method in ArcTools (ESRI, 1969), we constructed landscapes of activity from visitation rates and duration of stay for lions. To aid visual inspection of the association between animals, we ran HotSpots, a geoprocessing tool designed to identify statistically significant hotspots in ArcTools, from visitation rates and duration of stay; thus areas of high lion visitation rates had high pixel values when the activity landscapes were constructed for visitation rates and similarly, areas that the lions spent long durations of time had high pixel values when landscapes for the duration of stay were constructed for lions. We used the extraction tool in ArcTools (ESRI, 1969) to extract values from the lion activity landscapes to leopard GPS fixes. The values extracted were then used to determine the association between leopard GPS fixes and the lion activity landscapes for visitation rates and for the duration of stay.

### 2.3. Data analysis

Statistical analyses were performed using statistical software R 3.1.0 (R Core Team, 2014) and program Excel 2013 (Windows Office 2013). We plotted visitation rates against duration of stay for all the leopards in the study to evaluate their relationship (Lyons et al., 2013). All the data from the variables were continuous. Associations were not outright linear. Data were therefore analyzed using Generalized Additive Models (GAMs), which use non-parametric smoothers, which complement linear models, to indicate the relationships between variables (Crawley, 2007). GAMs were run in the package "mgcv" in statistical software R (R Core Team, 2014). GAMs were used because there were multiple continuous explanatory variables and that we did not want to prejudge the relationships between the response variables (visitation rates and duration of stay by leopards) and predictor variables, namely: lion visitation rates, lion duration of stay, enhanced vegetation indices for growing and dry seasons, woody cover percentage, distances to roads and streams, and water distribution. Models were ranked according to the generalized cross validation (GCV) and an unbiased risk estimator, which in essence, is a rescaled Akaike Information Criterion (Crawley, 2007). Associations were considered significant when the *P*-value was less than 0.01.
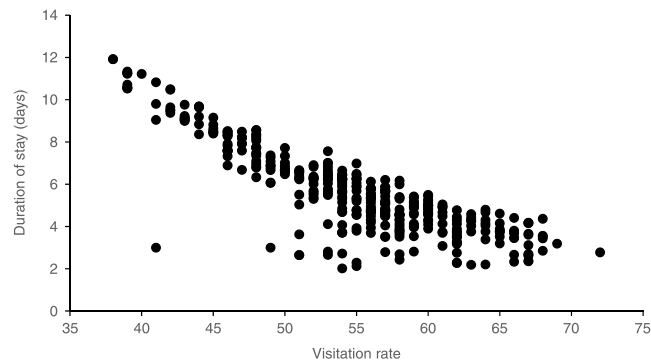
**Fig. 2.** Scatter plot depicting the relationship between visitation rate and duration of visits to different hulls for the female leopard from Skukuza, Kruger National Park in South Africa.
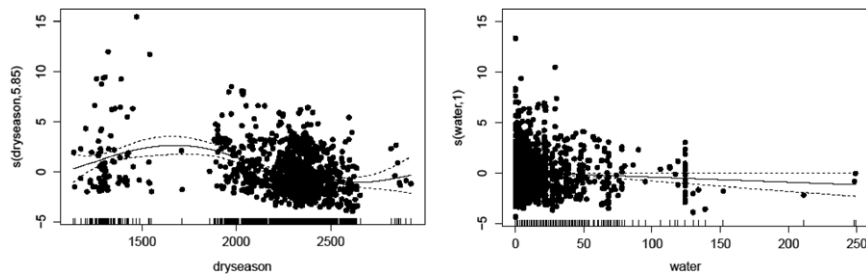


**Fig. 3.** Associations between the duration of stay by female leopards and two predictor variables enhanced vegetation index (dryseason) – in pixels –, and water distribution (water) – in pixels – in the Kruger National Park (KNP), South Africa. The etchings on the *x*-axis are the positions of the predictor variables on the axis. On the *y*-axis are the residuals based on the smoothed values from the predictor variables. Numbers following the predictor variables on the *y*-axis are the effective degrees of freedom.

## 3. Results

### 3.1. Duration of visit and visitation rates

On average, leopard collars yielded 533 ($n = 8$) geographical fixes per leopard that ranged from 1009 fixes and 125 fixes (Fig. 1). There was a young female of approximately two years old. This individual was not used in the analysis as it was not a fully grown adult leopard. Lion geographical fixes on the other hand yielded 3984 ($n = 3$) points ranging from 5303 fixes and 1809 fixes (Fig. 1). Basic statistics for the leopards collared in the Kruger revealed that on average leopards ($n = 6$) spent 5.35 (range: 2–15 days) days per hull. Leopard movements were characterized by areas that were visited frequently, but for short durations, usually less than five days; and a few areas that were less frequently visited, but with long durations of stay (Fig. 2). This pattern was observed in Skukuza ($n = 2$) and Crocodile Bridge ($n = 1$) where the collars were active for seven or more months. Leopards in the Nwanedzi study site ($n = 3$) showed a similar pattern albeit less pronounced because the collars there remained active for three or less months each (Fig. 1). The Timbavati male leopard used the landscape differently to the leopards collared in Kruger. Basic statistics revealed that the leopard stayed on average for 2.33 (range: 1.6–3.8 days) days per hull during the six months that the collar was active.

### 3.2. Resources and visitations

#### 3.2.1. Females

In the dry season, duration of stay by female leopards marginally associated with water distribution ($F_{1;\ 1206} = 4.3$; $P = 0.04$) and strongly associated with the enhanced vegetation index model ($F_{5.9;\ 1206} = 16$; $P < 0.01$) (Fig. 3). This model however, was poorly supported, explaining only 13% of the variation (GCV = 4.7). Similarly, the model that looked at the interactions between variables was poorly supported, explaining 17% of the variation (GCV = 4.66). The only highly significant association between the duration of stay by female leopards was with the interaction between the enhanced vegetation index model and the proximity to roads (Table 1).

Visitation rates by female leopards on the other hand were significantly associated with all the variables used in the study including woody cover ($F_{4.5;\ 1206} = 8.46$; $P < 0.01$), water distribution ($F_{8.7;\ 1206} = 22.28$; $P < 0.01$), enhanced vegetation index model ($F_{8.2;\ 1206} = 164.19$; $P < 0.01$), proximity to streams ($F_{2.3;\ 1206} = 10.27$; $P < 0.01$) and finally proximity to roads ($F_{3.3;\ 1206} = 67.71$; $P < 0.01$) (Fig. 4). The model explained 72% of the observed deviance (GCV = 331.99). The second model investigating association between visitation rates by female leopards in the dry season explained 81.4% of the

**Table 1**
Parameters used in the models that were selected from Generalized Additive Models for the dry season association between female leopard visitation rates/duration of stay and smoothed (using non-parametric smoothers) values for variables including woody cover percentage (wcp), water distribution (water), enhanced vegetation index (evi), proximity to streams (streams), and proximity to roads (roads) as well as their interactions; from the Kruger National Park, South Africa. Significant associations are in bold.

| Visitation rates by females in the dry season | | | | | Duration of stay by females in the dry season | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Variables | Effective degrees of freedom | Reference degrees of freedom | F-statistic | p-value | Variables | Effective degrees of freedom | Reference degrees of freedom | F-statistic | p-value |
| s(wcp) | 4.48 | 5.54 | 1.77 | 0.11 | s(water) | 1.00 | 1.00 | 1.49 | 0.22 |
| **s(water)** | **8.07** | **8.69** | **10.56** | **<0.001** | s(evi) | 2.04 | 2.29 | 0.23 | 0.82 |
| s(evi) | 3.09 | 3.70 | 0.68 | 0.59 | s(wcp,water) | 1.00 | 1.00 | 0.02 | 0.88 |
| s(streams) | 1.00 | 1.00 | 0.03 | 0.86 | s(wcp,evi) | 0.18 | 27.00 | 0.01 | 0.02 |
| s(roads) | 1.00 | 1.00 | 0.39 | 0.53 | s(wcp,streams) | 1.00 | 1.00 | 0.55 | 0.46 |
| s(wcp,water) | 0.00 | 27.00 | 0.00 | 0.74 | s(wcp,roads) | 1.00 | 1.00 | 0.20 | 0.65 |
| **s(wcp,evi)** | **24.01** | **27.00** | **2.37** | **<0.001** | s(water,evi) | 1.34 | 27.00 | 0.06 | 0.03 |
| s(wcp,streams) | 0.00 | 27.00 | 0.00 | 0.42 | s(water,streams) | 0.00 | 27.00 | 0.00 | 0.99 |
| s(wcp,roads) | 8.87 | 27.00 | 0.44 | 0.02 | s(water,roads) | 10.75 | 27.00 | 0.38 | 0.06 |
| **s(water,evi)** | **19.63** | **27.00** | **4.11** | **<0.001** | s(evi,streams) | 0.47 | 27.00 | 0.02 | 0.24 |
| s(water,streams) | 5.60 | 27.00 | 0.34 | 0.03 | **s(evi,roads)** | **13.90** | **27.00** | **1.09** | **<0.001** |
| s(water,roads) | 0.00 | 27.00 | 0.00 | 0.09 | s(streams,roads) | 1.43 | 27.00 | 0.06 | 0.29 |
| **s(evi,streams)** | **21.88** | **27.00** | **1.84** | **<0.001** | | | | | |
| **s(evi,roads)** | **21.14** | **27.00** | **3.19** | **<0.001** | | | | | |
| **s(streams,roads)** | **6.91** | **27.00** | **1.24** | **<0.001** | | | | | |

Parametric coefficients: Intercept = 62.4; Std. err = 0.44; t-value = 140.8; P < 0.01 Adjusted $R^2$ = 0.79; Deviance explained = 81.4%; GCV score = 264.73; n = 1206

Parametric coefficients: Intercept = 5.79; Std. err = 0.061; t-value = 94.6; P < 0.01 Adjusted $R^2$ = 0.14; Deviance explained = 16.2%; GCV score = 4.66; n = 1206
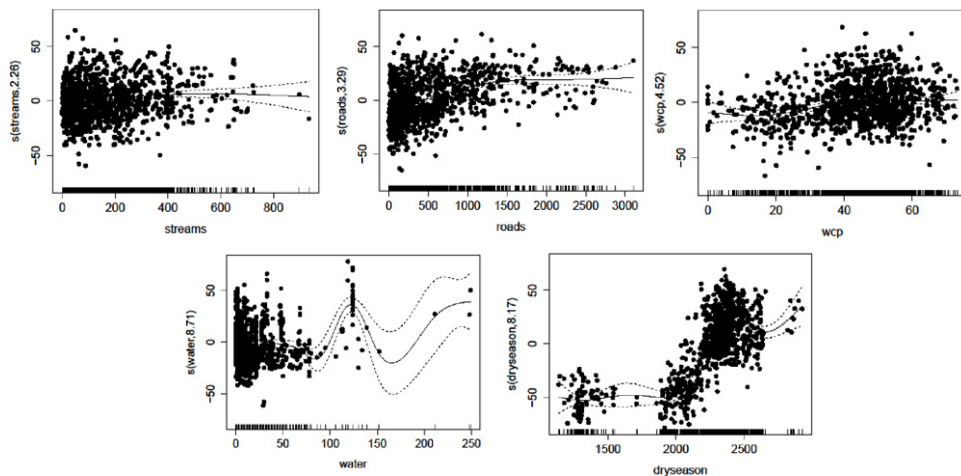


**Fig. 4.** Association between visitation rates by female leopards and different variables in the dry season in the Kruger National Park, South Africa. The models include proximity to streams (streams) – in meters –, proximity to roads (roads) – in meters –, the woody cover percentage (wcp), enhanced vegetation index model (dryseason) – in pixels – in the dry season, and water distribution—in pixels. The etchings on the *x*-axis are the positions of the predictor variables on the axis. On the *y*-axis are the residuals based on the smoothed values from the predictor variables. Numbers following the predictor variables on the *y*-axis are the effective degrees of freedom.

variation (GCV = 264.73). It revealed a highly significant association with water distribution and also with the interaction between woody cover and enhanced vegetation index model, water distribution and enhanced vegetation index model, enhanced vegetation index model and proximity to streams, enhanced vegetation index model and proximity to roads, and proximity to streams and proximity to roads (Table 1).

Visitation rates in the wet season by female leopards were significantly associated with the variables including woody cover ($F_{3.6; 1125}$ = 4.53; $P < 0.01$), water distribution ($F_{8.4; 1125}$ = 16.5; $P < 0.01$), enhanced vegetation index model ($F_{7.76; 1125}$ = 494.13; $P < 0.01$), and proximity to roads ($F_{7.57; 1125}$ = 6.25; $P < 0.01$) (Fig. 5). The model explained 90.1% of the deviance (GCV = 145). The second model, which also investigated interacting variables, explained 93.7% of the variation (GCV = 114.46). Water distribution and association between visitation rates and interacting variables were highly significant for the following interactions: woody cover and water distribution, water distribution and enhanced vegetation index model, water distribution and proximity to roads, enhanced vegetation model index and proximity to roads, and lastly, proximity to streams and proximity to roads (Table 2).
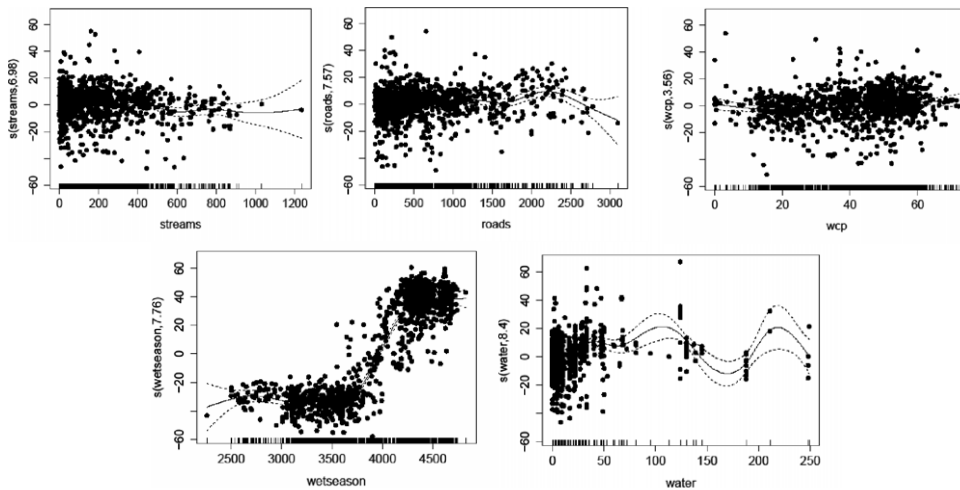
**Fig. 5.** Association between visitation rates by female leopards and different variables in the wet season in the Kruger National Park, South Africa. The models include proximity to streams (streams) – in meters –, proximity to roads – in meters –, the woody cover percentage (wcp), enhanced vegetation index model (wetseason) – in pixels – in the wet season, and water distribution (water)—in pixels. The etchings on the *x*-axis are the positions of the predictor variables on the axis. On the *y*-axis are the residuals based on the smoothed values from the predictor variables. Numbers following the predictor variables on the *y*-axis are the effective degrees of freedom.

**Table 2**
Parameters used in the models that were selected from Generalized Additive Models for the wet season association between female leopard visitation rates/duration of stay and smoothed (using non-parametric smoothers) values for variables including woody cover percentage (wcp), water distribution (water), enhanced vegetation index (evi), proximity to streams (streams), and proximity to roads (roads) as well as their interactions. Significant associations are in bold. The study was conducted in the Kruger National Park, South Africa.

| Visitation rates by females in the wet season | | | | | Duration of stay by females in the wet season | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Variables | Effective degrees of freedom | Reference degrees of freedom | F-statistic | p-value | Variables | Effective degrees of freedom | Reference degrees of freedom | F-statistic | p-value |
| s(wcp) | 5.30 | 6.69 | 1.82 | 0.08 | s(water) | 1.00 | 1.00 | 2.30 | 0.13 |
| **s(water)** | **9.00** | **9.00** | **3.64** | **<0.001** | s(wcp,water) | 7.37 | 10.42 | 1.16 | 0.31 |
| s(evi) | 1.00 | 1.00 | 1.74 | 0.19 | s(wcp,evi) | 1.00 | 1.00 | 0.02 | 0.89 |
| s(streams) | 1.00 | 1.00 | 0.46 | 0.50 | s(wcp,streams) | 7.44 | 9.93 | 0.21 | 0.995 |
| s(roads) | 4.38 | 4.93 | 0.59 | 0.71 | s(wcp,roads) | 1.00 | 1.00 | 0.63 | 0.43 |
| **s(wcp,water)** | **20.20** | **27.00** | **1.50** | **<0.001** | **s(water,evi)** | **18.99** | **27.00** | **2.31** | **<0.001** |
| **s(wcp,evi)** | **10.90** | **27.00** | **0.80** | **<0.001** | **s(water,streams)** | **16.95** | **27.00** | **0.91** | **<0.001** |
| s(wcp,streams) | 0.00 | 27.00 | 0.00 | 0.1 | s(water,roads) | 7.18 | 27.00 | 0.29 | 0.02 |
| **s(wcp,roads)** | **14.50** | **27.00** | **0.78** | **<0.001** | **s(evi,streams)** | **2.49** | **27.00** | **0.28** | **0.001** |
| **s(water,evi)** | **20.00** | **27.00** | **3.01** | **0.001** | **s(evi,roads)** | **13.58** | **27.00** | **1.52** | **<0.001** |
| s(water,streams) | 5.68 | 27.00 | 0.27 | 0.04 | s(streams,roads) | 4.52 | 27.00 | 0.31 | 0.01 |
| **s(water,roads)** | **6.12** | **27.00** | **0.35** | **0.003** | | | | | |
| s(evi,streams) | 9.02 | 27.00 | 0.46 | 0.07 | | | | | |
| **s(evi,roads)** | **27.00** | **27.00** | **5.19** | **<0.001** | | | | | |
| **s(streams,roads)** | **7.14** | **27.00** | **1.01** | **<0.001** | | | | | |

| | |
|---|---|
| Parametric coefficients: Intercept = 56.55; Std. err = 0.3; t-value = 189.7; P < 0.01 Adjusted $R^2$ = 0.93; Deviance explained = 93.7%; GCV score = 114.46; n = 1125 | Parametric coefficients: Intercept = 5.91; Std. err = 0.06; t-value = 101.5; P < 0.01 Adjusted $R^2$ = 0.27; Deviance explained = 32.3%; GCV score = 4.11; n = 1125 |

There was poor support for the association of the duration of stay by female leopards and the majority of the variables selected for the study in the wet season. Only 15% of the variation could be explained (GCV = 4.58) with a highly significant association with enhanced vegetation index model ($F_{8.26; 1125}$ = 12.1; $P < 0.01$) (Fig. 6).

The model outlining association between the duration of stay with interactions between variables was slightly better, explaining 32.3% of the variation (GCV = 4.11). There were significant association with water distribution and roads and highly significant association with the following interactions: water distribution and enhanced vegetation index model, water distribution and proximity to streams, enhanced vegetation index model and proximity to streams, and finally, enhanced vegetation index model and proximity to roads (Table 2).

### 3.2.2. Males

All but one male leopard had data for the wet season only. The first model for assessing the association between visitation rates and the predictor variables explained 79.9% of the variation (GCV = 384.82). The visitation rates by males are signif-
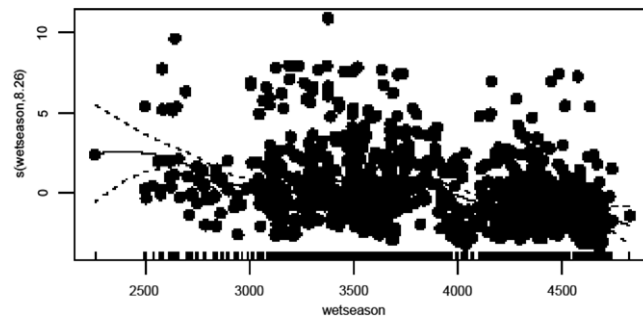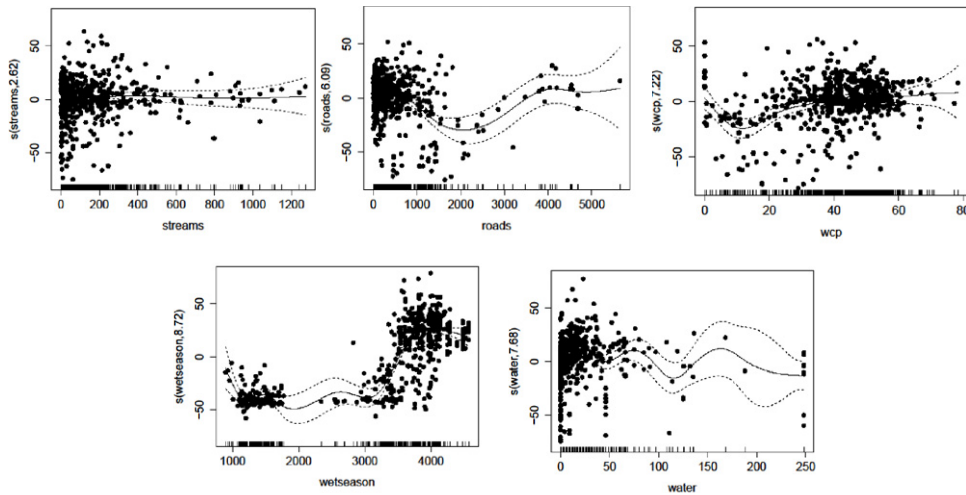
**Fig. 6.** Association between duration of stay by female leopards and the enhanced vegetation index (wetseason) – in pixels – in the dry season in the Kruger National Park, South Africa. The etchings on the *x*-axis are the positions of the predictor variables on the axis. On the *y*-axis are the residuals based on the smoothed values from the predictor variables. Numbers following the predictor variables on the *y*-axis are the effective degrees of freedom.



**Fig. 7.** Association between visitation rates by male leopards and different variables in the wet season in the Kruger National Park, South Africa. The models include proximity to streams (streams) – in meters –, proximity to roads (roads) – in meters –, the woody cover percentage (wcp), enhanced vegetation index model in the wet season (wetseason) – in pixels –, and water distribution (water)—in pixels. The etchings on the *x*-axis indicate positions of the predictor variables on the axis. On the *y*-axis are the residuals based on the smoothed values from the predictor variables. Numbers following the predictor variables on the *y*-axis are the effective degrees of freedom.

icantly associated with woody cover ($F_{7.2;\ 646} = 5.45; P < 0.01$), water distribution ($F_{7.7;\ 646} = 10.3; P < 0.01$), enhanced vegetation index model ($F_{8.7;\ 646} = 72.61; P < 0.01$), and proximity to roads ($F_{6.1;\ 646} = 8.7; P < 0.01$) (Fig. 7). There was poor support for the visitation rates and proximity to streams ($F_{3.1;\ 695} = 2.14; P = 0.08$). The second model that looked at interactions explained 91% of the variation (GCV = 254.21). The model revealed highly significant associations with woody cover and with interactions between variables including woody cover and water distribution, woody cover and enhanced vegetation index model, woody cover and proximity to roads, water and enhanced vegetation index model, enhanced vegetation index and proximity to roads, and the interaction between proximity to roads and proximity to streams (Table 3).

The model assessing the duration of stay by male leopards strongly associated with all the variables including woody cover ($F_{7.4;\ 646} = 3.47; P < 0.01$), water distribution ($F_{6.8;\ 646} = 5.94; P < 0.01$), enhanced vegetation index model ($F_{6.4;\ 646} = 14.59; P < 0.01$), proximity to streams ($F_{2.7;\ 646} = 3.92; P < 0.01$), and proximity to roads ($F_{8.2;646} = 7.85; P < 0.01$) (Fig. 8). However, only 52% of the variation could be explained (GCV = 24.25). The model explaining association of the duration of stay by male leopards explained 83% of the variation observed (GCV = 14.78). The model revealed strong significant associations with woody cover and with interactions between several variables including woody cover and water distribution, woody cover and proximity to streams, woody cover and proximity to roads, water distribution and enhanced vegetation index, water distribution and proximity to streams, water distribution and proximity to roads, and proximity to streams with proximity to roads (Table 3).

### 3.2.3. Site specific associations: Resources and lion landscapes of activity

*Skukuza female*—In the Skukuza area, there were differences and similarities in the response of visitation rates and durations of stay by the female and the male leopards given different variables. Visitation rates by the female leopard were strongly associated with the lion visitation rates landscapes ($F_{3.8;\ 440} = 3.25; P < 0.01$) and the duration of stay

**Table 3**
Parameters used in the models that were selected from Generalized Additive Models for the wet season association between male leopard visitation rates/duration of stay and smoothed (using non-parametric smoothers) values for variables including woody cover percentage (wcp), water distribution (water), enhanced vegetation index (evi), proximity to streams (streams), and proximity to roads (roads) as well as their interactions. Significant associations are in bold. The study was conducted in the Kruger National Park, South Africa.

| Visitation rates by male leopards | | | | | Visitation rates by male leopards | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Variables | Effective degrees of freedom | Reference degrees of freedom | F-statistic | p-value | Variables | Effective degrees of freedom | Reference degrees of freedom | F-statistic | p-value |
| **s(wcp)** | **8.68** | **8.95** | **5.85** | **<0.001** | **s(wcp)** | **8.68** | **8.92** | **7.09** | **<0.001** |
| s(water) | 1.00 | 1.00 | 2.41 | 0.12 | s(water) | 1.00 | 1.00 | 1.22 | 0.27 |
| s(evi) | 1.00 | 1.00 | 0.55 | 0.46 | s(evi) | 1.76 | 1.93 | 0.02 | 0.97 |
| s(streams) | 1.04 | 1.05 | 0.80 | 0.37 | s(streams) | 1.00 | 1.00 | 0.74 | 0.39 |
| s(roads) | 1.01 | 1.01 | 0.62 | 0.43 | s(roads) | 1.15 | 1.24 | 0.13 | 0.77 |
| **s(wcp,water)** | **26.97** | **27.00** | **5.52** | **<0.001** | **s(wcp,water)** | **26.65** | **27.00** | **4.15** | **<0.001** |
| **s(wcp,evi)** | **16.59** | **27.00** | **0.73** | **<0.001** | s(wcp,evi) | 0.91 | 27.00 | 0.04 | 0.23 |
| s(wcp,streams) | 0.026 | 27.00 | 0.00 | 0.35 | **s(wcp,streams)** | **18.09** | **27.00** | **1.57** | **<0.001** |
| **s(wcp,roads)** | **26.94** | **27.00** | **3.67** | **<0.001** | **s(wcp,roads)** | **26.31** | **27.00** | **2.02** | **<0.001** |
| **s(water,evi)** | **9.15** | **27.00** | **0.36** | **0.002** | **s(water,evi)** | **25.85** | **27.00** | **1.41** | **<0.001** |
| s(water,streams) | 0.03 | 27.00 | 0.00 | 0.38 | **s(water,streams)** | **16.82** | **27.00** | **0.85** | **0.002** |
| **s(water,roads)** | **26.94** | **27.00** | **3.61** | **<0.001** | **s(water,roads)** | **14.69** | **27.00** | **2.62** | **<0.001** |
| s(evi,streams) | 8.48 | 27.00 | 0.55 | 0.01 | s(evi,streams) | 5.31 | 27.00 | 0.43 | 0.01 |
| **s(evi,roads)** | **7.11** | **27.00** | **0.67** | **0.001** | s(evi,roads) | 0.00 | 27.00 | 0.00 | 0.70 |
| **s(streams,roads)** | **6.15** | **27.00** | **0.50** | **0.002** | **s(streams,roads)** | **26.01** | **27.00** | **2.33** | **<0.001** |

Parametric coefficients: Intercept = 48.74; Std. err = 0.55; t-value = 87.97; P < 0.01 Adjusted $R^2$ = 0.89; Deviance explained = 91%; GCV score = 254.21; n = 646

Parametric coefficients: Intercept = 9.56; Std. err = 0.13; t-value = 74.06; P < 0.01 Adjusted $R^2$ = 0.77; Deviance explained = 83%; GCV score = 14.78; n = 646
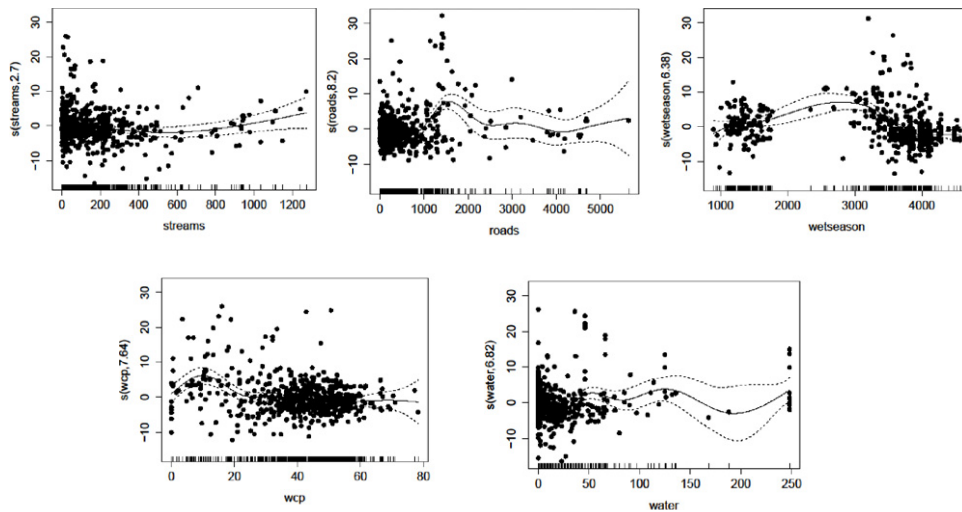


**Fig. 8.** Association between duration of stay by male leopards and different variables in the wet season in the Kruger National Park, South Africa. The models include proximity to streams (streams) – in meters –, proximity to roads (roads) – in meters –, the woody cover percentage (wcp), enhanced vegetation index model in the wet season (wetseason) – in pixels –, and water distribution (water)—in pixels. The etchings on the x-axis indicate positions of the predictor variables on the axis. On the y-axis are the residuals based on the smoothed values from the predictor variables. Numbers following the predictor variables on the y-axis are the effective degrees of freedom.

by lions ($F_{7.6; 440} = 2.91$; $P < 0.01$) (Fig. 9). Visitation rates were also associated, albeit not significantly, with woody cover ($F_{4.8; 440} = 2.27$; $P = 0.04$) (Fig. 9). There was poor support for the duration of stay by the female with lion landscapes of activity. However, there was support for the association between durations of stay by the female leopard and water distribution ($F_{7.4; 440} = 4.71$; $P < 0.01$); and slight evidence with poor support for the association with woody cover ($F_{3.8; 440} = 2.54$; $P = 0.03$) (Fig. 10).

Visitation rates by the male leopard from Skukuza were strongly associated with enhanced vegetation index ($F_{1; 335} = 22.59$; $P < 0.01$) and also with visitation rates by the lion pride from the Skukuza area ($F_{2.7; 335} = 4.63$; $P < 0.01$) (Fig. 11). There was poor support for the association between visitation rates by the male leopard and other variables including woody cover, water distribution, distances to streams distances to roads and land use by lions based on their duration of stay in the area. With regard to the duration of stay by the male leopard, there was poor support for the association between the duration of stay by the leopard and any of the selected variables.
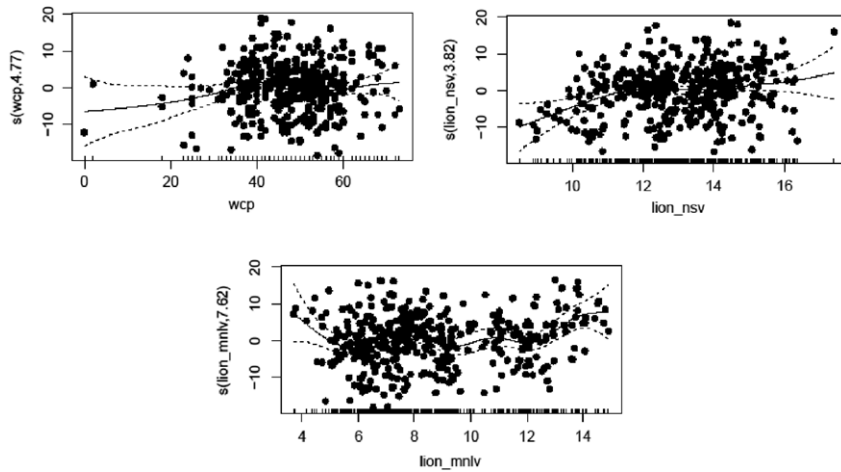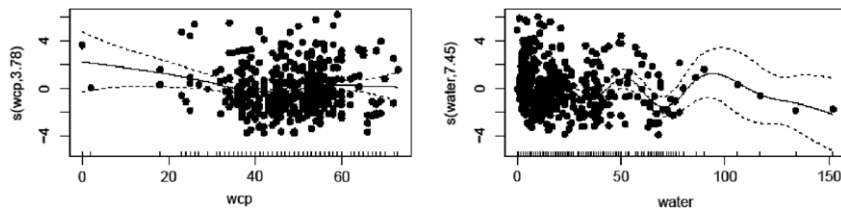
**Fig. 9.** Association between visitation rates by the Skukuza female leopard and (i) the woody cover percentage (wcp); (ii) lion visitation rates (lion_nsv) – in pixels –, and lion duration of stay (lion_mnlv)—in pixels. The etchings on the *x*-axis indicate positions of the predictor variables on the axis. On the *y*-axis are the residuals based on the smoothed values from the predictor variables. Numbers following the predictor variables on the *y*-axis are the effective degrees of freedom.



**Fig. 10.** Association between the duration of stay by the Skukuza female leopard and water distribution (water) – in pixels – and the woody cover percentage (wcp). The etchings on the *x*-axis indicate positions of the predictor variables on the axis. On the *y*-axis are the residuals based on the smoothed values from the predictor variables. Numbers following the predictor variables on the *y*-axis are the effective degrees of freedom.
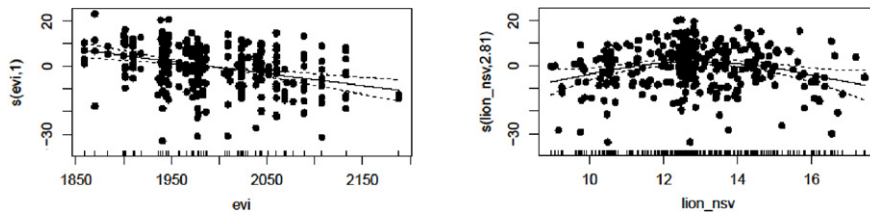


**Fig. 11.** Association between visitation rates by the Skukuza male leopard and the enhanced vegetation index model – in pixels – and lion visitation rates (lion_nsv)—in pixels. The etchings on the *x*-axis indicate positions of the predictor variables on the axis. On the *y*-axis are the residuals based on the smoothed values from the predictor variables. Numbers following the predictor variables on the *y*-axis are the effective degrees of freedom.

Visitation rates by the Timbavati leopard were significantly associated with enhanced vegetation index model ($F_{8.2; 308} = 4.1$; $P < 0.01$), visitation rates by the lion pride ($F_{4.4; 308} = 5.79$; $P < 0.01$), duration of stay by the pride ($F_{7.9; 308} = 11.43$; $P < 0.01$), visitation rate by the nomadic male lion ($F_{4.4; 308} = 5.09$; $P < 0.01$) (Fig. 12). There was slight evidence of significant association between the visitation rate by the leopard and the duration of stay by the nomadic male lion ($F_{4.6; 308} = 2.98$; $P = 0.01$) (Fig. 13).

Duration of stay by the Timbavati male leopard poorly associated with enhanced vegetation index model ($F_{4.3; 308} = 1.79$; $P = 0.11$), but strongly associated with visitation rates by the lion pride ($F_{7.3; 308} = 3.12$; $P < 0.01$), duration of stay by the pride ($F_{4.3; 308} = 4.93$; $P < 0.01$), visitation rate by the nomadic male lion ($F_{7.9; 308} = 6.57$; $P < 0.01$), and duration of stay by the nomadic male lion ($F_{4.3; 308} = 7.05$; $P < 0.01$) (Fig. 13).

## 4. Discussion

The use of T-Locoh (Lyons et al., 2013) has enabled us to account for time in our analysis and to show strong territorial behavior predicted for leopards. The study also revealed a shift in these associations depending on the season. Leopard visits and durations of stay were positively associated with resources and in particular areas with high enhanced vegetation index
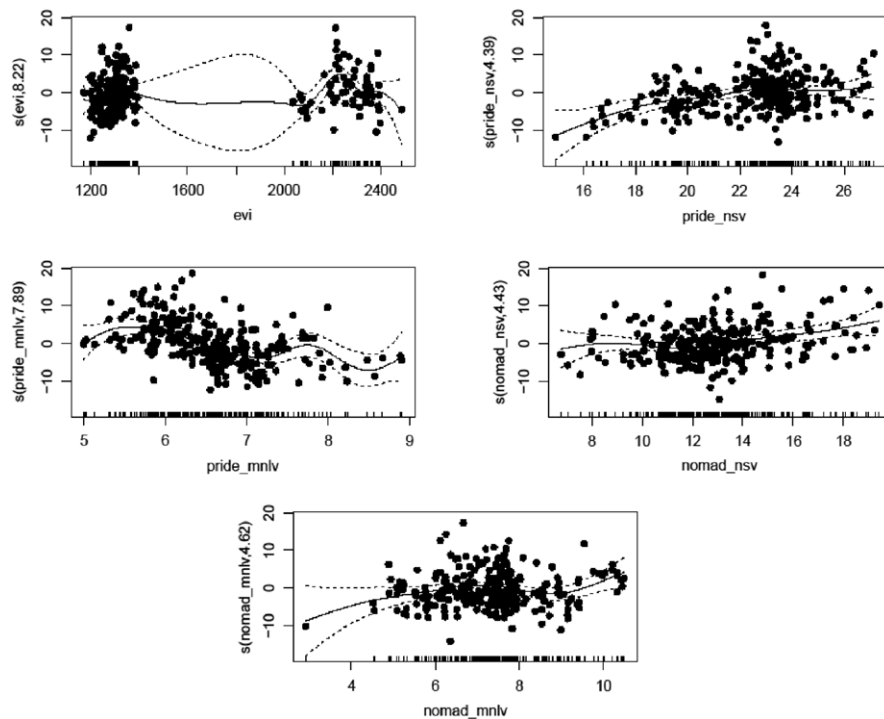
**Fig. 12.** Association between visitation rates by the Timbavati male leopard and (i) the enhanced vegetation index model (evi); (ii) lion pride visitation rates (pride_nsv) – in pixels –; (iii) and lion pride duration of stay (pride_mnlv) – in pixels –; (iv) visitation rates of nomadic male lion (nomad_nsv) – in pixels –; and (v) nomadic male lion's duration of stay (nomad_mnlv)—in pixels. The etchings on the *x*-axis indicate positions of the predictor variables on the axis. On the *y*-axis are the residuals based on the smoothed values from the predictor variables. Numbers following the predictor variables on the *y*-axis are the effective degrees of freedom.

model values, close to drainage lines, high woody cover percentage and close to permanent water points; more so during the dry season than the wet season. In the Skukuza study site in Kruger, lion visitation rates and durations of stay did not seem to play a significant role in how leopards used the landscape, except that there were subtle indications of positive association with the female leopard and with the male leopard. However, in the Timbavati study area, lions seemed to play a significant role on the movement behavior of the male leopard collared there. We note that there were no nomadic male lions collared in the Skukuza study site and thus their role on leopard visitation rates and durations of stay cannot be substantiated. Equally, the role of spotted hyaenas cannot be substantiated for all study sites at this stage. Despite that, the present data revealed that lions may be responsible for the land use behavior by the male leopard from the Timbavati. Thus this study revealed site specific differences in large carnivore assemblages between Kruger and Timbavati. Overall, the results indicate strong territorial behavior in leopards.

Strong positive relationship between leopards and resources are in agreement with the prediction that leopard movements in Kruger were mostly resource driven. As expected, leopard visitation rates were associated significantly with their proximity to roads. Roads play an important role as leopards use them to traverse and possibly for patrolling their territories (Bailey, 1993). Woody cover and proximity to streams appeared to be important variables on visitation rates for the female and male leopards that were collared in Kruger; more so for females in the dry season. This is indicative of the foraging behavior described for leopards in southern Africa (see Bailey, 1993; Hayward et al., 2006). There was a shift in the association between visitation rates by females and proximity to streams associated with the dry and the wet seasons. In the dry season visitation rates were significantly associated with proximity to streams, but in the wet season there was not enough evidence to suggest a positive association. Similarly, visitation rates did not associate significantly with proximity to streams in the wet season. This observation agrees with our prediction that prey animals were likely to concentrate around permanent water points in the dry season and move away from these during the wet season; thus explaining the shift observed in the female leopards. The Kruger is very heterogeneous since animal behavior is a function of a host of variables as a result of a patchy distribution of resources (Du Toit, 2003). Interestingly, leopard visitation rates were significantly associated with the dense herbaceous layer, which we used as a proxy for food resources for leopard prey and by extension, for the leopards. Duration of stay by female leopards associated significantly with water distribution, herbaceous layer and proximity to streams. However, in the wet season there was poor association between female leopards and all the variables except for the herbaceous layer; thus highlighting the importance of water resources for leopards in Kruger. In contrast to the patterns observed for the duration of stay by female leopards, duration of stay by males significantly associated with all the variables used during the analysis; highlighting differences between males and females on landscape use. The differences
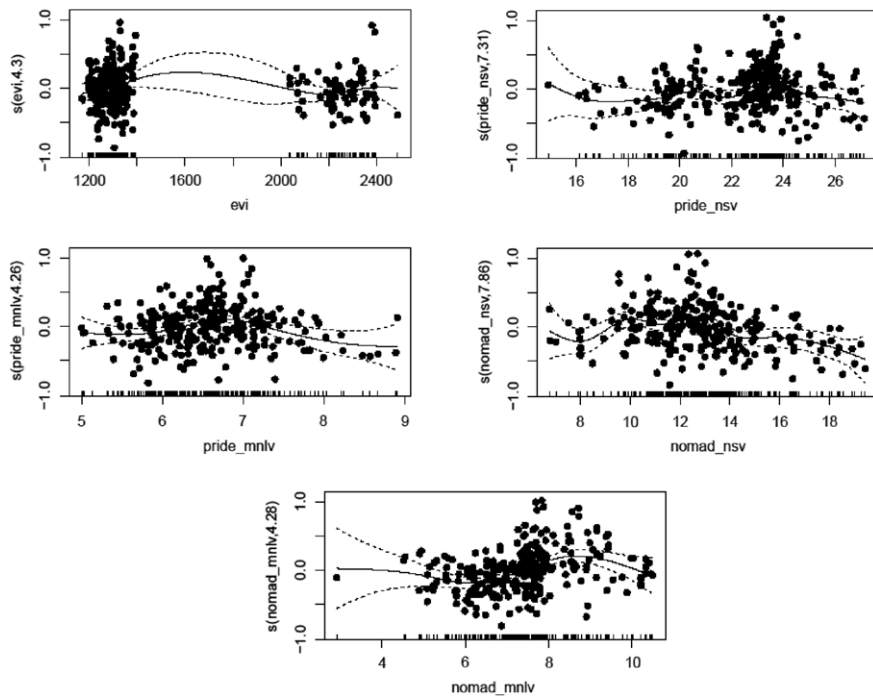
**Fig. 13.** Association between the duration of stay by the Timbavati male leopard and (i) the enhanced vegetation index model (evi); (ii) lion pride visitation rates (pride_nsv) – in pixels –; (iii) and lion pride duration of stay (pride_mnlv) – in pixels –; (iv) visitation rates by the nomadic male lion (nomad_nsv) – in pixels –; and (v) nomadic male lion's duration of stay (nomad_mnlv)—in pixels. The etchings on the *x*-axis indicate positions of the predictor variables on the axis. On the *y*-axis are the residuals based on the smoothed values from the predictor variables. Numbers following the predictor variables on the *y*-axis are the effective degrees of freedom.

between male and females may be as a result of dissimilarities in home range sizes and ranging behavior. For example, Bailey (1993) noted that males spend a considerable amount of time patrolling their territories and females may happen to be rearing the young (Steyn and Funston, 2009). These observations make a strong case for the prediction that leopard foraging behavior was likely to associate with the herbaceous layer; following the extrapolations that high scores obtained for vegetation cover from satellite imagery associated with high herbaceous layer biomass (Wessels et al., 2006) and that ruminants tended to associate with highly productive patches in the landscape as suggested by Smit (2011).

It is interesting that there was significant association between the visitation rate by the female leopard and the lion landscapes of visitation rates and duration of stay. However there was insufficient evidence to suggest that the duration of stay by the female leopard was impacted by the landscapes of activity by lions. Similarly, the visitation rate by the male leopard significantly associated with the lion visitation rates, but not with the duration of stay by lions. This suggests that the leopard visitation rates were impacted by the same resources that drove landscape use by lions, but the leopards stayed for extended periods in areas where lion activity was minimal. Although lions were suggested as possible drivers of leopard movement behavior, in the Kruger study area, they did not come out as strongly as the predictions suggested. Possible reasons for this are firstly that there were not enough data to draw outright conclusions for the observed patterns in leopard movements against the lion landscape of activity. Secondly, the overlap between the male leopard and the lion home range was not complete—only the female leopard home range fell within the lion pride home range (unpublished data). Thirdly, male lions were not collared during the Kruger study site, thus weakening the predictions around the influence of lions on leopard movement behavior. However, the observation that leopards in Kruger could stay in an area for more than ten consecutive days suggest that lion space use did not have a significant impact on leopard space use. This may be because while there is some overlap, diet partitioning is quite profound for lions and leopards in Kruger as suggested by Owen-Smith and Mills (2008b). The lion-specific prey may just be using the terrain differently to movement behavior by leopard-specific prey species (see Du Toit, 2003). This does not negate the fact that given lion presence, leopards are likely to move away (Du Preez et al., 2015). The results therefore concur with results published by Vanak et al. (2013), where leopard movements were minimally affected by lions whereas cheetah and wild dogs were more affected. Results from the Timbavati study area paints a different picture. The visitation rate and duration of stay by the leopard significantly associated with duration of stay and visitation rates by both the pride and the nomadic male. That means the likelihood of encounters were quite high in the Timbavati; thus allowing the leopard movements there to be strongly influenced by lions. This was shown by the leopard's duration of visits, which were markedly shorter than those observed for leopards from the Kruger study site. This may be an example of risk avoidance behavior, thus supporting the findings of Broekhuis et al. (2013) and Du Preez et al. (2015) that suggested that cheetahs and leopards avoided immediate presence of lions respectively. Similarly, in India findings

by Harihar et al. (2011) suggested that leopards moved to the periphery of the reserve after tigers were re-introduced. Whereas the Kruger study site did not have sufficient data to support the influence of lions on leopards, the reason for profound separation between observed trends in the Kruger leopards and the solitary Timbavati leopard may simply be that lion presence was much stronger in the Timbavati than at the Kruger study site. The second reason is that the two study areas are managed differently. Whereas there is no hunting in the Kruger, there is occasional legal hunting in the Timbavati including carnivore hunting and culling of impala. These two reasons and that fences dominate land demarcation in western section of the reserve, where the study was undertaken, suggest that movement behavior of the leopard was subjected to different variables to the Kruger study area. These results therefore, are pre-emptive of the roles that different management regimes play in the persistence of species of concern depending on the objectives.

## 5. Conclusion

Results from this study agree with the predictions that leopards in the study area are primarily resource-driven and secondarily, lion driven although lion data were scanty. This is especially true in the Skukuza study site. Although the prediction did not come out as clearly in the Timbavati study site as in the Kruger, resources and lions are the likely drivers of the leopard movement and these results are attributed to differences in management regimes between the two reserves. Furthermore, our results strengthen conclusions that meso-predator release mechanisms are unlikely to be realized in the Kruger ecosystem based on heterogeneity and high abundance of prey species (Maputla, 2014). We attribute our observations to co-evolution between lions and leopards in the absence of constraints such as small reserves and strict management criteria. In conclusion, we suggest that in the management of leopards, adaptive management strategy, that encompasses resources, competitors and landscape heterogeneity be adopted in order for the species to persist.

## Acknowledgments

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