

## Use of site occupancy models for targeted monitoring of the cheetah

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## Abstract

The cheetah (*Acinonyx jubatus*) has suffered dramatic range contractions and population declines as a result of habitat degradation, prey depletion and conflict with humans. Of further concern is that many of Africa's remaining cheetah populations persist in human-dominated and highly fragmented landscapes, where their ecology is poorly understood and population data are lacking. Presence-absence surveys may be a practical means to collect these data, however, failing to account for detection error can lead to biased estimates and misleading inferences; potentially having deleterious consequences for species conservation. The goal of this study was to identify how an occupancy modelling technique that explicitly accounts for detectability could be used for quantifying cheetah status in human-impacted landscapes. Replicated camera-trap and track surveys of 100 km<sup>2</sup> sample units were used to estimate the proportion of area occupied by cheetah and to determine the survey effort required to inform conservation planning. Based on our results, 16 km (±SE = 12-22) of walking or 193 camera-trap nights (±SE = 141-292) are required to confirm cheetah absence at a given 100 km<sup>2</sup> grid cell (with 95% certainty). Accounting for detection resulted in an overall cheetah occurrence estimate of 0.40 (SE = 0.13), which is 16% higher than the traditional presence-absence estimate that ignores detection error. We test *a priori* hypotheses to investigate factors limiting cheetah using an occurrence probability model of their preferred prey. The results show that both cheetah and their prey were strongly negatively influenced by human settlements. Our study provides an unbiased estimate of occurrence that can be used to compare status across different sites and as a basis for long-term monitoring. Based on our results, we suggest that track and/or camera-trap surveys coupled with site occupancy models may be useful for targeted monitoring of cheetah across their distribution.

## Introduction

Prey depletion, habitat degradation and conflict with humans have resulted in considerable population declines and range contractions of the cheetah *Acinonyx jubatus* (Ray, Hunter & Zigouris, 2005). Of further concern is that many of Africa's remaining cheetah populations persist in human-dominated, highly fragmented landscapes where they are at risk of persecution (IUCN/SSC, 2007). Cheetah conservation management is hindered because few studies have investigated their ecology in human-impacted landscapes (but see Marker *et al.*, 2003).

Evidence-based management requires reliable population data as well as sound knowledge of the factors driving system change (Conroy & Carroll, 2009). A targeted monitoring approach that uses hypothesis testing to gain knowledge of the underlying mechanisms behind system change can be an efficient means to meet these goals (Yoccoz, Nichols & Boulinier, 2001).

Acquiring absolute abundance or density estimates for cheetah is both time and resource consuming and many of the required methodologies cannot be practically implemented across their distribution (Bashir *et al.*, 2004). The collection of presence-absence data is cost-effective and surveys can be implemented rapidly across large areas, however, neglecting to account for detection error can provide biased estimates and misleading inferences (Anderson, 2001; MacKenzie *et al.*, 2002). For example, detection error can lead to inaccurate species distribution models (Lobo, Jiménez-Valverde & Hortal, 2010), underestimates of areas where conservation interventions are required (Rondinini *et al.*, 2006) and distorted species-habitat relationships (Gu & Swihart, 2004). Efforts to standardize data collection methodologies cannot account for all heterogeneity in detection over space and time (Anderson, 2001; Yoccoz *et al.*, 2001; MacKenzie *et al.*, 2006).

Where absolute abundance estimates cannot be practically obtained, occupancy (i.e., the proportion of area occupied or probability of site use) is considered a robust alternative state variable (MacKenzie *et al.*, 2004; Karanth, Nichols & Kumar, 2004). Occupancy is a useful metric for assessing species status (Conroy & Carroll, 2009) and is a natural state variable for investigating species distribution, habitat relationships and meta-population dynamics. Since detection/non-detection data are relatively easy to obtain, occurrence models are useful for long-term monitoring programs and can be used to estimate the dynamic processes of local extinction and colonization (MacKenzie *et al.*, 2006). The occupancy models of MacKenzie *et al.*, (2002) use replicated detection/non-detection surveys to estimate a detection probability and derive unbiased estimates of occurrence. Hierarchical ranking of covariates are used to explain heterogeneity in occupancy and detectability simultaneously; thereby permitting the testing of ecological hypothesis and providing inferences about variables that affect distribution and resource selection (MacKenzie *et al.*, 2006).

The goal of this study was to identify how an occupancy modelling approach could be used to quantify cheetah status and to obtain inferences on the factors limiting their occurrence in a human-impacted landscape. We provide initial occupancy and detectability estimates for the species that can be used to explore sampling design trade-offs and illustrate how detection data can be used to design robust ecological studies and occupancy monitoring programs. Our study was conducted in the Limpopo National Park (LNP) in Mozambique, a legally protected area that is inhabited by both humans and livestock. LNP is potentially important habitat for cheetah because it borders on a protected population in the Kruger National Park (KNP) in South Africa, and could facilitate dispersal to other areas in Mozambique. However, prior to this study there had been no empirical investigation into cheetah status in the region. We applied replicated track

and camera-trap surveys across a 2400 km<sup>2</sup> study area to provide baseline data on the status of cheetah in LNP and test *a priori* hypotheses to investigate factors that may be limiting cheetah using an occurrence probability model of their preferred prey.

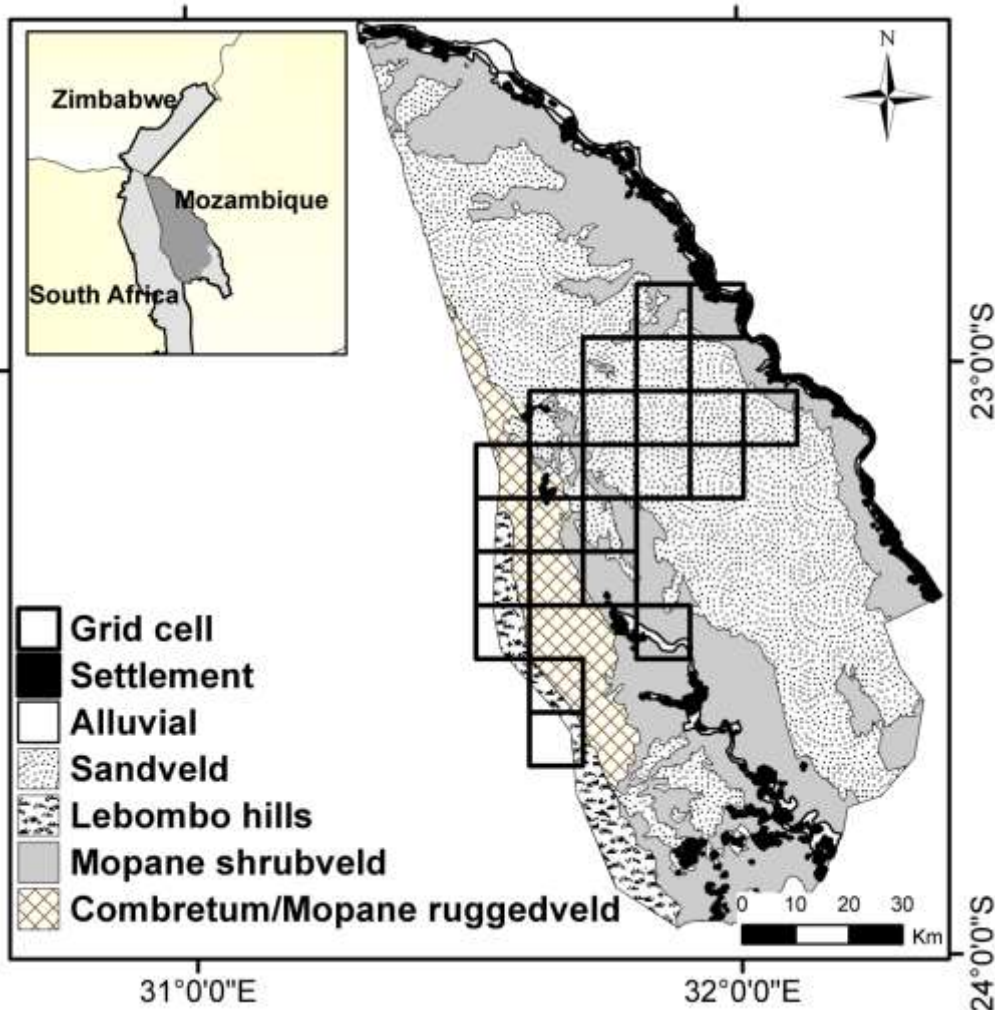
## Materials and Methods

### Study area

The 8, 238 km<sup>2</sup> LNP is located in south-western Mozambique and forms a component of the Greater Limpopo Transfrontier Park. South Africa's KNP forms the western boundary, characterized by high wildlife densities, and the Limpopo River forms the northern and eastern boundaries, characterized by human settlements and habitat degradation. LNP is inhabited by approximately 6,500 humans residing in eight villages located in the core area of the park (Huggins *et al.*, 2003) (Fig. 1). There is a limited road network and limited infrastructure. Settlements are characterized by free-grazing of livestock, packs of free-roaming domestic dogs (*Canis lupus familiaris*), land clearing for subsistence farming and 'bushmeat poaching' (illegal hunting of wildlife for local consumption). Large mammal populations were significantly depleted during armed conflict (1980-1992) in Mozambique (Hatton, Couto & Oglethorpe, 2001); however, the formation of LNP (2000) and removal of sections of fence along the KNP boundary provided the potential for movement of wildlife into the area.

As habitat generalists, cheetahs are able to persist in a broad array of woodland savannahs and were once widely distributed across southern Africa (IUNC/SSC, 2007). LNP comprises continuous woodland savannah plains with short to tall woodlands, shrublands and thickets. The

predominant landscape is sandveld, which is comprised of short woodlands and thickets on sandy substrates, characterized by the absence of well-defined drainage lines and the presence of pans (depressions flooded for long periods) (Stalmans *et al.*, 2004).



**Figure 1.** The Limpopo National Park (LNP) in Mozambique, bounded to the west by the Kruger National Park in South Africa, characterized by high wildlife densities, and to the east by the Limpopo River, characterized by human agro-pastoralist settlements; Surveyed grid cells overlaid across a gradient of distinguishing landscapes and settlement areas. Inset map: Location of LNP (dark grey) in relation to the Greater Limpopo Transfrontier Park (light grey) and to Zimbabwe and South Africa.

## Survey design

### Model assumptions and identification of covariates

In this study, the parameter of interest is the proportion of area occupied by cheetah, and the following assumptions of an occupancy ( $\Psi$ ) model are made: (1) Sites are closed to changes in occupancy (i.e., are either occupied or unoccupied *by the species* during the sampling period) (2) Detection histories at each site and survey are independent (3) Species are never falsely identified (4) Heterogeneity in occupancy and detection probability is modelled with covariates (MacKenzie *et al.*, 2006). Cheetah home ranges have been estimated at 126-185 km<sup>2</sup> in the adjoining KNP (Broomhall, Mills & du Toit, 2003). To interpret our estimator ( $\Psi$ ) as the proportion of area occupied, we defined sample units (sites) as 10 x 10 km grid cells, considering this a conservative size to assume that if cheetah were detected within a grid cell the entire unit was occupied, but large enough to minimize the risk of spatial autocorrelation among neighbouring grid cells. Our survey design was limited by lack of accessibility to large portions of LNP. Given these constraints, we selected 24 grid cells to be surveyed such that the resulting area represented approximately one third of LNP and followed a gradient of distinguishing biophysical features and thus incorporated important environmental strata (Fig. 1).

Cheetahs become independent of their mother at approximately 18 months, but will often remain in their natal range for several additional months. Males are known to centre their territories on areas where females cluster around prey resources (Caro, 1994). To minimize the chance that an unoccupied cell would become colonized by dispersers or that an occupied cell would become permanently vacated by the species during our survey, we sampled over a 5 month period (May 7 to October 13, 2012) in the dry season.

The utilization of multiple detection methods may increase survey efficiency and the probability of detecting low density carnivores (O'Connell & Bailey, 2011). We chose to use

two sampling methodologies; camera-traps and track transects. Sample occasions were represented by 14 day camera-trap surveys and temporally replicated 3 km track transects (replicates separated by  $\geq 14$  days). Twenty grid cells were sampled with cameras ( $\bar{x} = 90$  camera-trap nights/grid cell) and 23 were sampled with track surveys ( $\bar{x} = 13$  km/grid cell). We note that the occupancy model accounts for unequal sampling across sites (MacKenzie *et al.*, 2002). Due to the limited road network, track transects were conducted along game trails on foot. Within each grid cell, camera stations ( $\bar{x} = 2$ ) and/or fixed length track transects ( $\bar{x} = 2$ ) were established to optimize spatial representation. Grid cells were sub-divided into quadrants and one from each cell was randomly selected for obligate sampling. Because of logistical constraints three cells were sampled in only one quadrant while the rest were sampled in 2-4. Multiple surveys were not conducted within the same quadrant over the same 14 day interval. Detections were represented by unambiguously identified cheetah tracks or photographs.

We identified three predictor variables (covariates) to explain heterogeneity in cheetah occurrence in LNP. These were prey resource, anthropogenic pressure and landscape structure for prey capture (Table 1). We investigated the influence of prey availability on cheetah occurrence using a probability of occurrence model of their main prey species. The preferred prey of cheetah in the region are impala (*Aepyceros melampus*) (Hayward *et al.*, 2007), which are a non-migratory, comparatively abundant antelope (Estes, 1992). We assume that our occurrence probability model is biologically representative of the encounter probability of preferred prey for cheetah.



**Table 1** Predictor variables (covariates) expected to influence cheetah occupancy, their unit, relationship to cheetah fitness, range of values and *a priori* prediction of the direction of impact.

<b>Covariates (unit)</b>	<b>Relationship to cheetah fitness</b>	<b>Range of values (mean)</b>	<b><i>A priori</i> prediction</b>
Preferred prey (occurrence probability)	Encounter probability of food resources	0.11-0.79 (0.44)	+
Agro-pastoralist settlement (km)	Persecution from livestock herders, harassment from domestic dogs, loss of cover	2.01-20.41 (11.17)	-
Open habitat patches (%)	Landscape structure for prey capture (large edge for concealment and suitable terrain for high speed chase)	0.09-5.85 (2.63)	+

A prey occupancy model for the probability of impala site use ( $\Psi$ ) was developed for each grid cell based on detection/non-detection surveys of 260 sites ( $\bar{x} = 11/$  grid cell) conducted during September 9, 2011-October 13, 2012. Sampling occasions ( $\bar{x} = 5$  /site) were represented by temporally replicated 1 km transects ( $n = 602$ ) or by 7 day camera-trap intervals ( $n = 666$ ). Detections were represented by sightings of impala along transects or photographs recorded by camera-traps. Of the 260 sites, 184 were sampled only by transects, 48 were sampled by both a transect and a camera station and 28 were sampled only by camera-traps. Where sites were surveyed by both methods during the same 7 day interval, occasions/detections were pooled. We note that the closure assumption could be relaxed because our parameter of interest was site use (MacKenzie *et al.*, 2006). An impala occupancy model was developed from 360 camera-trap

detections and 154 sightings along transects (maximum value = 1). To explain heterogeneity in impala site use, we included landscape covariates based on vegetation communities, in addition to the proximity to water and to agro-pastoralist settlements (Table 2). Mean impala occurrence for each grid cell was extracted using Spatial Analyst ArcGIS 9.3.1 from the inverse weighted distance of impala  $\hat{\Psi}$ .

Other than prey resources, cheetah may also be influenced by anthropogenic factors including persecution by livestock herders, accidental snaring (IUCN/SSC, 2007) and harassment from domestic dogs. We considered the proximity to human-settlements as a proxy for these factors, calculated as the mean Euclidean distance of each 30 m x 30 m pixel in a grid cell to the nearest human settlement using Spatial Analyst ArcGIS 9.3.1.

Cheetahs are specialized predators, requiring concealment for stalking and suitable terrain for short high-speed chases (Estes, 1992). In woodland savannahs where there is adequate cover for concealment, cheetahs have been shown to center their territories on more open habitats (Broomhall *et al.*, 2003). LNP is characterized by continuous woodland, shrubland or bushland with small, discrete open patches of land (i.e., pans) (Stalmans *et al.*, 2004). Considering that these features may be limiting for cheetah, we included a covariate ‘open habitat patches’ as proxy for the landscape structure offering suitable prey capture. The proportion of a grid cell represented by open habitat patches was evaluated using remotely sensed data of landscape cover classified as ‘bare’ or ‘grassland’ (Peace Parks Foundation, Stellenbosch).

**Table 2** Predictor variables (covariates) expected to influence impala site use in the Limpopo National Park, Mozambique, their description and value.

<b>Covariate</b>	<b>Description</b>	<b>Value</b>
Mopane shrubveld	Shrublands and thickets on calcareous soils	1 or 0
Sandveld	Short woodlands and thickets on sandy substrates	1 or 0
Lebombo Hills	Short woodland to tall shrubland on stony, rhyolite soils, undulating hills	1 or 0
Combretum/Mopane Ruggedveld	Short to tall woodlands and tall shrublands on shallow clay soils	1 or 0
Water	Drainage lines/seepage points	Proximity (km)
Anthropogenic	Cultivation and livestock grazing (agro-pastoralist settlements)	Proximity (km)

### Data collection

Fixed length, 3 km track transects were walked on suitable substrate by LA and KE during morning and afternoon hours. One digital remote camera (Reconyx HC500, Bushnell Trophy Cam, or SpyCam) was placed at each camera station approximately 0.15 m from the ground, towards the trail. Sampling (hereafter surveys) were conducted where one would expect to find cheetah if they were present (i.e., trails, waterholes, open habitat patches). Male cheetah exhibit scent-marking behaviour and will deposit their faeces and urine on conspicuous objects (e.g., termite mounds, fallen trees or exposed rocks) (Caro, 1994). We actively searched for locations that cheetahs may have scent-marked in an effort to increase the probability that they would be detected.

## Data analysis

The maximum likelihood estimates for cheetah and impala occupancy ( $\Psi$ ) and detection probability ( $p$ ) were estimated in program PRESENCE ver 4.4 using single season occupancy models.

### *Prey occupancy model*

Impala detection histories from camera and track surveys were compiled into a single detection matrix for each site ( $n = 260$ ), assigning a '1' for surveys where impala were detected and '0' where impala were not detected. Following this, a survey-specific matrix was constructed to account for differences in sampling methods, recording a '1' for camera-trap surveys and a '0' for transect surveys (excluding pooled samples). An additional survey-specific matrix was constructed, recording a '1' for occasions represented by both a camera-trap and a transect survey (pooled samples) and a '0' for occasions represented by only one method. Finally, a survey-specific matrix was constructed, recording a '1' or '0' for surveys conducted during wet (November 1-April 30) and dry (May 1-October 31) seasons, respectively. Continuous variables were assessed for collinearity ( $r = 0.5$ ) prior to inclusion into models (none found) and were standardized using a z-transformation. Akaike's Information Criterion adjusted for small sample sizes (AICc) (Burnham & Anderson, 2002) was used in the model selection procedure to rank the relative support for different models in order of parsimony, with the effective sample size defined conservatively as the number of sites. First, we considered covariates for impala detectability ( $p$ ). We include survey method (Mm), pooled samples (Mp) and season (SN) as covariates for impala  $p$  in subsequent analysis of impala site use ( $\Psi$ ); models containing these covariates were strongly supported ( $\sum w > 0.99$ ;  $\Delta AICc < 2$ ) and ranked higher than the constant model ( $\Delta AICc =$

12.77). To determine the factors that best explained impala occurrence, we compared all possible combinations of  $\Psi$  covariates ( $n = 63$  models). AICc weights were used to evaluate the weight of evidence for each model, and were summed for all models containing each predictor variable. Variables resulting in high summed model weights were considered more important in explaining heterogeneity in occupancy. Parameter estimates were obtained from a 95% confidence set ( $\sum w > 0.95$ ) using a model-averaging technique. Goodness of fit for the general model was tested using chi-square tests and 10,000 boot strap samples (Burnham & Anderson, 2002)

### *Cheetah occupancy model*

Cheetah detection histories from camera and track surveys were compiled into a single detection matrix for each sample unit (100 km<sup>2</sup> grid cell,  $n = 24$ ), assigning a '1' for surveys where cheetah were detected, and a '0' where cheetah were not detected. Following this, a survey-specific matrix was constructed to account for differences in sampling methods (as above). Five scent-marking sites were located in three grid cells over the survey period. Considering that multiple detections at these sites were likely due to a dependent behavioural response, we applied a 'removal design' as recommended by MacKenzie *et al.* (2006); removing surveys conducted at scent-marking sites after cheetah were first detected.

To investigate factors that may be limiting cheetah occurrence in LNP, we used AICc to compare a simple set of three univariate models representing our *a priori* hypothesis (Table 1) to the model that accounts for variation in detectability with survey method,  $\Psi(.)p(M)$  (the inclusion of method outranked the constant model ( $\Delta AICc = 6.45$ )). Models with  $\Delta AICc < 2$  were considered more strongly supported (Burnham & Anderson, 2002). The above mentioned procedures for parameter estimation and goodness of fit were applied.

To provide data that can be used to design occupancy surveys for cheetah, we generated detectability curves and calculated the minimum number of surveys required to infer absence with a given certainty. The probability  $P_k$  of detecting cheetah at least once at an occupied site after  $k$  repeat surveys was calculated as  $P_k = 1 - (1 - p)^k$  where  $p$  is the per-survey detection probability of the species MacKenzie & Royle, (2005). Following this, the minimum number of surveys required ( $N_{min}$ ) to infer cheetah absence with a 95% certainty was calculated as (Kéry, 2002):  $N_{min} = \log(0.05) / \log(1 - p)$ . We estimated the optimal number of sites ( $S$ ) to survey to achieve a given model precision in the occupancy estimate for  $\Psi = 0.2-0.9$  using MacKenzie & Royle (2005):

$$S = \frac{\psi}{\text{Var}(\hat{\psi})} \left[ (1 - \psi) + \frac{(1 - p^*)}{p^* - Np(1 - p)^{N_{min}-1}} \right]$$

Where  $p^*$  is the expected probability of detecting cheetah at least once (i.e.,

$$p^* = 1 - (1 - p)^{N_{min}} \text{ where } p \text{ is the averaged parameter estimate of cheetah detectability}).$$

## Results

A total survey effort of 1903 camera trap nights across 47 camera stations and 303 km of transects resulted in 60 cheetah photographic events and 22 sets of cheetah tracks. The final data set consisted of 197 surveys, with each cell sampled on  $\bar{x} = 8$  occasions ( $\bar{x} = 5$  camera,  $\bar{x} = 4$  track).

### *Prey occupancy model*

The factor contributing the most to impala site use was proximity to agro-pastoralist settlements ( $\sum w = 0.96$ ; Table 3), which strongly decreased with increasing proximity ( $\hat{\beta} = -1.569$ , SE 0.385; Table 4; Fig. 2). The model averaged estimate of impala detectability was  $<1$  ( $\hat{p} = 0.285$ , SE = 0.038) and the overall estimate of occurrence was  $\hat{\Psi} = 0.482$  (SE = 0.090), or impala used approximately 48% of the sites we surveyed. Impala occurrence was significantly higher in the Lebombo hills ( $\hat{\beta} = 1.511$ , SE = 0.558) than in the other landscapes (Table 4). There was no evidence of lack of fit ( $p = 0.22$ ) or overdispersion ( $\hat{c} = 1.09$ ).

**Table 3** Model selection procedure for factors influencing impala site occupancy ( $\Psi$ ) in the Limpopo National Park, Mozambique. Covariates considered are mopane shrubveld (MS), Lebombo hills (LH), combretum/mopane ruggedveld (CM), sandveld (SV), agro-pastoralist settlements (S) and water (W). Impala detectability (p) varies with method (Mm), pooled samples (Mp) and season (SN). Number of sites = 260.

Model	AICc	$\Delta$ AICc	w	k	-2L
$\Psi$ (S,MS,CM,SV)p(Mm,Mp,SN)	770.13	0.00	0.27	9	751.41
$\Psi$ (S,CM,LH)p(Mm,Mp,SN)	771.05	0.92	0.17	8	754.48
$\Psi$ (S,CM,LH,SV)p(Mm,Mp,SN)	771.71	1.58	0.12	9	752.99
$\Psi$ (S,LH,SV)p(Mm,Mp,SN)	771.72	1.59	0.12	8	755.15
$\Psi$ (S,CM,LH,W)p(Mm,Mp,SN)	773.03	2.90	0.06	9	754.31
$\Psi$ (S,CM,LH,MS)p(Mm,Mp,SN)	773.08	2.95	0.06	9	754.36
$\Psi$ (S,CM,SV,W)p(Mm,Mp,SN)	773.80	3.67	0.04	9	755.08
$\Psi$ (S,CM)p(Mm,Mp,SN)	773.91	3.78	0.04	7	759.47
$\Psi$ (S,CM,SV)p(Mm,Mp,SN)	775.54	5.41	0.02	8	758.97
$\Psi$ (S,CM,MS)p(Mm,Mp,SN)	775.61	5.48	0.02	8	759.04
$\Psi$ (S,CM,W)p(Mm,Mp,SN)	775.64	5.51	0.02	8	759.07
$\Psi$ (S,CM,MS,SV)p(Mm,Mp,SN)	776.37	6.24	0.01	9	757.65
$\Psi$ (.)p(Mm,Mp,SN)	795.81	25.68	0.00	5	785.57

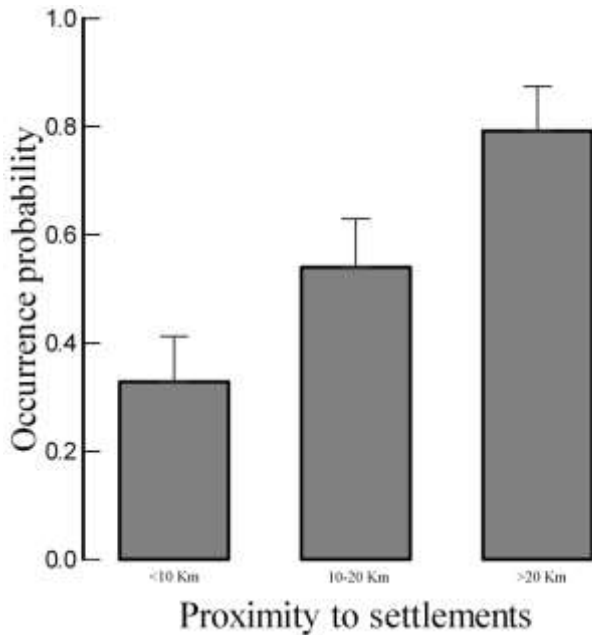
AICc values; the relative difference in AICc values between each model and the model with the lowest AICc ( $\Delta$ AIC); AICc model weights (w); the number of parameters in the model (k); twice the negative log-likelihood (-2L). (.) assumes the parameter is constant.

**Table 4** Covariates influencing impala site use ranked according to their relative contribution (summed model weights  $\sum w$ ),  $\beta$ -coefficients and associated standard errors (SE).

Covariate	$\hat{\beta}$	SE	$\sum w$
Agro-pastoralist settlements	<b>-1.569</b>	<b>0.385</b>	0.96
Combretum/Mopane	<b>-3.398</b>	<b>0.938</b>	0.85
Sandveld	<b>-1.894</b>	<b>0.672</b>	0.59
Lebombo hills	<b>1.511</b>	<b>0.558</b>	0.52
Mopani shrubveld	-1.229	0.654	0.36
Water	0.114	0.258	0.12

+/- sign indicates direction of influence; bold entries indicate robust impact ( $\beta \pm 1.96 \times SE$  not overlapping zero).

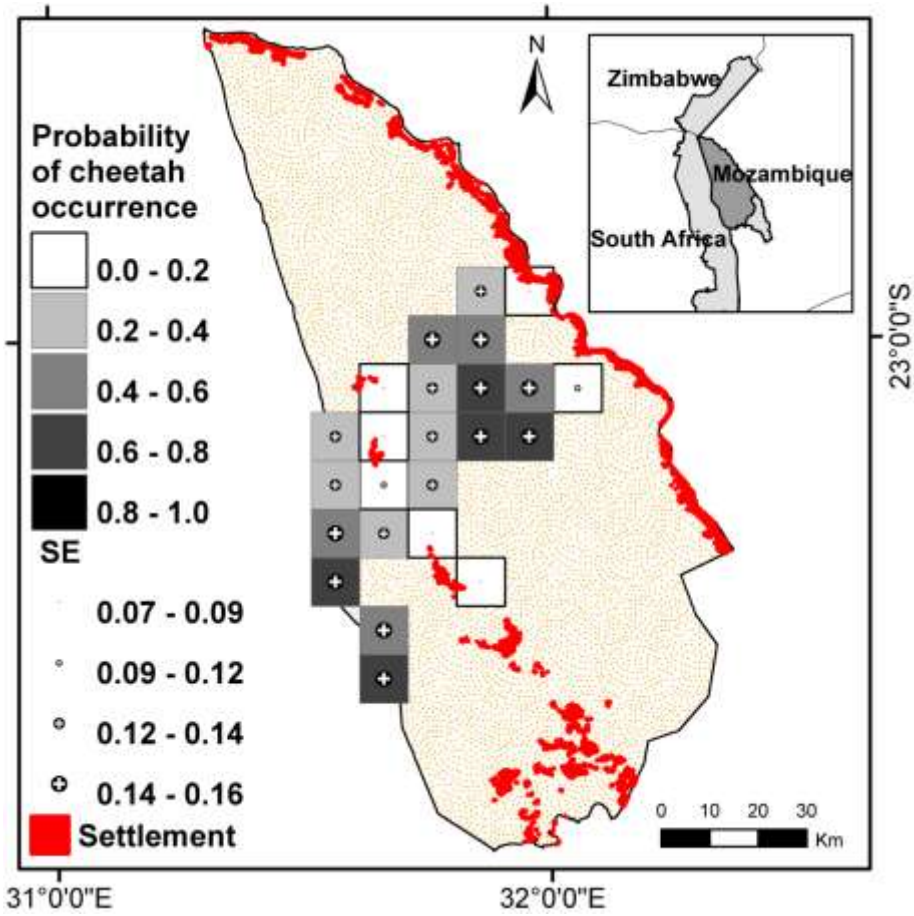




**Figure 2.** Influence of agro-pastoralist settlements use on the occurrence probability of cheetahs preferred prey. Site occupancy estimates are based on the averaged model ( $\sum w > 0.95$ ). Error bars show +SE.

### *Cheetah occupancy and detectability*

Given presence in a grid cell, the probability of detecting cheetah on a single survey was  $< 1$ ,  $\hat{p} = 0.295$  (SE = 0.076) (Table 5). Accounting for detectability resulted in a model averaged ( $\sum w > 0.95$ ) estimate of  $\hat{\Psi} = 0.395$  (SE = 0.129), or cheetah occupied approximately 40% of a 2400 km<sup>2</sup> sample of potential habitat. This estimate is 16% higher than the naïve estimate (0.333) that fails to account for detection error. We mapped the variation in site occupancy estimates of cheetah across grid cells (Fig. 3).



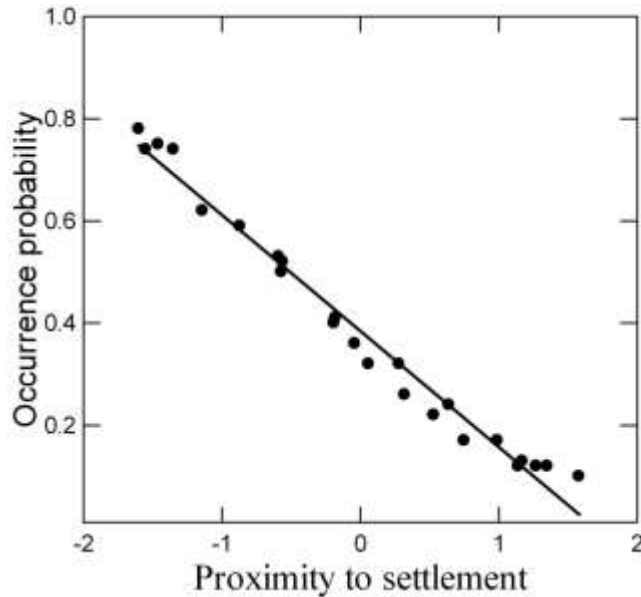
**Figure 3.** Spatial variation in site occupancy ( $\Psi$ ) estimates of cheetah and associated standard errors (SE) in the Limpopo National Park, Mozambique. Estimates are based on the averaged model ( $\sum w > 0.95$ ) from 197 surveys. Probability of occurrence accounting for occurrence probability of preferred prey and agro-pastoralist use and accounting for variation in detection probability

There was considerable support for the hypothesis that human disturbance was a limiting factor of cheetah occurrence ( $\Delta\text{AICc} < 2$ ;  $\sum w = 0.69\%$ ). Cheetah occurrence strongly decreased with proximity to settlements ( $\hat{\beta} = -1.599$ ,  $\text{SE} = 0.781$ ; Fig. 4). Mean site occupancy was  $\hat{\Psi} = 0.558$  ( $\text{SE} = 0.145$ ) at sites that were  $>10$  km from settlements ( $n = 13$ ) compared to  $\hat{\Psi} = 0.179$  ( $\text{SE} = 0.101$ ) at sites that were  $<10$  km from settlements ( $n = 11$ ). Cheetah occurrence was greater in grid cells with greater impala occurrence ( $\beta = 1.062$ ,  $\text{SE} = 0.630$ ), however, there was less support for the prey hypothesis ( $\Delta\text{AICc} = 3.01$ ), which only slightly outperformed the constant model ( $\Delta\text{AICc} = 3.80$ ). There was little evidence that cheetah were limited by per cent openness at this spatial scale ( $\Delta\text{AICc} = 6.34$ ;  $\hat{\beta} = -0.285$ ,  $\text{SE} = 0.480$ ). A goodness of fit test showed no evidence of lack of fit ( $p = 0.56$ ) or overdispersion ( $\hat{c} = 0.25$ ).

**Table 5** Model selection procedure for factors influencing cheetah site occupancy ( $\Psi$ ) obtained from 197 surveys of 24 (100 km<sup>2</sup>) grid cells in the Limpopo National Park, Mozambique. Hypothesis considered are the influence of prey (P) agro-pastoralist settlements (S) and open-habitat patches (O). Cheetah detectability (p) varies with survey method (M).  $\Psi(\cdot)$  assumes the parameter is constant.  $\beta$  coefficients for the variables direction and strength of influence on  $\Psi$  are also shown.

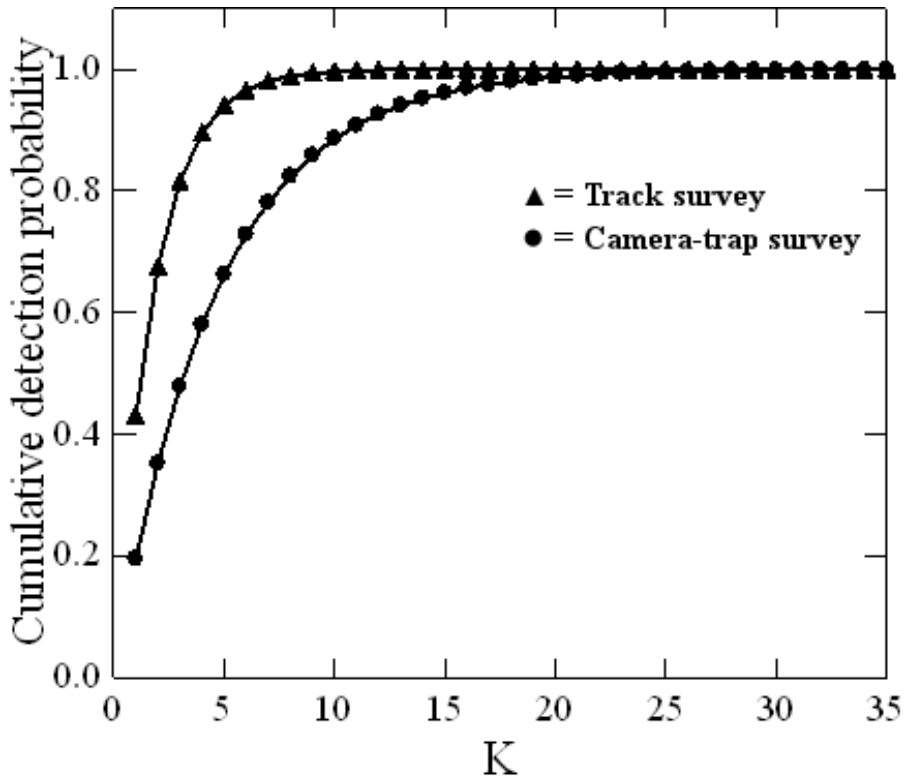
Model	AICc	$\Delta\text{AICc}$	w	K	-2L	$\hat{\Psi}(\text{SE})$	$\hat{p}(\text{SE})$	$\hat{\beta}(\text{SE})$
$\Psi(\text{S}) \text{ p}(\text{M})$	113.27	0.00	0.69	4	103.16	0.40(0.13)	0.29(0.08)	<b>-1.60 (0.78)</b>
$\Psi(\text{P}) \text{ p}(\text{M})$	116.28	3.01	0.15	4	106.17	0.40(0.13)	0.30(0.08)	1.06 (0.63)
$\Psi(\cdot) \text{ p}(\text{M})$	117.07	3.80	0.10	3	109.87	0.39(0.11)	0.30(0.08)	
$\Psi(\text{O}) \text{ p}(\text{M})$	119.61	6.34	0.03	4	109.50	0.39(0.15)	0.29(0.08)	-0.29 (0.48)
$\Psi(\cdot) \text{ p}(\cdot)$	119.72	6.45	0.03	2	115.15	0.41(0.12)	0.29(0.06)	
<b>Model Average</b>						<b>0.40(0.13)</b>	<b>0.30(0.08)</b>	

Model AICc values; the relative difference in AICc values between each model and the model with the lowest AICc ( $\Delta\text{AICc}$ ); AICc model weights (w); the number of parameters in the model (k); twice the negative log-likelihood (-2L); mean estimated occupancy ( $\hat{\Psi}$ ) and detectability ( $\hat{p}$ ) parameters; associated standard errors (SE). Bold entries for  $\hat{\beta}$  indicate robust impact ( $\beta \pm 1.96 \times \text{SE}$  not overlapping zero).

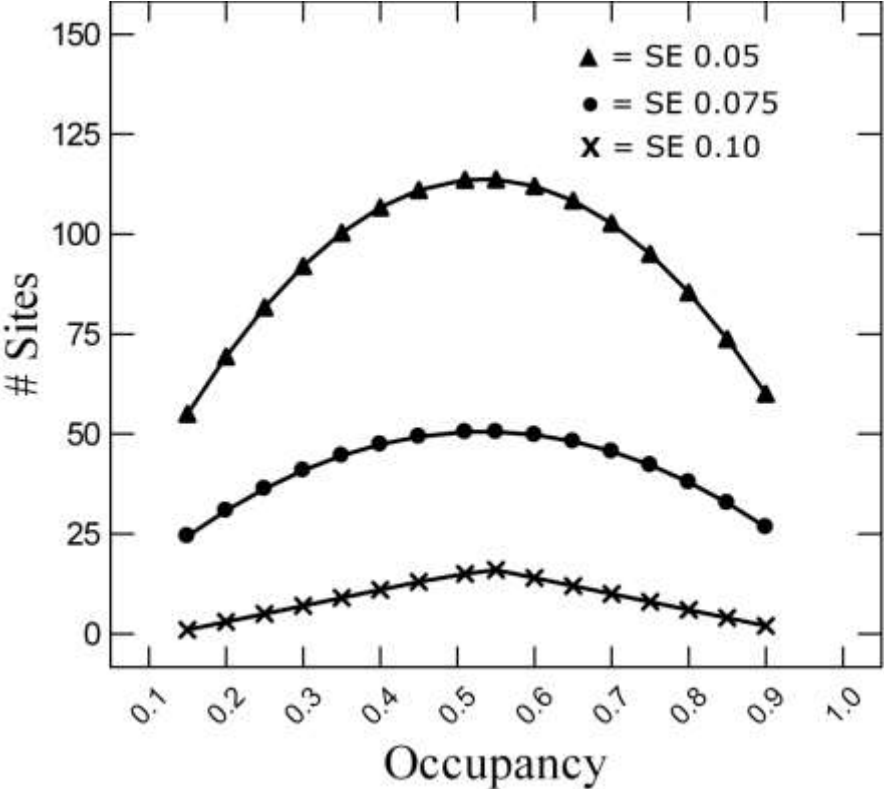


**Figure 4.** Influence of agro-pastoralist settlements use on the probability of cheetah occurrence. The variable proximity to settlement is normalized; Site occupancy estimates are based on the averaged model ( $\sum w > 0.95$ ).

Based on the model averaged estimate of cheetah detectability (0.295) and our mean number of surveys per grid cell (8.21), the power of our survey was  $1 - (1 - 0.295)^{8.21} = 0.94$ , that is, we can confirm cheetah absence with 94% certainty. Given cheetah presence in a  $100 \text{ km}^2$  grid cell, the probability ( $\hat{p} = 0.431$ ,  $\text{SE} = 0.094$ ) of detecting the species on a 3 km track survey was greater than on a 14 day camera-trap survey ( $\hat{p} = 0.195$ ,  $\text{SE} = 0.062$ ). The power of track and camera surveys to detect cheetah at least once in an occupied grid cell is provided in Fig. 5. We estimate that 16 km ( $\pm \text{SE} = 12\text{-}22$ ) of walking or 193 camera-trap nights ( $\pm \text{SE} = 141\text{-}292$ ) are required to confirm cheetah absence in a given grid cell (with 95% certainty). The optimal number of grid cells to survey to achieve standard errors of 0.10, 0.075 and 0.05 (where  $\Psi = 0.2\text{-}0.9$ ) was estimated to be 28, 50 and 113 sites, respectively (Fig. 6).



**Figure 5.** Probability of detecting cheetah at least once at 100 km<sup>2</sup> site that is in use after k surveys using different survey methodologies; where a camera-trap survey is a 14 day sample and a track survey is a (temporally replicated) 3 km transect. Detection probability estimates are based on the averaged model ( $\sum w > 0.95$ ).



**Figure 6.** Total number of 100 km<sup>2</sup> grid cells to survey to achieve a given precision in the occupancy estimate as a function of occupancy probability. Curves are based on the averaged model ( $\sum w > 0.95$ ) estimates of detectability and the estimated the minimum number of surveys required to be 95% certain of cheetah absence. The optimal number of sites to survey corresponds to value that can achieve a given precision at all occupancy rates.

## Discussion

Informed conservation management of the cheetah requires reliable status assessments and inferences on their ability to utilize human-influenced landscapes. However, there are few quantitative data on cheetah population status or distribution and current estimates are primarily based on questionnaire surveys (Bashir *et al.*, 2004). This study provides the first quantification of cheetah status in a recently established National Park in Mozambique, which is also the first for the country. Our results thus provide an important benchmark that future change can be measured against.

This study has demonstrated the feasibility of quantifying cheetah status in a location with limited infrastructure using an occupancy modelling approach that explicitly accounts for species detectability. The use of replicated detection/non-detection surveys enabled us to estimate the probability of detecting cheetah and to provide an unbiased estimate of occurrence that can be used to compare status across different sites and as a basis for long-term monitoring. Given presence, the probability of detecting cheetah on a single survey was  $<1$  ( $p = 0.295$ ). By accounting for detectability, we estimate that cheetah occupy approximately 40% of a 2400 km<sup>2</sup> sample of potential habitat. This estimate is 16% higher than the naïve estimate that fails to account for detection error. Failing to account for detectability in distributional assessments of cheetah is problematic because it can lead to populations being overlooked that require conservation interventions and misleading inferences on factors influencing their occurrence.

Knowledge of the survey effort required to provide robust occupancy estimates is critical for the design of ecological studies that seek to inform conservation plans. Our study demonstrates the value of using detectability estimates to construct robust survey design for

monitoring cheetah occurrence. The power of a study to detect a decline in occupancy corresponds to the number of surveys required to infer absence (MacKenzie & Royle, 2005). Based on our results, 16 km of walking or 193 camera-trap nights are required to confirm cheetah absence at a given 100 km<sup>2</sup> grid cell (with 95% certainty) in LNP. We recommend surveying 50 or 113 grid cells to achieve a standard error of 0.075 or 0.05 in the occupancy estimate (Fig. 6). This may be most logistically feasible using spatially replicated track surveys (Karanth *et al.*, 2011) given the limited accessibility.

An occupancy approach is advantageous because it permits comparison between studies that differ in their survey methodologies, thereby allowing researchers to employ the method(s) that are best suited for their location and study objectives. That unequal sampling across sites can be accounted for is logistically advantageous when accessibility is limited. Robust occurrence estimates require sufficiently high detection probabilities (i.e., >0.15) (MacKenzie *et al.*, 2002). In our study, the probability of detecting cheetah using either method was adequate; however, track surveys out-performed camera surveys: Given presence in a 100 km<sup>2</sup> grid cell, the probability of detecting cheetah was 55% greater on a 3 km track survey than on a 14 day camera-trap survey. Incorporating scent-marking sites helped us to achieve an adequate detection rate; however, incorporating these sites may cause dependency between sampling occasions. Cheetahs visit scent-marking sites frequently (Caro, 1994) and therefore once a surveyor knows where one is located the probability of detecting cheetah on subsequent surveys is increased. We suggest following a ‘partial removal design’ (MacKenzie *et al.*, 2006), halting surveys at scent-marking sites after cheetah have been detected.

We selected grid cells to be slightly smaller than home ranges to reduce the likelihood of over-estimating the proportion of area occupied by cheetah. We acknowledge that sampling



adjacent cells may have introduced spatial dependency; however, we aimed to reduce spatial autocorrelation by selecting grid cells that were approximate to home range size. Previous authors have raised concern that cheetah's tendency to temporarily cluster around resources may result in biased estimates (Bashir *et al.*, 2004). Future studies might consider multi-scale models (Mordecai *et al.*, 2011) or sampling in a checkerboard fashion for addressing spatial dependency.

Our results demonstrate that cheetah can persist in landscapes impacted by cultivation and livestock. However, we found that both cheetah and their preferred prey were strongly negatively influenced by proximity to agro-pastoralist human settlements (Tables 3-5). Cheetah occurrence was low in the core area of the park that contains villages and near agro-pastoralist communities along the eastern park boundary (Fig. 3). These results indicate spatial avoidance of agro-pastoralist settlements, which may be a result of persecution. Alternatively, cheetah may be avoiding settlement areas due to harassment and/or kleptoparasitism from packs of free-ranging domestic dogs. LNP is presently undergoing resettlement of communities from the core area of the park (*pers. comm.* LNP Park Management) and it can be anticipated that cheetah will expand into these areas. A robust occupancy monitoring program in LNP could be achieved by conducting 16 km ( $\pm 12-22$ ) of track surveys within 50 grid cells (Fig. 6). Replicating occupancy surveys over time will permit the estimation of vital rates such as local extinction and colonization probabilities.

The status of cheetah in LNP has positive implications for other nearby protected areas in Mozambique (e.g., Banhine and Zinave National Parks) where cheetah are thought to have been extirpated but status is unknown (IUCN/SSC, 2007). Our study has shown that cheetah can persist in an agro-pastoralist landscape characteristic of these areas. As occupied range, LNP has the potential to facilitate cheetah recolonization to other locations and to prevent genetic

impoverishment by providing connectivity to populations in South Africa. On the other hand, that cheetah exhibited low occurrence along the eastern park boundary may be indicative of edge effects (Woodroffe & Ginsberg, 1998), and therefore the ability for cheetah to exploit potential corridor areas needs to be assessed. Landscape-scale occupancy surveys could be used to identify meta-populations, which if coupled with prey occurrence models and anthropogenic information could permit the delineation of important corridors and suitable locations for reintroductions (Hebblewhite *et al.*, 2011).

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