## Title

# Resource selection of reintroduced lions and the influence of intergroup interactions

## Running title

Resource selection of reintroduced lions

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Image of the study species to be used for the table of contents and considered for the publication cover.

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## Abstract

Optimal resource selection is crucial for maximising fitness and survival. Animals introduced to a new area need time to explore the environment, which could result in a time lag before optimal selection occurs. Furthermore, intra-specific interactions (particularly in territorial species) also play a role in shaping resource selection patterns, with weaker individuals being displaced from optimal resources. We assessed within-home range habitat selection of lions (*Panthera leo*) introduced to a South African wildlife reserve, to examine changes in their resource selection patterns across three years from the time of introduction, and the effect of intra-specific interactions on these selection patterns. After initial exploration, lions selected low altitudes and flat slopes that facilitate movement, high tree densities that provide cover and refuge, and areas close to water sources and floodplains that have high prey density. Responses to human disturbances differed between males and females, with males being more tolerant to high densities of roads and buildings. These patterns were however disrupted by deaths due to intergroup conflicts and by introductions of new individuals, with the dominant groups remaining within favourable resources and subordinate groups shifting to suboptimal resources. Our findings support the spatio-temporal dynamic nature of habitat selection processes for reintroduced large carnivores and emphasise the role of intra-specific interactions in influencing the landscape determinants of habitat selection.

## Keywords

African lion; intraspecific conflict; large carnivore; *Panthera leo*; resource selection function

## Introduction

An understanding of habitat selection patterns is important for informed wildlife management decisions as these patterns affect most components of animal fitness (Holbrook et al. 2017). The process of habitat selection is a function of time and space, and is influenced by ecological processes that determine the spatial and temporal distribution of resources (Boyce 2006). In addition, it is a scale-dependent process (Mayor et al. 2009) as the animals could respond differently to the same environmental cue at different scales (DeCesare *et al.*, 2012), or be influenced by different factors at different scales (Zeller *et al.*, 2014). Home range utilization and resource selection within the home ranges are of particular importance because resource preferences of animals influence home range locations while the latter in turn limits the type of resources the animals can acquire (Johnson, 1980).

To maximize fitness, animals must optimize resource selection by balancing the trade-off between resource exploration and exploitation (Eliassen et al. 2007). This trade-off is not only affected by the distribution of resources, but also by inter- and intra-specific behavioural interactions. Inter- and intra-specific behavioural interactions are especially important for territorial species that defend their resources and home ranges. Competition for resources could result in suboptimal habitat selection, with subordinate individuals of the same species or subdominant species being forced to select less favourable resources. For example, in black-footed ferrets (*Mustela nigripes*), resident and dominant individuals showed a stronger preference for habitats with high densities of burrows providing refuges than the newly introduced subordinate individuals (Biggins *et al.*, 2004). Between different species, Alpine chamois (*Rupicapra rupicapra*) increased their habitat specialization in the presence of the Himalayan tahr (*Hemitragus jemlahicus*) (Forsyth 2000), while the least weasel (*M. nivalis*) selected for less productive habitats compared to the stoat (*M. erminea*) when in the same area (Aunapuu & Oksanen, 2003). In large carnivores, territoriality resulted in reduced dispersal and home ranges for less dominant individuals (Funston *et al.*, 2003), but to date studies on the impact of competition on resource selection within home ranges remain limited.

The establishment of small reserves (<1000 km$^2$) and introduction of large carnivores, especially lions (*Panthera leo*), has increased in recent years in South Africa due to growing demand for ecotourism (Hayward *et al.*, 2007). These reserves are entirely fenced, leading to intense competition for resources and territories (Ferreira & Hofmeyr 2014). Introduced animals also face the additional challenge of being in an unfamiliar environment where they need to explore and learn the locations of resources (Berger-Tal *et al.*, 2014). The fitness and survival of introduced large carnivores are therefore directly affected by their spatial responses to competitors and resource distribution. Successful establishment of introduced animals thus depends on the ability of individuals to optimize selection of suitable resources and avoid competitors (Le Gouar, Mihoub & Sarrazin, 2012).

In a previous study we assessed the home range utilization of a lion population introduced to a small South African reserve over their first three years of release (Yiu *et al*2017), and found that the pattern changed over time due to inter-group interactions. In this paper, we investigate within-home range resource selection of those same lions, in order to understand their habitat selection decisions at a finer spatial scale compared to the previous study, and the impacts of inter-group interactions on selection patterns at this scale. We hypothesised that lions would show a progressive change from no selection to selection for favourable resources as they learn the area. However, we expected this process to be influenced by intra-specific interactions and result in selection of suboptimal resources by the subordinate individuals. Using resource selection functions (RSF; Manly *et al.*, 2002), we examined the effects of topography, water availability, vegetation type and structure, human disturbances, and probability of occurrence of potential competitors and mates in shaping within-home range habitat selection patterns of lions. We expected no evident within-home range selection patterns after introduction (i.e. equal probability to use any resource within the home range) but more consistent patterns over time, with lions selecting landscape features that could facilitate movement (low topographic roughness), attract prey (areas close to water sources, floodplains and riparian vegetation) and had low level of human disturbances (away from roads and buildings). We expected these patterns to be affected by competition and mating opportunities, with lions selecting areas with low probability of occurrence of individuals they had territorial conflicts with, while selecting areas with high probability of occurrence of potential mates.

## Materials and Methods

### Study area

The study was conducted in Dinokeng Game Reserve (DGR), South Africa. The reserve is fenced, spanning an area of 185 $km^2$ that ranges from 1025 m above sea level (a.s.l) in the southeast to 1258 m a.s.l. in the northwest. The average annual rainfall is 626 mm, with distinct wet (October-April) and dry (May-September) seasons (New *et al.* 2002). Perennial water sources include the Pienaars River in the north, joined by the Kaallaagte Spruit in the southwest and the Boekenhout Spruit in the southeast, and more than 40 natural and artificial dams. The reserve is situated within the savanna biome, consisting primarily of mixed Bushveld, Kalahari thornveld and sourish mixed Bushveld (Mucina and Rutherford 2006). Fifteen vegetation types are identified in the reserve, each representing a plant community with distinct vegetation density and structure. Large predators were absent before the introduction of lions, except for leopards (*P. pardus*) but sightings were rare (Contour Project Managers CC, unpublished report). The most common mammalian herbivore species include blue wildebeest (*Connochaetes taurinus*), impala (*Aepyceros melampus*), Burchell's zebra (*Equus quagga burchellii*), blesbuck (*Damaliscus pygargus phillipsi*), greater kudu (*Tragelaphus strepsiceros*) and warthog (*Phacochoerus africanus*) (aerial census data, 2012). DGR incorporates lands owned by the Gauteng Provincial Government and more than 250 landowners, most of whom reside in the reserve. There are at least 188 fenced residential buildings and lodges in the reserve and an extensive road network.

### Lion data

We obtained data from eleven lions that had been fitted with satellite collars (African Wildlife Tracking, Pretoria, South Africa) by the Dinokeng Game Reserve Management Association (DGRMA) for their monitoring purposes. The introductions and collaring operations were planned and managed in compliance with the ethical standard set by the Department of Environmental Affairs and Tourism (DEAT) and the Gauteng Department Agriculture, Conservation and Environment (GDACE). The lions were introduced to DGR in three separate releases in October 2011 (two females, two years of age, and two males, two and a half year of age), November 2011 (two females and two males, all two years of age) and November 2013 (two females, five years of age, and one female two years of age). Lions from the first two releases were set free from an enclosure at the same location, while lions from the last release were held in the same enclosure as the previous lions for one month and then set free in another part of the reserve 12.5 km away (Fig. 1). The previously released lions were observed to frequent the enclosure when new lions were kept in it; therefore, all lions were aware of the existence of other individuals. The GPS collars recorded locations every four hours for the lions in the first two releases, and every five hours for the lions in the third release. The recording frequency was set by DGRMA. Locations spanned from October 2011 to September 2014 and consisted of three wet seasons (October–April 2011–12, 2012–13, 2013–14) and three dry seasons (May–September 2012, 2013, 2014). Information on group structure and the deaths of individuals due to intergroup fights were obtained through field observations.

Lions from the first two releases separated on their own into four same-sex pairs (M-release 1, F-release 1, M-release 2, and F-release 2; Table 1). The females from the third release separated themselves into one pair (F-release 3) and one lone individual (LF-release 3, the two-year-old female; Table 1). All same-sex pairs were genetically related brothers and sisters, respectively, while LF-release 3 was an offspring from one of the females from F-release 3. Lion groups remained associated throughout the study or until one or both of the members died. One of the males (M4) in M-release 2 and both females in F-release 2 were killed in February and May 2012 respectively by M-release 1, during inter-group territorial conflicts (Table 1). The remaining male from M-release 2 was translocated from northwest to southeast DGR at the start of the wet season 2012-13 as a management decision. Data were not available for M-release 2 during the dry season 2013 due to collar failure, but the collar was replaced at the start of the following season.

## Environmental data

Eight environmental variables were categorised into features related to topography, water availability and vegetation, and human disturbance (Fig. 1; Table 2). We obtained elevation data at 30 m spatial resolution from the ASTER Global Digital Elevation Model (GDEM) (NASA LP DAAC, 2009), and derived the slope using the Slope tool in ArcGIS 10.2. We downloaded the 250 m Terra MODIS Vegetation Continuous Fields (VCF) imagery (Townshend *et al.*, 2011), representing the annual percentage of tree cover, from 2011 to 2014 and resampled the data to the same spatial resolution as the GDEM. A vegetation map identifying 15 distinct vegetation types from SPOT images (<20 m resolution) and vegetation survey was obtained from Contour Project Managers CC (unpublished report; Table 2). We created shapefiles of roads, rivers, dams and buildings from satellite images in Google Earth (Google Earth Version 7.1, http://www.google.com/earth/, accessed 5 Nov 2014). Road density was calculated using the kernel density tool in ArcGIS 10.2, with radius defined as the average distance between roads (230 m). The main tarred road in the reserve carried a double weight in the calculation due to higher traffic flow compared to secondary roads.

**Habitat selection modelling and model validation**

Due to different GPS intervals, introduction procedures and events that happened to each lion group, we analysed each group separately using the data of one individual from each group (Table 1). Despite the low sample size, our study includes the entire lion population in the reserve and therefore inferences made from selection patterns through time and the influences of inter-group interactions are still valid (Millspaugh *et al.*, 2015).

We assessed within-home range habitat selection of each lion group by building resource selection functions using generalised linear models (GLM) and logistic regression implemented in R3.1.3. Models were built under the used-availability design (Manly *et al.*, 2002). Used resources were defined as GPS locations of the lions within their respective seasonal Time Local Convex Hull (T-LoCoH) home ranges calculated in Yiu et al. (2017) following Lyons et al. (2013), as T-LoCoH excludes locations where the animals explore only occasionally thus did not represent the daily use of resources. Within-home range available resources were defined as random points created within seasonal minimum convex polygon (MCP) home ranges (Marshal et al. 2010; DeCesare et al. 2012; Davidson et al. 2012), as MCP are includes all areas available to that animal in that time period (Northrup *et al*, 2013). We sampled random points at a ratio of 1:1 to the number of used locations to ensure that the random points representing the available resources were accessible to the animals at the specific spatial and temporal scale (Recio *et al.*, 2014). For each used and random location, we calculated distances to rivers, dams, human infrastructures and extracted the values of road density, elevation, and vegetation.

Multicollinearity between the independent variables was tested using the variance inflation factor (VIF) with a cut-off value of two (Zuur et al. 2010) and a set of seven a priori models was constructed for each lion group for each season (Table 3). Distance to buildings was removed from the analyses for M-release 2 for the dry season 2012 due to multicollinearity with distance to dams (VIF > 5). We calculated the Akaike weights (ω) of the models based on AIC values and selected the best-fit model using w ≥ 0.90 (Burnham and Anderson 2002). When none of the models had ω ≥ 0.90, we used the multi-model inference approach by computing the average model parameters weighted by the Akaike weights of each model (Burnham, Anderson & Huyvaert, 2011). Model fit was assessed using 10-fold cross validation (Aarts *et al.*, 2008; Northrup *et al.*, 2013).

We evaluated the impact of deaths from territorial conflicts on the within-home range resource selection of the remaining lions and the impact of introduction of new individuals on the previously released lions. Specifically we tested the impact of: 1) the death of M4 (member of M-release 2, Table 1) on the remaining males, 2) the death of F-release 2 on M-release 1 and the other female group (F-release 2), and 3) the third introduction on the existing male (M-release 1) and female (F-release 2) groups (Table 4). We built RSFs that tested the interactive effects of two independent variables on the resource selection of each group: 1) time period relative to death from intergroup conflict or new introduction event (categorical variable coded as before or after), and 2) predicted probability of occurrence of other lion groups (continuous variable) (Table 4). Predicted probability of occurrence of the lion groups was mapped using the raster calculator in ArcGIS 10.2 and the equation (Supplementary material Fig. S1-5; Manly *et al.*, 2002):

$$P = exp(a + bx_1 + bx_2 + \cdots + bx_\infty)$$

where *P* is the predicted probability of occurrence of a lion group, $a$ is the intercept and $b$ is the coefficient of each independent variable x extracted from the seasonal RSF built for each group. F-release 3 and LF-release 3 were released at the same time and represented one introduction. We therefore obtained their combined probabilities using the equation (Ash, 2008):

P(females from the third release) = P(F-release 3) + P(LF-release 3) - P(F-release 3) × P(LF-release 3)

The values of predicted probability of occurrence associated with used and random points were extracted for the periods before and after each event. When testing the effect of the death of M4 on the within-home range habitat selection of the remaining male lions, a 67-day time period before and after the death of M4 was selected to remove any possible seasonal effects, as it was the maximum number of days that fell within the same season (Table 4). For the death of F-release 2, we used the wet season 2011-12 as the before and the dry season 2012 as the after event period. Because F-release 2 were killed at the start of the dry season 2012, potential seasonal effect could not be removed. Similarly, the third introduction was carried out at the start of a season (wet season 2013-14), therefore we defined the dry season 2014 as the time period before and the wet season 2013-14 as the time period after the reintroduction.

## Results

### Model selection and environmental variables

The global model (model 7) with all the eight environmental variables was the best-fit model ($\omega \geq 0.99$) in 17 out of 42 instances (Table 3). In the remaining cases, no single model had a weight > 0.90. The most common models to add up to a value greater than 0.90 together with the global model were model 2 (features related to water and vegetation), model 4 (features related to topography, water and vegetation), and model 6 (features related to water, vegetation and human presence). Ten-fold cross validation for each final model always provided a model fit above 0.93.

Within home ranges, lions appeared to select low elevations throughout the study period following release, except for M-release 2, which changed from lower elevation to higher elevation after it was translocated at the start of the wet season 2012-13 (Fig. 2). There was not much selection for slope within home ranges during the first seasons after release, but selection for less steep slopes as time progressed (Fig. 3). At the beginning all lions selected locations further away from rivers, but the selection became weaker over time with M-release 2 shifted to selection for locations close to rivers from wet season 2012-13 (Fig. 4). Throughout the study period, lions selected locations closer to dams but occasionally showed no selection or negative selection for distance to dams (dry season 2012: M-release 2; wet season 2013-14: M-release 1 and F-release 3) (Fig. 5). However, the changes in the selection for rivers and dams were minimal (differences between coefficients < 0.002). Males increasingly selected denser vegetation after release, but the magnitude of selection decreased between the dry season 2013 and dry season 2014, going back to levels similar to the first season of release by the end of the study (Fig. 6). F-release 1 showed no selection the first two season after release, but shifted to selecting dense vegetation except in the wet season 2013-14.

Within home ranges, M- and F-release 1 selected the floodplains and riparian vegetation complex more than all of the other vegetation types in the wet season 2011-12 and the dry season 2012, but included bushvelds and thornvelds of various openness and rhyolitic floodplains from the wet season 2012-13 onwards (Supplementary material Fig. S6 and S7). After the territorial conflict in the wet season 2012-13, M-release 2 showed a drastic change from using 11 types to 3 types of vegetation and selected *Terminalia sp.* and *Tarchonanthus sp.* velds that were avoided by M-release 1, but only during the dry season 2012. (Supplementary material Table S8). Females from the third release selected rhyolitic floodplains over other vegetation types (Supplementary material Fig. S9). Overall, there was an increase in the number of vegetation types being used by the lions over time.

Male and female lions differed in their responses to human disturbances. In general males selected higher road density compared to within-home range availability, after not showing any selection the first season after release (Fig. 7). Females either showed no selection or used locations with lower road density compared to what was available within their home range (Fig. 7). Females selected for locations closer to buildings compared to within-home range availability with selection becoming weaker in time (Fig. 8). In comparison, males responded to buildings differently, with M-release 1 showing signs of habituation (i.e. selection of locations closer to buildings with time) (Fig. 8) while M-release 2 remained away from buildings over the study period (Fig. 8). However, the changes in the responses of all of the lions to buildings were minimal (differences between coefficients $< 0.002$; Fig. 8).

### Intra-specific interactions

and probability of occurrence of M-release 1 explained the effect that the death of M4 had on the surviving member of M-release 2 ($p < 0.001$; Table 5). M-release 1 switched from locations with low probabilities to locations with high probabilities of occurrence of M-release 2, i.e. after the death of M4, M-release 1 preferred landscape features that used to be selected by M-release 2. At the same time, M-release 2 changed from areas with high probabilities to areas with low probabilities of occurrence of M-release 1, i.e. M-release 2 avoided the landscape features selected by M-release 1. The interaction between time of event and probability of occurrence of F-release 2, explained the effect that the death of F-release 2 had on the other lions ($p < 0.01$; Table 5). Both M-release 1 and F-release 1 selected areas with high probability of occurrence of F-release 2 after the death of the latter, i.e. the males were using the landscape features selected by F-release 2 before their deaths. Interactions between time of event and probability of occurrence of females from the third introduction explained the habitat selection of the existing lions ($p < 0.001$; Table 5). After the third introduction, both M-release 1 and F-release 1 shifted to avoid areas with high predicted probability of occurrence of the newly released females.

## Discussion

Lions showed progressive and consistent changes in within-home ranges selection patterns following introduction in the new area. These patterns were therefore a result of increasing selective use within their home range space. Inter-group interactions had a clear role in shaping habitat selection patterns of the introduced lions, as individuals released later showed signs of selection for suboptimal resources, with intra-specific interactions altering selection patterns.

Within home ranges, lions selected areas with low elevation, gentle slopes, and high tree cover after release. Selection of lower elevations and gentler slopes after initial exploration is in line with other studies on large carnivores (Dickson & Beier, 2006; Abade, Macdonald & Dickman 2014), suggesting preference for landscape features that can facilitate movement. However, M-release 2 shifted from low elevations to high elevations after one member was killed, despite availability of low elevations, indicating how competitive interactions can result in a reversed habitat preference by the weaker individual (in this case the lone male) to avoid further conflicts (Winker, Rappole & Ramos, 1995; Vanak *et al.*, 2013). High tree density improves prey ambushing success (Loarie, Tambling & Asner, 2013) and provides shelter from competitors and human disturbances (Spong, 2002), which explains the initial selection of high tree density by the lions. The reduction in selection for high tree density by the males after the third introduction was likely triggered by the males need for greater visibility to detect the newly introduced females for mating opportunities, and the females need to avoid territorial conflict. This is in line with Funston et al. (1998), which reported higher encounter frequencies between male and female lions in ecosystems with open habitat structures (e.g. Serengeti, Kalahari) than ecosystems with closed habitat structures (e.g. Kruger National Park, Rwenzori Mountains National Park), suggesting the importance of visibility for the detection of conspecifics. The changes suggest that lions optimize their resource selection based on food accessibility as well as inter-group interactions. We had found similar responses at the home range scale, with males expanding their home ranges to overlap with those of the newly introduced females, and the previously released females shifting theirs to avoid the new females

(Yiu et al., 2017). Males were more tolerant to human disturbances than females. As males increase their fitness by maximizing mating opportunities and females by maximizing offspring survival (Clutton-Brock, 2006), female lions are more risk sensitive than males thus more likely to avoid human disturbances that are often perceived as a form of predation risk (Frid & Dill, 2002; Beale & Monaghan 2004).

As expected based on the fact that the lions home ranges were established around the largest dam (0.43 $km^2$) in the reserve (Yiu *et al.*, 2017), within their home ranges lions further selected areas close to the dams where prey density could be high. A similar pattern was observed in Hwange National Park, Zimbabwe, where lions preferred areas close to waterholes (Valeix *et al.*, 2010). Although lions did not show significant signs in the selection of rivers within their home ranges, their home ranges included the rivers throughout the study period (Yiu *et al.*, 2017), suggesting a scale-dependent response. The shift to selecting locations closer to rivers by M-release 2 after one member was killed corresponded to the time period when M-release 2 was translocated to the south-eastern part of the reserve, where it has gained access to a stretch of the river away from other lions (Yiu *et al*., 2017). This has likely reflected the need of M-release 2 for cover and refuges in woody riparian vegetation to avoid further territorial conflicts (Vanak et al. 2013).

Riparian vegetation and floodplains support the growth of grass species with high palatability, e.g. *Panicum maximum*, *Cynodon dactylon* and *Setaria megaphylla* (Contour Project Managers CC, unpublished report), which could attract a high number of herbivores and thus attract the lions. These types of vegetation are known to be preferred by lions across geographic areas due to high prey abundance (Spong, 2002; Cozzi *et al.*, 2013). The increased number of vegetation types selected over time again indicates exploration behaviour, and corresponded with expansion of home ranges to another part of the reserve during the same time (Yiu *et al.*, 2017). The impact of intra-specific competition on vegetation selection was evident. After territorial conflict, the males from the second release used less vegetation types and selected vegetation types not preferred by lions from the first release. However, the selected vegetation types subsequently became avoided again by the male after one season, suggesting selection of suboptimal resources following conflict, which is commonly observed in sympatric competitors (Durant, 1998; Vanak et al., 2013).

Intra-sexual competition for territory is intense in lions, with males maximizing their mating opportunities and females the survival of their young by expanding their territories (Mosser & Packer, 2009; Rosvall, 2011). After the deaths of three individuals due to inter-group fights, all other lions selected locations that used to be selected by the dead lions (except the surviving male whose coalition member was killed, who since begun avoiding other lions). We had observed a similar response at the home range scale: home range expansion by the dominant individuals and home range contraction by the subordinate individual (Yiu *et al.*, 2017). Surprisingly all the already released lions avoided locations that had high predicted probability of occurrence of females from the third introduction. The females might have been cautious to avoid potentially fatal conflicts with the new individuals, as suggested by their shifting home ranges (Yiu *et al.*, 2017). Males however expanded their home ranges to overlap with that of the females (Yiu *et al.*, 2017), suggesting a scale dependent response to the presence of mates.

Our findings demonstrate the influence of scale depended responses and intra-specific interactions on the optimization of habitat selection by introduced large carnivores, thus reinforcing the need for multi-scale analyses on habitat selection of reintroduced animals. In addition, multiple introductions should be planned to maximize the initial distance between different groups such that inter-group conflicts and suboptimal resource selections could be minimized during initial stages of release.

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**Table 1.** Information on the release, grouping and data availability of lions introduced to Dinokeng Game Reserve, South Africa, October 2011-September 2014. Grey shading = data available. * indicates the individual of which data was used for the analyses. †Death of M4 and translocation of M3 to southeast; data available represent M3 only thereafter.

| Date of release | Individuals | Coalition | Wet season 2011-2012 | Dry season 2012 | Wet season 2012-2013 | Dry season 2013 | Wet season 2013-1014 | Dry season 2014 |
|---|---|---|---|---|---|---|---|---|
| October 2011 | M1*, M2 | M-release 1 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| | F1*, F2 | F-release 1 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| November 2011 | M3*, M4 | M-release 2 | ▨ | ▨ | ▨ † | | ▨ | ▨ |
| | F3*, F4 | F-release 2 | ▨ | | | | | |
| November 2013 | F5*, F6 | F-release 3 | | | | | ▨ | ▨ |
| | F7* | LF-release 3 | | | | | ▨ | ▨ |

**Table 2.** Vegetation types in Dinokeng Game Reserve, South Africa.

| Vegetation types | |
|---|---|
| 1 | Open *Combretum apiculatum* veld |
| 2 | Dense *Combretum apiculatum* & *Combretum zeyheri* bushveld |
| 3 | Open *Mundulea sericea* & *Combretum molle* veld |
| 4 | Rhyolitic floodplains and riparian vegetation complex |
| 5 | Dense *Combretum apiculatum* bushveld |
| 6 | *Terminalia sericea* & *Burkea Africana* bushveld |
| 7 | *Peltophorum africanum* & *Terminalia sericea* bushveld |
| 8 | Grassy floodplains with scattered *Terminalia sericea* |
| 9 | Floodplain and riparian vegetation complex |
| 10 | *Tarchonanthus camphorates* & *Boschia albitrunca* veld |
| 11 | Open *Vachellia tortilis* floodplains |
| 12 | Dense *Vachellia tortilis* & *Combretum apiculatum* bushveld |
| 13 | *Vachellia tortilis* & *Senegalia mellifera* & *Terminalia sericea* complex |
| 14 | Mixed Bontveld with bushblumps |
| 15 | *Vachellia robusta* & *Euclea undulata* brackish thornveld |

**Table 3.** Environmental variables (A), a priori resource selection function (RSF) model set (B), and final model selection (C) for lions in Dinokeng Game Reserve, South Africa, October 2011-September 2014.

A. Environmental variables

| Feature categories | Variable |
|---|---|
| Topography | Elevation, slope |
| Water availability and vegetation | Distance to the nearest river, distance to the nearest dam, Vegetation Continuous Fields (VCF), vegetation types |
| Human disturbances | Density of roads, distance to the nearest building |

B. A priori RSFs models

| Model number | Model |
|---|---|
| 1 | Elevation + slope + VCF |
| 2 | Distance to river + distance to dam + VCF + vegetation types |
| 3 | Density of roads + distance to building |
| 4 | Elevation + slope + VCF + distance to river + distance to dam + vegetation types |
| 5 | Elevation + slope + VCF + density of roads + distance to building |
| 6 | Distance to river + distance to dam + VCF + vegetation types + density of roads + distance to building |
| 7 (global model) | Elevation + slope + VCF + distance to river + distance to dam + vegetation types + density of roads + distance to building |

C. Model selection (Models with a sum of AIC weight > 0.90 are listed)

| Season | Wet 2011-12 | Dry 2012 | Wet 2012-13 | Dry 2013 | Wet 2013-14 | Dry 2014 |
|---|---|---|---|---|---|---|
| M-release 1 | 6 7 | 4 7 | 4 7 |  | 4 7 | 4 7 |
| F-release 1 | 7 | 7 | 7 | 4 7 | 4 7 | 4 7 |
| M-release 2 | 7 | 7 4 | 7 |  | 6 7 | 6 7 |
| F-release 2 | 7 |  |  |  |  |  |
| F-release 3 |  |  |  |  | 4 2 7 6 | 7 |
| LF-release 3 |  |  |  |  | 7 |  |

**Table 4.** Events and variables used to test for the effect of intraspecific interactions on resource selection of lions in Dinokeng Game Reserve, South Africa.

| Event | Response variable (used vs available) | Independent variables | |
|---|---|---|---|
| | | Time of event | Presence of other lions |
| Death of M4 | M-release 1 | Before:<br>67 days before death<br>After:<br>67 days after death | Probability of occurrence of M-release 2 |
| | M-release 2 | | Probability of occurrence of M-release 1 |
| Death of F-release 2 | M-release 1 | Before:<br>wet season 2011-2012<br>After:<br>dry season 2012 | Probability of occurrence of M-release 2 |
| | F-release 1 | | |
| 3rd introduction | M-release 1 | Before:<br>dry season 2013<br>After:<br>wet season 2013-2014 | Probability of occurrence of F-release 3 & LF-release 3 |
| | F-release 1 | | |

**Table 5.** Resource selection function (RSF) results of lions in response to the predicted probability of occurrence (P) of lion groups and the time of events (before and after) of territorial conflicts and introduction of new individuals in Dinokeng Game Reserve, South Africa.

| Independent variable | Estimate | Standard error | z value | p value |
|---|---|---|---|---|
| Territorial conflict event: Death of M4 from M-release 2 | | | | |
| **Response group: M-release 1** | | | | |
| P(M-release 2) | -0.74301 | 0.23124 | -3.213 | 0.001 |
| Time of event (after) | -1.49777 | 0.19308 | -7.757 | <0.001 |
| P(M-release 2) X Time of event (after) | 3.08545 | 0.3513 | 8.783 | <0.001 |
| **Response group: M-release 2** | | | | |
| P(M-release 1) | 9.6946 | 0.9219 | 10.516 | <0.001 |
| Time of event (after) | 1.3885 | 0.1787 | 7.768 | <0.001 |
| P(M-release 1) X Event (after) | -13.0711 | 2.1278 | -6.143 | <0.001 |
| Territorial conflict event: Death of F-release 2 | | | | |
| **Response group: M-release 1** | | | | |
| P(F-release 2) | 0.53955 | 0.41745 | 1.293 | 0.196 |
| Time of event (after) | -0.56479 | 0.08481 | -6.66 | <0.001 |
| P(F-release 2) X Event (after) | 5.53428 | 0.65813 | 8.409 | <0.001 |
| **Response group: F-release 1** | | | | |
| P(F-release 2) | -0.1404 | 0.55694 | -0.252 | 0.801 |
| Time of event (after) | -0.12363 | 0.07653 | -1.615 | 0.106 |
| P(F-release 2) X Event (after) | 2.48017 | 0.88139 | 2.814 | <0.01 |
| New introduction event: 3rd reintroduction | | | | |
| **Response group: M-release 1** | | | | |
| P(F- & LF-release 3) | 0.62454 | 0.32711 | 1.909 | 0.056 |
| Time of event (after) | 0.29537 | 0.08373 | 3.528 | <0.001 |
| P(F- & LF-release 3) X Event (after) | -3.2076 | 0.58633 | -5.471 | <0.001 |
| **Response group: F-release 1** | | | | |
| P(F- & LF-release 3) | 0.30973 | 0.25141 | 1.232 | 0.218 |
| Time of event (after) | 0.29312 | 0.08714 | 3.364 | <0.001 |
| P(F- & LF-release 3) X Event (after) | -2.55021 | 0.48389 | -5.27 | <0.001 |

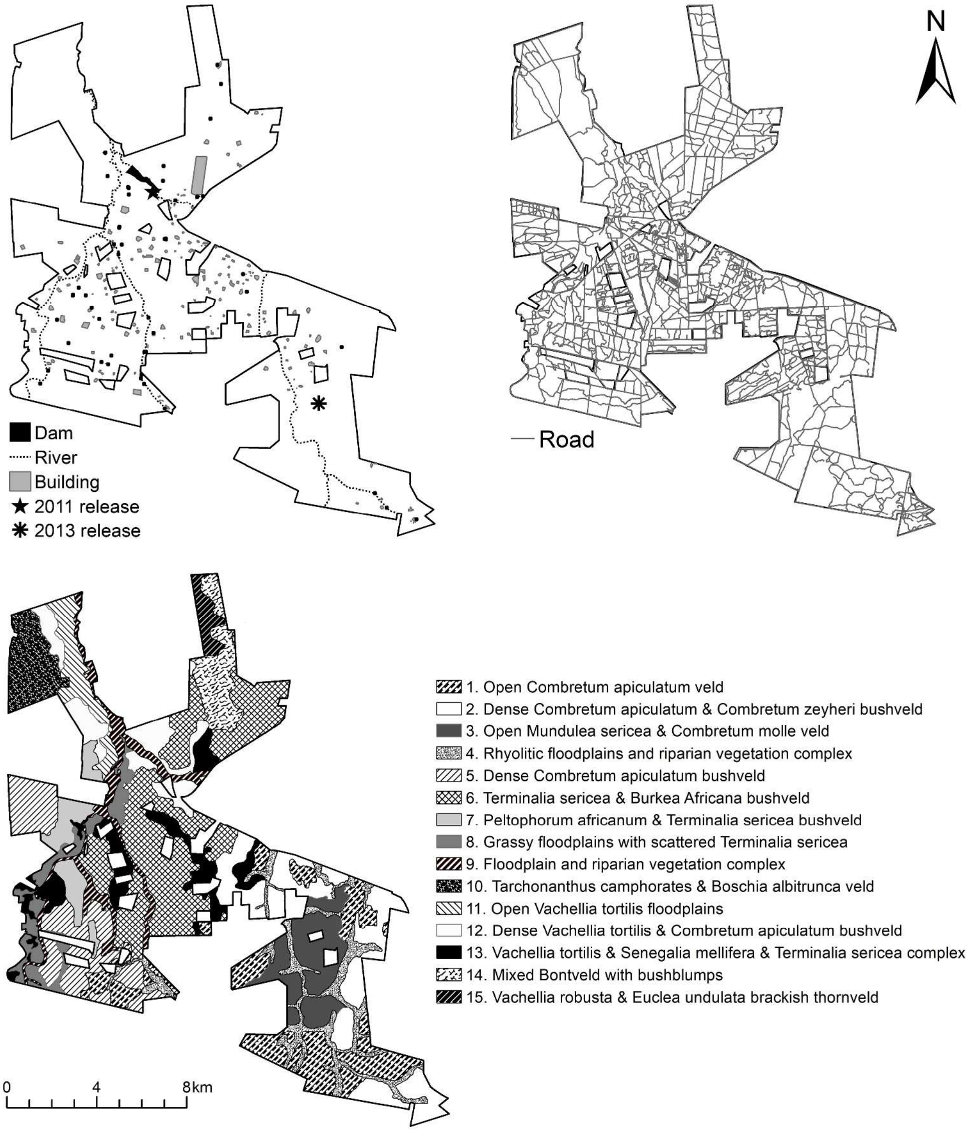

Figure 1. Maps of Dinokeng Game Reserve, Gauteng, South Africa.

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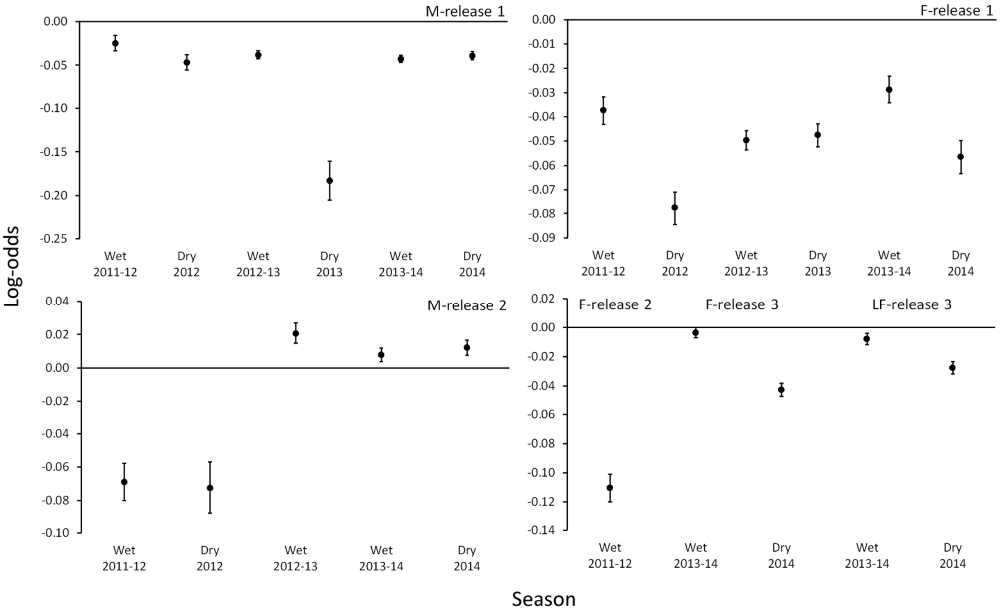

Figure 2. Regression estimates and 95% confidence intervals for elevation in the resource selection function of lion groups in Dinokeng Game Reserve, October 2011-September 2014.

790x484mm (72 x 72 DPI)

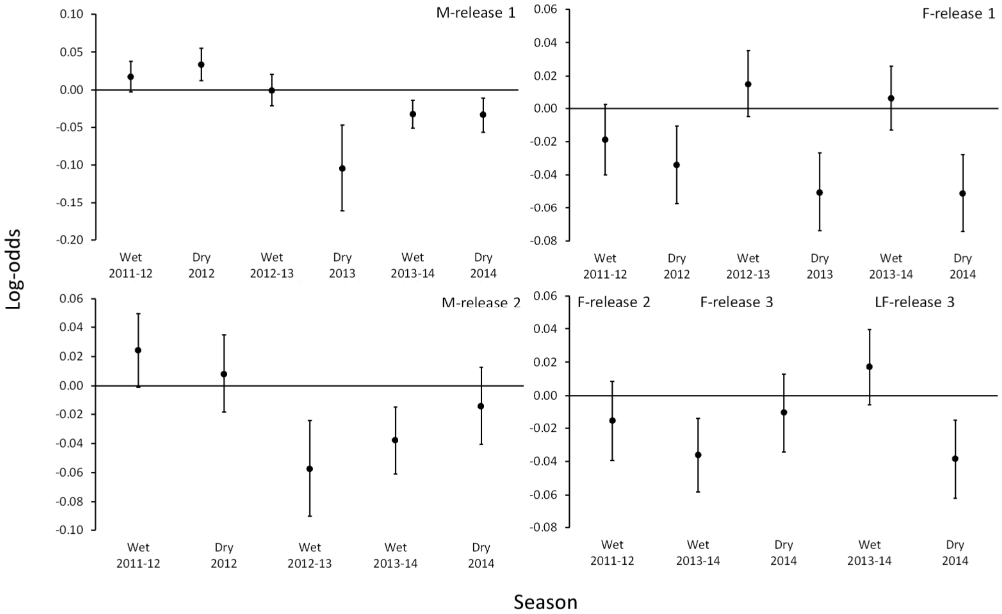

Figure 3. Regression estimates and 95% confidence intervals for slope in the resource selection function of lion groups in Dinokeng Game Reserve, October 2011-September 2014.

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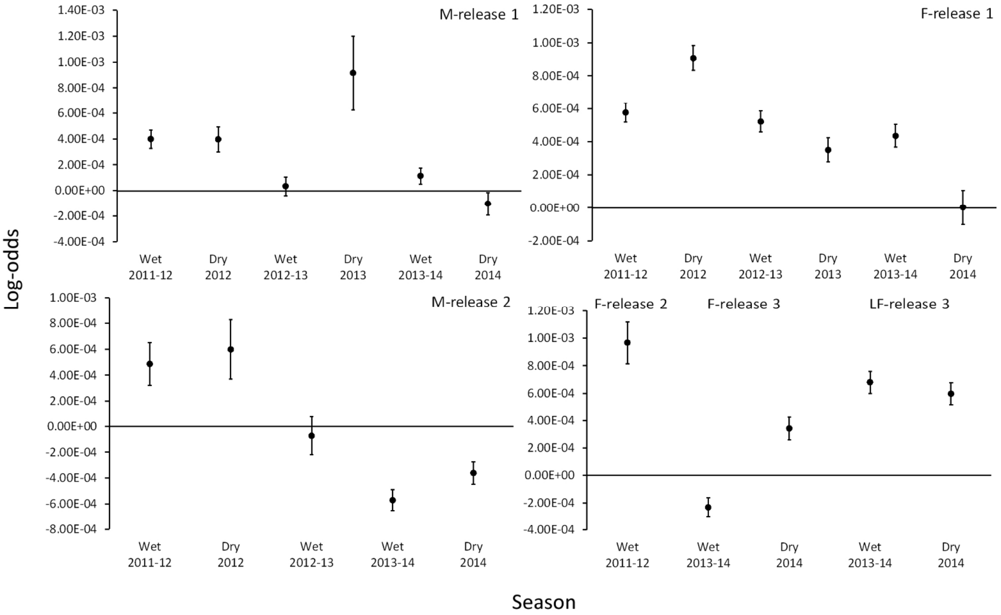

Figure 4. Regression estimates and 95% confidence intervals for distance to the nearest river in the resource selection function of lion groups in Dinokeng Game Reserve, October 2011-September 2014.

790x484mm (72 x 72 DPI)

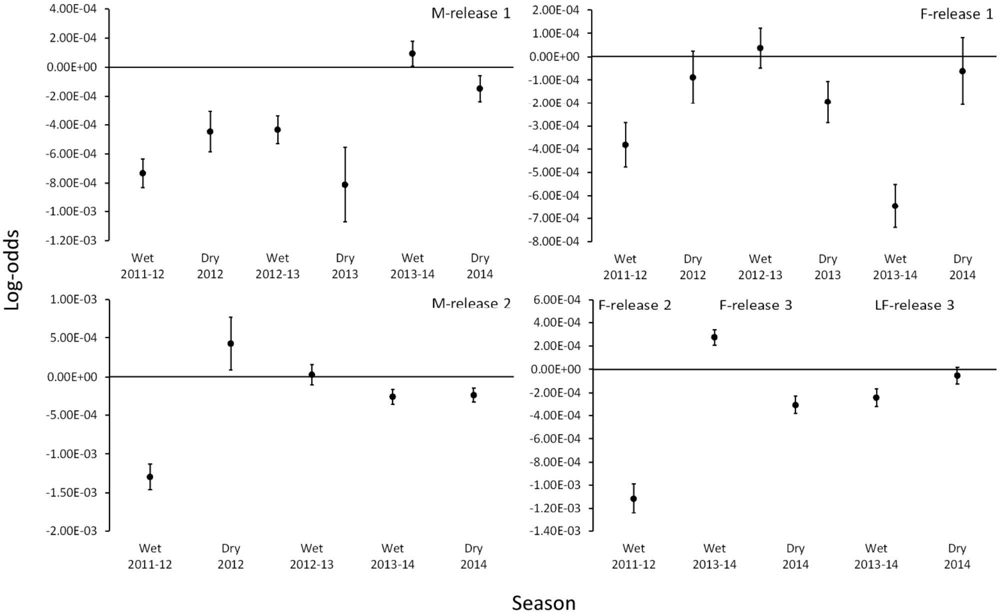

Figure 5. Regression estimates and 95% confidence intervals for distance to the nearest dam in the resource selection function of lion groups in Dinokeng Game Reserve, October 2011-September 2014.

790x484mm (72 x 72 DPI)

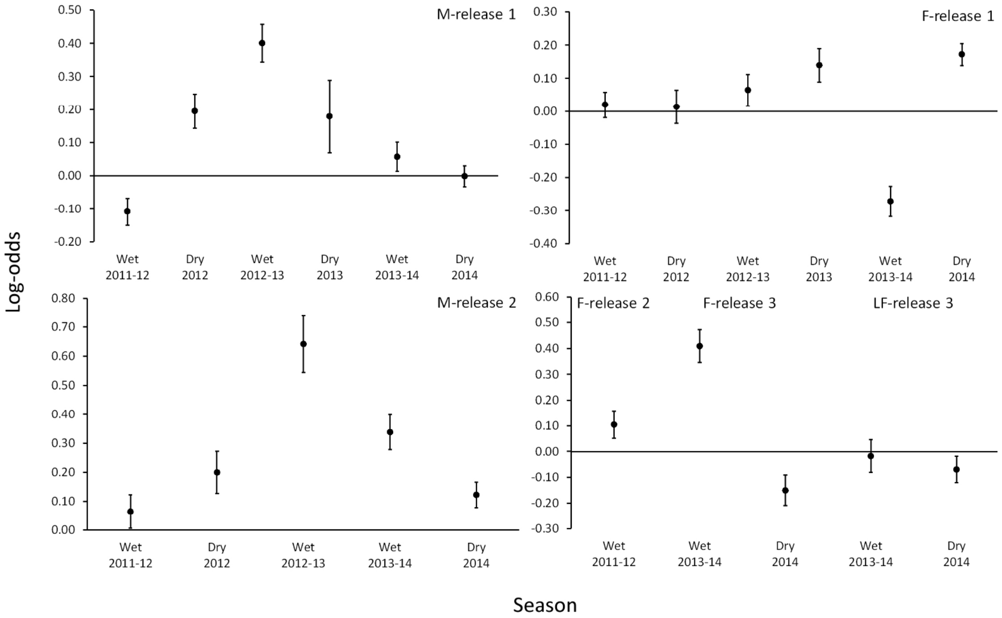

Figure 6. Regression estimates and 95% confidence intervals for vegetation continuous fields (VCF) in the resource selection function of lion groups in Dinokeng Game Reserve, October 2011-September 2014.

790x484mm (72 x 72 DPI)

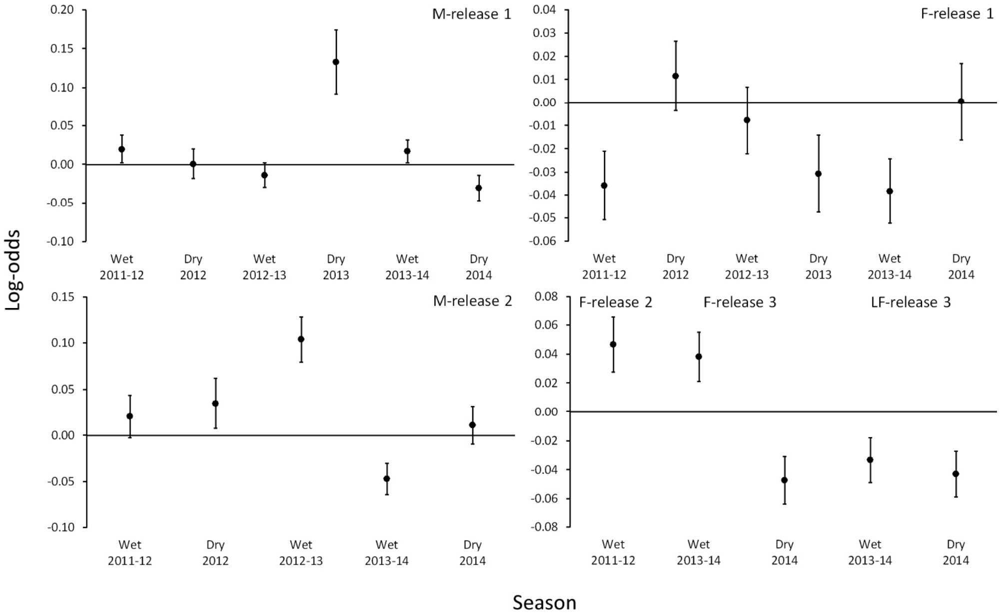

Figure 7. Regression estimates and 95% confidence intervals for road density in the resource selection function of lion groups in Dinokeng Game Reserve, October 2011-September 2014.

790x484mm (72 x 72 DPI)

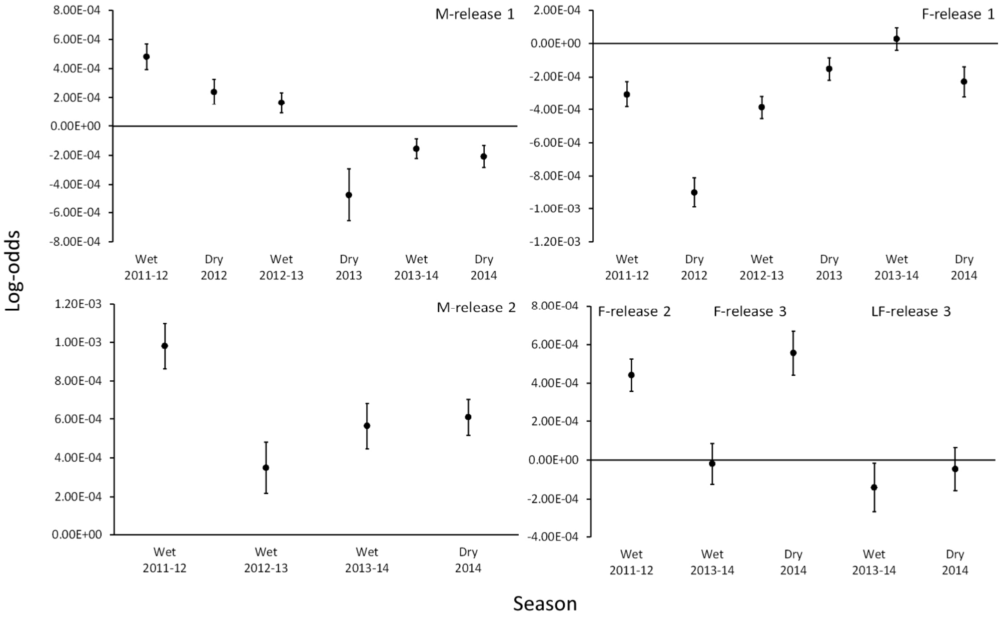

Figure 8. Regression estimates and 95% confidence intervals for distance to the nearest building in the resource selection function of lion groups in Dinokeng Game Reserve, October 2011-September 2014.

790x484mm (72 x 72 DPI)

Supplementary Materials

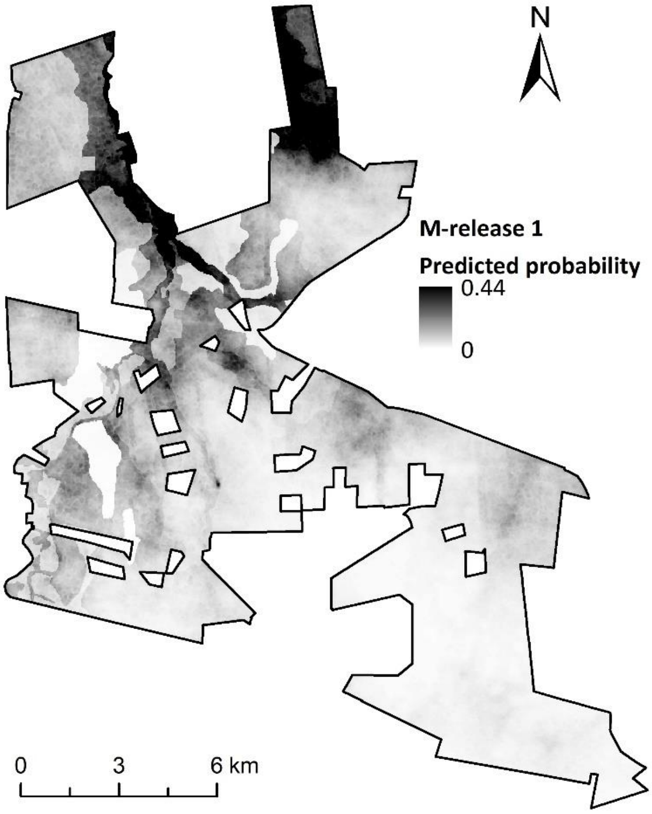

Figure S1. Predicted probability of occurrence of lion group M-release 1 in Dinokeng Game Reserve, wet season 2011-12.

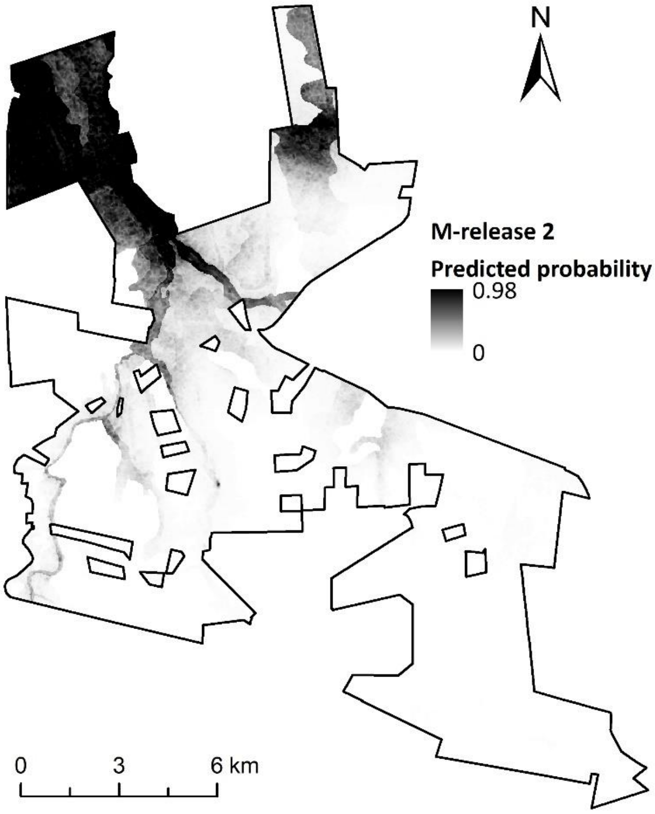

Figure S2. Predicted probability of occurrence of lion group M-release 2 in Dinokeng Game Reserve, wet season 2011-12.

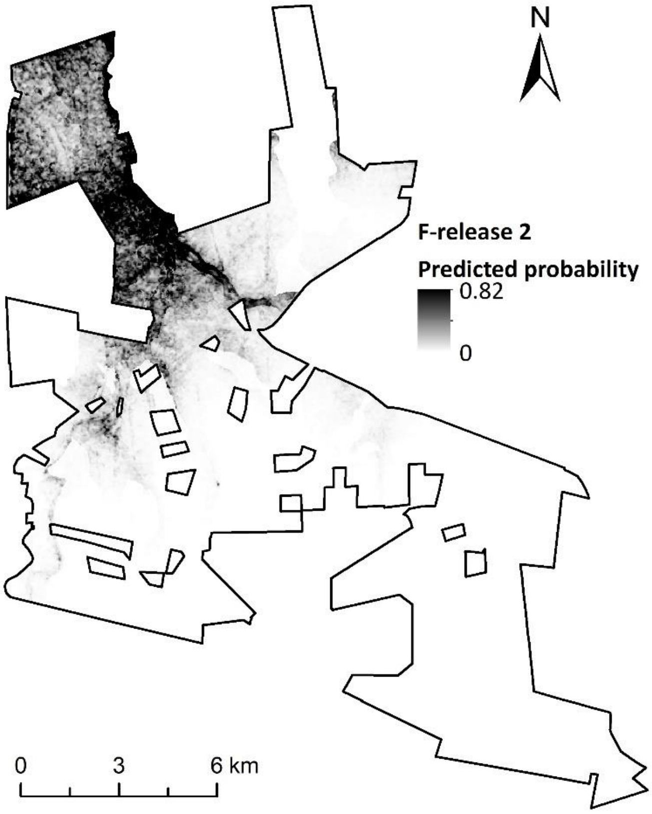

Figure S3. Predicted probability of occurrence of lion group F-release 2 in Dinokeng Game Reserve, wet season 2011-12.

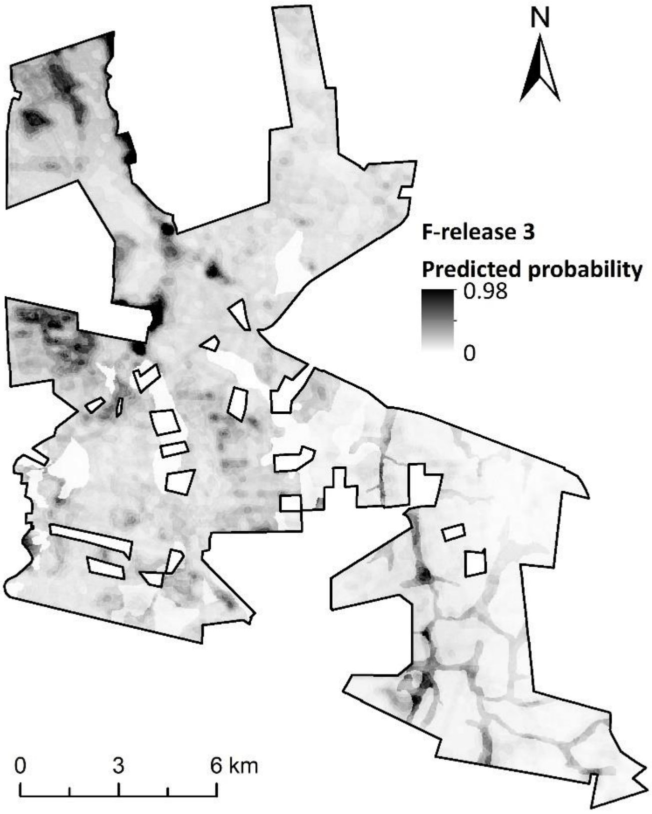

Figure S4. Predicted probability of occurrence of lion group F-release 3 in Dinokeng Game Reserve, wet season 2013-14.

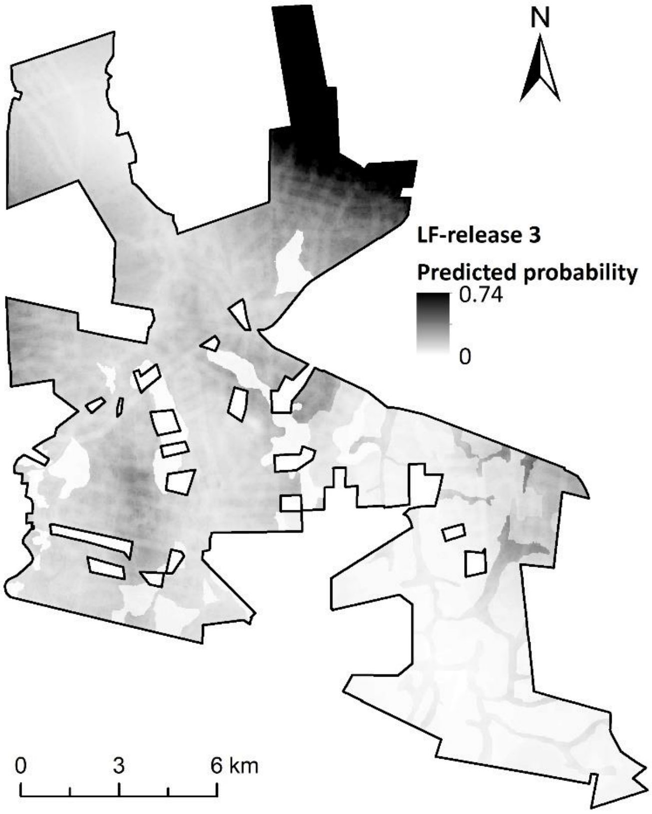

Figure S5. Predicted probability of occurrence of lion group LF-release 3 in Dinokeng Game Reserve, wet season 2013-14.

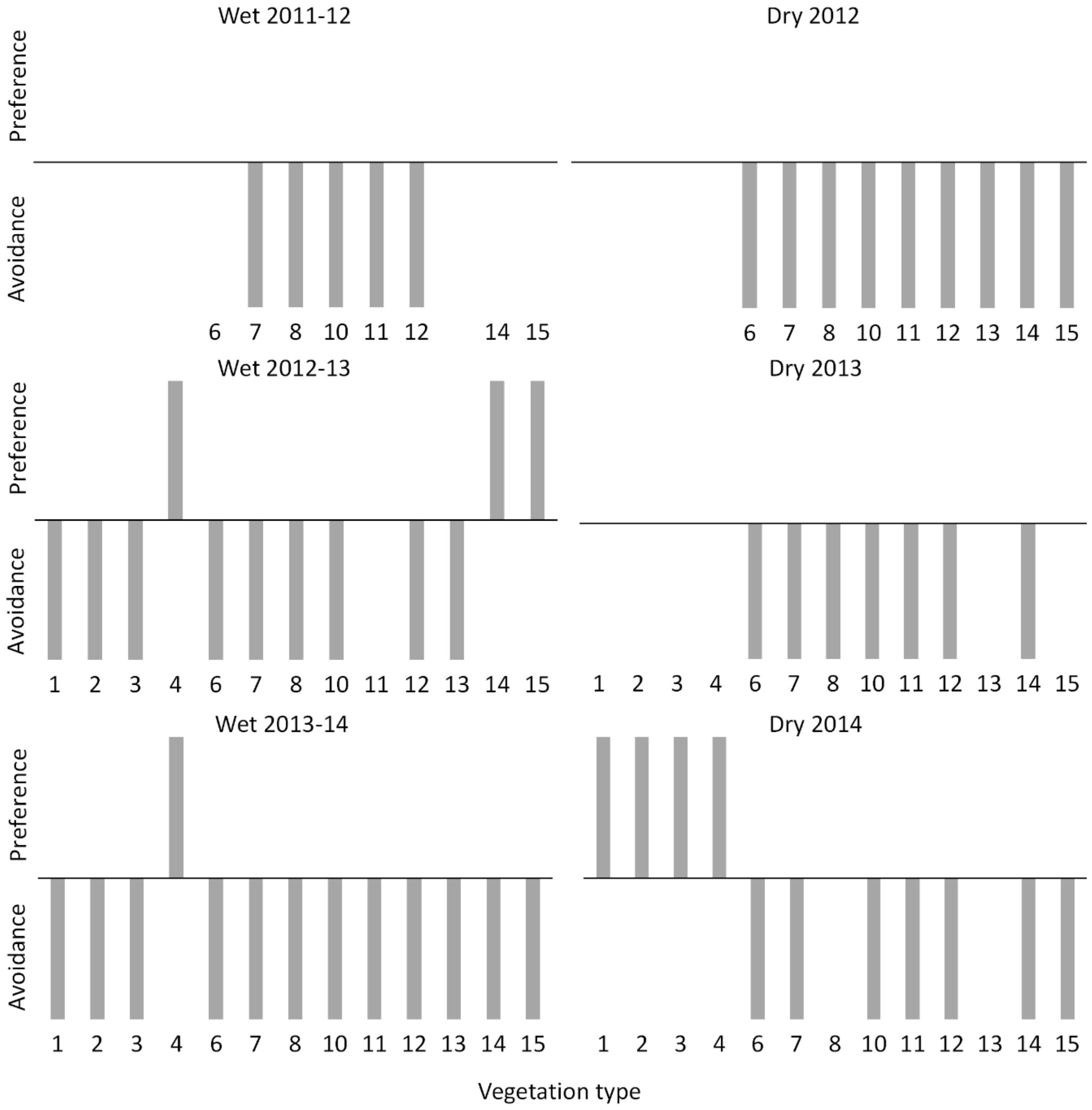

Figure S6. Vegetation selection by lion group M-release 1 in Dinokeng Game Reserve (reference level: type 9), 2011-14. Vegetation type numbers with no grey bars = no selection in comparison to the reference level.

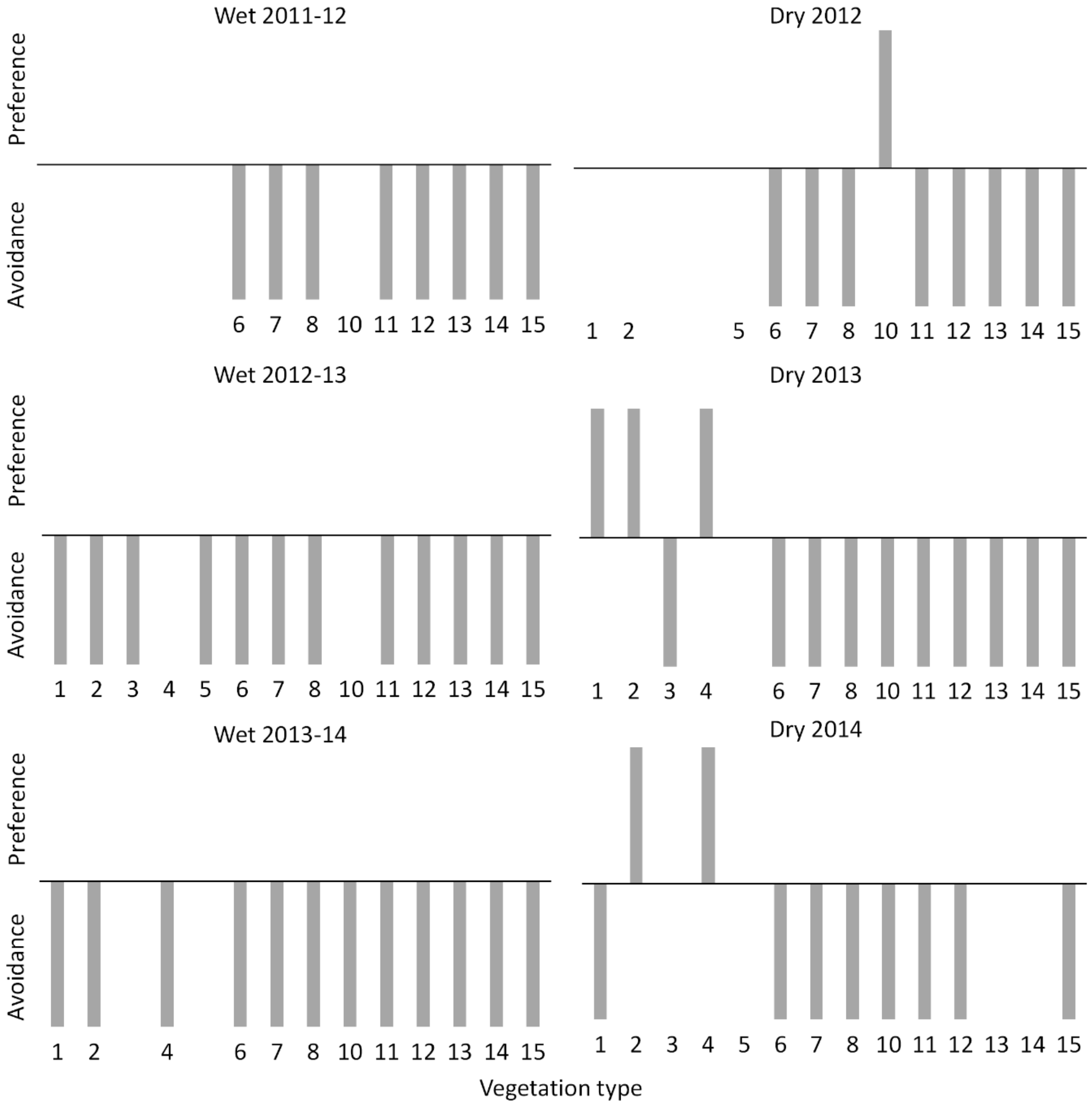

Figure S7. Vegetation selection by lion group F-release 1 in Dinokeng Game Reserve (reference level: type 9), 2011-14. Vegetation type numbers with no grey bars = no selection in comparison to the reference level.

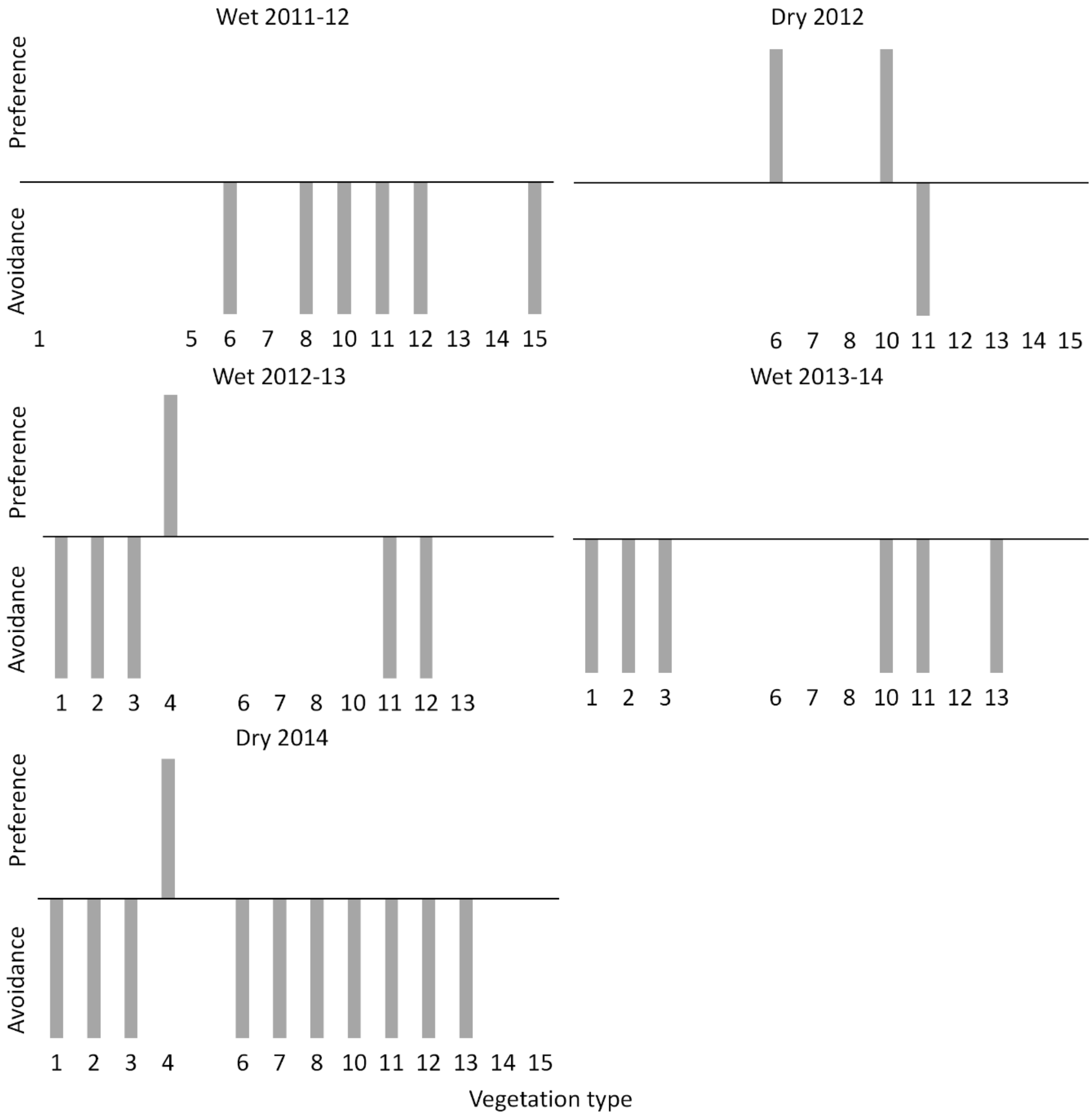

Figure S8. Vegetation selection by lion group M-release 2 in Dinokeng Game Reserve (reference level: type 9), 2011-14. Vegetation type numbers with no grey bars = no selection in comparison to the reference level.

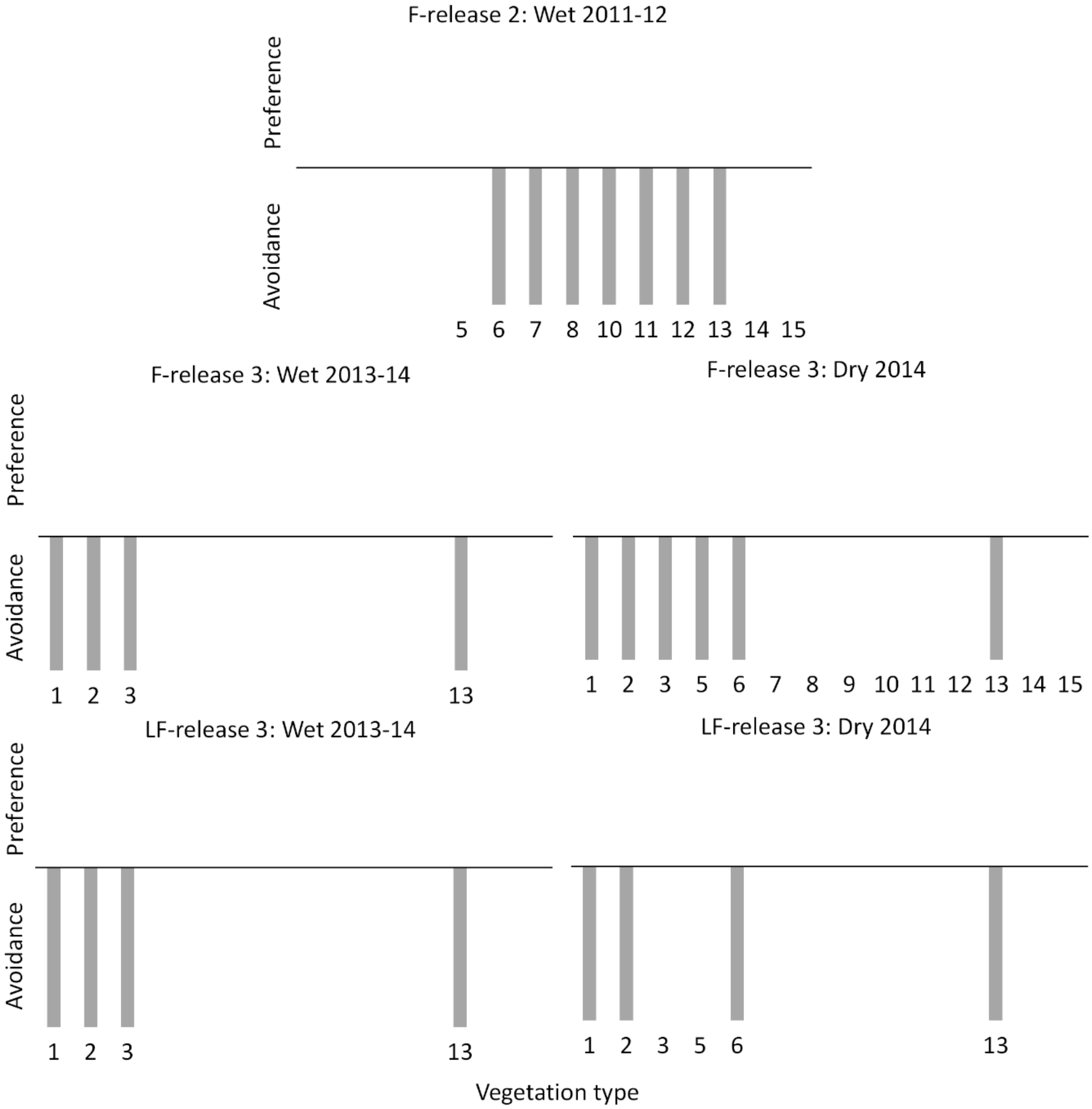

Figure S9. Vegetation selection by lion group F-release 2 (reference level: type 9), F-release 3 (reference level: type 4) and LF-release 3 (reference level: type 4) in Dinokeng Game Reserve (reference level: type 9), 2011-14. Vegetation type numbers with no grey bars = no selection in comparison to the reference level.