Movement choices of persecuted caracal on farmlands in South Africa

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ABSTRACT

Landscapes used for livestock agriculture are common worldwide and have the potential for wildlife-human conflict, particularly when carnivores prey on livestock. Identifying habitat features that influence carnivore movements in livestock areas can help mitigate conflict. Caracal (*Caracal caracal*) are a common mesopredator on farms in southern Africa. We used Step Selection Functions to identify habitat selection of GPS collared male caracal (n = 8) along their movement paths on private farmlands in a semi-arid region of South Africa. In the wet season, some caracal selected rugged terrain but high elevations were avoided by certain individuals. Electric fences were avoided, whereas some animals moved close to farm buildings. Many caracal selected shrubland and avoided main roads, but the opposite movement choices were documented for some individuals. Plowed fields were consistently avoided In the dry season, caracal movements were similar to those recorded in the wet season, but there was greater variability in individual choices. Based on model averaging, caracal appeared to move closer to electric fences in the dry season, but such patterns were not significant from individual-level analyses. Because some caracal avoided whereas others selected the same habitats or anthropogenic features, and model averaging could not detect those differences, we recommend that whenever possible individual movement choices of predators are assessed. For caracal and other carnivores that prey on livestock, understanding the ecology of individuals as opposed to exclusively population-level habitat choices may be more informative for conflict mitigation.

RUNNING TITLE

KEYWORDS

Caracal caracal, Habitat selection, Human-wildlife conflict, Livestock predation, Movement ecology, Namaqualand, Rangeland ecology, Step Selection Function, SSF

BACKGROUND

Landscapes used for livestock grazing or browsing are becoming increasingly common across the globe and lead to the loss and fragmentation of natural vegetation and habitats, contributing to the imperilment and extinction of wildlife species (IUCN, 2014; Wolf & Ripple, 2016). Agricultural operations including livestock farming have been linked to geographic range contraction and population declines of multiple wildlife species (Wolf & Ripple, 2017).In contrast, some wildlife may benefit from agricultural operations increasing both in range and numbers and often coming into conflict with farmers over livestock predation (Treves *et al.,* 2002; Drouilly *et al.,* 2017). At the global level, predator-human conflict is projected to increase particularly in lower and middle-income countries (Woodroffe, 2000) and with raising demand for livestock production (Ripple *et al.*, 2014).

Carnivore persistence on livestock farms depends both on farmer tolerance and whether the carnivores can use human-modified landscapes. Cultivated lands both attract and deter carnivore species (Ramesh *et al.,* 2016; Ramesh *et al.*, 2017; Reed *et al.*, 2016), likely because such an area can function as both a prey source and a human risk area. For example, serval (*Leptailurus serval*) avoided cultivated lands (Ramesh *et al.*, 2016) while caracal (*Caracal caracal*) use them (Ramesh *et al.,* 2017). Predicting habitat types selected by carnivores on farming landscapes can reduce predator-farmer conflict but needs to be assessed on a per species basis.

Habitat selection is the disproportionate use of available resources that involves the animals' temporal and spatial responses to real or perceived costs and benefits (Mayor *et al.*, 2009). Similar species may respond to habitat features differently. For example, leopards (*Panthera pardus*) in South Africa strongly select for rugged terrain (Swanepoel *et al.*, 2013), while elevation is the best predictor of Amur leopard (*Panthera pardus orientalis*) density in northeastern China (Qi *et al.,* 2015). Top predators respond differently to road types; heavily used roads are avoided by grizzly bears (*Ursus arctos*) while roads with infrequent traffic are used and crossed frequently (Northrup *et al.*, 2012). Roads also have a direct effect on felid mortality (Kerley *et al.*, 2002; Teichman *et al.*, 2013). For example, Kerley *et al.,* (2002) found that, over a 9-year period, all female Amur tigers (*Panthera tigris*) survived in areas with no roads and no female tiger survived in areas with primary roads.

Habitat selection varies due to seasonal fluctuations in resource availability. Consequently, seasonal differences in habitat selection are widespread for predators including bobcat (*Lynx rufus*, Lovallo & Anderson, 1996), serval (Ramesh *et al.*, 2016) and mountain lion (*Puma concolor*, Cristescu *et al.,* 2019). By contrast, Balme *et al.,* (2007) demonstrated that there were no seasonal differences in feeding habitat selection of leopards in South Africa on a private game reserve. Accounting for season when trying to understand habitat use patterns may yield more accurate results and may enable season-specific conflict mitigation.

Our knowledge of habitat selection and movement patterns by African wildlife species is limited, particularly for carnivores. Of the African large carnivores, lions are some of the most studied species with regard to movement patterns (Valeix *et al.*, 2010, Oriol-Cotterill *et al.*, 2015). For leopards in South Africa, 64% of research has focused on leopard diet in protected areas (Balme *et al.*, 2013), with few studies analyzing movement or habitat selection. Most cheetah (*Acinonyx jubatus*) research has also been carried out in protected areas (Cristescu *et al.*, 2017), although much of the cheetah’s range is unprotected (Durant *et al.*, 2017). While many large carnivores are most at risk outside protected areas and particularly on farmlands, due to direct (i.e. persecution) or indirect threats (i.e. habitat alteration, loss, or fragmentation) (Lamarque *et al.*, 2009), some mesocarnivores may benefit from lower numbers or absence of dominant carnivores on farms (Curveira-Santos *et al.*, 2021). Overall, research on Africa carnivores has focused on large carnivores and neglected mesocarnivores (Ray *et al.*, 2005). Considerable knowledge gaps exist in understanding the natural or anthropogenic habitat characteristics that large carnivores (Balme *et al.*, 2013, Johnson *et al.*, 2017), and especially mesocarnivores (du Plessis *et al.*, 2015) select or avoid on human-dominated landscapes of Africa, despite the importance of such information to conservation practice (Greggor *et al*., 2016).

On South African farmlands, wildlife-human conflict is extensive and poses immediate challenges to biological conservation, human livelihoods, and food security (Maconald & Service, 2007; Drouilly *et al.*, 2017). This conflict can have negative effects on farming productivity via livestock predation (Woodroffe *et al.*, 2004) and on wildlife, particularly predators, which on farmland are often indiscriminately persecuted in attempts to minimize livestock losses. Understanding carnivore habitat selection on farmlands has the potential to limit livestock losses by assisting farmers in livestock management decisions. For example, season-specific information on areas preferred by carnivores can help farmers rotate livestock into areas that are less frequented by predators, while also achieving more efficient monitoring of livestock and improving grazing conditions (Constant *et al.*, 2015, Bogezi *et al.*, 2021).

Caracal are mammalian mesopredators that occur on livestock farms where they consume both wild and domestic prey, such as sheep and goats (Drouilly *et al.*, 2017, Jansen *et al.*, 2019). Despite their economic impact on livestock farmers and their ecological role in suppressing wildlife that may compete with livestock for forage, caracals remain understudied and heavily persecuted (Inskip & Zimmermann 2009, Kerley *et al.*, 2018). Focusing on caracal on arid farmland in South Africa, we identified habitat features that influence movement choices of this mesopredator in both the wet and dry seasons. We contrasted hypotheses related to natural habitat features, human-derived risk and combinations thereof as drivers of caracal movement (Tables 1, 2). We expected caracal to move in rugged terrain (Bouyer *et al.,* 2015), rocky outcrops, shrubland and treed areas (Reed *et al.,* 2016) while avoiding high elevations (Ramesh *et al.*, 2017) and open areas (Dickson & Beier, 2002) (Table 1). We also expected caracal to move along electric fences (Andersen *et al.,* 2017), in cultivated fields (Ramesh *et al.,* 2017) and along 4WD roads (Andersen *et al.*, 2017). Due to high risk of persecution, we expected caracal to avoid main roads and farm buildings.

METHODS

Study area

The study area encompassed 330 km^2 of commercial livestock farms near Namaqua National Park in the semi-arid shrubland of the Northern Cape, South Africa (Fig. 1). The region's main land use is farming, particularly with small stock such as sheep and goats. The area is a botanical biodiversity hotspot in the Succulent Karoo biome, hosting a wide variety of endemic plant species (Cowling *et al.*, 1998). Mean annual rainfall ranges from 100 – 250 mm (Desmet, 2007) and in our study region elevations are 330 – 1,120 m.

Common small mammalian herbivores on farmlands in this region include scrub hare (*Lepus saxatilis*) and rock hyrax (*Procavia capensis*), with red rock rabbit (*Pronolagus* spp.) being less common. Ungulate species include common duiker (*Sylvicapra grimmia*), steenbok (*Raphicerus campestris*) and klipspringer (*Oreotragus oreotragus*). In addition, red hartebeest (*Alcelaphus caama*), oryx (*Oryx gazella*) and springbok (*Antidorcas marsupialis*) were reintroduced into Namaqua National Park and are also occasionally found on farmlands due to escape from the park or farmer reintroductions (Jansen, 2016, Puls *et al.*, 2021).

The small carnivore guild consists of African wild cat (*Felis silvestris lybica*), grey mongoose (*Galerella pulverulenta*), yellow mongoose (*Cynictis penicillata),* bat-eared fox (*Otocyon megalotis*), Cape fox (*Vulpes chama*), common genet (*Genetta genetta*) and striped polecat (*Ictonyx striatus*) (Jansen, 2016, de Satgé *et al.*, 2017). Leopard is the only remaining large carnivore in the region while mesopredators include caracal, black-backed jackal (*Canis mesomelas*) and honey badger (*Mellivora capensis*) (Jansen, 2016, Cristescu *et al.*, 2020).

Both lethal and non-lethal predator control occur on farmlands. Lethal management included night hunts using spotlights and predator calls, opportunistic shooting, trapping to kill, and poison collars placed on livestock. Non-lethal management included electric fences and patrolling fencelines to cover holes made by wildlife that can be used by predators for moving between farms, rotating livestock between areas of the farm, as well as to a lesser extent enclosing livestock at night in kraals.

Caracal capture and monitoring

From March 2014 to February 2015, we live-trapped and GPS collared caracal on farmlands and in Namaqua National Park under the authority of research and collection licenses from the Northern Cape Department of Environment and Nature Conservation (permit #: 1157/2013) and South African National Parks (SANParks) (permit #: CRC-2013/029-2014). Permission for the study was also granted by the University of British Columbia Okanagan (A15-0204), the University of Cape Town (protocol #: 2013/V30/BC) and Stellenbosch University (protocol #: SU-ACUM14-00001). Trapping methods included single door cage traps and padded foothold traps (traps that secure the foot through a rubber padded spring mechanism). These were set to minimize bycatch by adjusting the pressure trigger plate to the weight of the target animals, and in the case of foot traps were anchored with concealed ground anchors and fitted with springs, elastic bands, and swivels to minimize the risk of injury to the trapped animal. Traps were physically checked every 24 hours or more frequently and also remotely monitored using VHF telemetry that detected uniquely identifiable frequencies of trap transmitters (Telonics, Mesa, Arizona, USA). We used bait, visual lures (i.e. wool, feathers, stuffed animals), and olfactory lures (i.e. gland scents, urine and blood) to improve capture probability.

Captured caracal were immobilized under veterinarian assistance by administering 3 mg/kg of tiletamine-zolazepam (Zoletil) using a CO_2 pistol (DanInject, Denmark) and then outfitted with GPS radio-collars (Followit Tellus Satellite UltraLight Iridium, Lindesberg, Sweden). The collars were selected due to their lightness (~200 g), small size, and remote satellite communication. Collars were programmed to acquire locations at 3-hour intervals and data were received via e-mail every 33 h. Collars had mortality sensors that detected lack of motion and data were also inspected visually to check on the status of the animals. Each collar was equipped with a drop-off mechanism and in the event that this failed a rot-off device to ensure animals did not wear collars for their lifetime.

Modelling approach

Caracal movement predictors

Using variables that we and other authors have deemed ecologically relevant for wild felid movement and habitat selection (Table 1), we created *a priori* candidate model sets (See Supplementary Material S1) to understand factors associated with caracal movement decisions. We used identical variable combinations for wet (March-October) and dry season (November-February) models. We opted to partition the data and run separate analyses by season to avoid interacting a dummy variable for season with other covariates of interest, to develop clear seasonal models that help management including how farmers manage their stock, and because our sample sizes allowed splitting the data in the dry vs. wet time of the year. We contrasted three competing sets of hypotheses denoting the movement response of caracal in relation to: 1) natural habitat features (five variables; six models), 2) human-derived risk (five variables; six models) and 3) combined natural habitat features–human-derived risk (10 variables; 21 models) (Table 1, Supplementary Material S1).

We used existing data layers or generated spatially explicit predictors of caracal habitat selection. Variables were either imported to or calculated in GIS (ArcMap 10.3.1) or R (R Core Team, 2022) using a 30 m raster resolution throughout.

Habitat variables included land cover, elevation and terrain ruggedness. We reclassified land cover (www.geoterraimage.com) into five vegetation types based on the probability that a pixel classified into a given category represented that category on the ground (user accuracy) and vegetation type description (Geoterraimage 2013-2014, Supplementary Material S2). Our final vegetation classes were treed areas, shrubland, open areas, plowed fields, and rock (Table 1). Elevation and terrain ruggedness were derived from a digital elevation model available for the region (https://earthexplorer.usgs.gov/) (United States Geological Survey, 2015). We opted to exclude quadratic terms for elevation and terrain ruggedness due to the absence of extremely high or overly rugged terrain.

Five human-related variables were used as surrogates of risk to caracal: distance to electric fence (because lethal traps can be set in holes at the base of fencelines in attempt to control caracal and other mesocarnivores, particularly black-backed jackal), distance to nearest major road (all unpaved but drivable by a 2WD vehicle, mostly for public use, and few major roads on private farms), distance to 4WD road (2-track dirt road, on private farms), distance to farm buildings, and cultivated/plowed fields (Table 1). We used hand-held GPS units to map fence networks by means of hiking along fence lines, recording the track log and importing the logs in GIS. We digitized 4WD roads, main farm roads, and buildings/shacks on screen from high-resolution Google Earth imagery and based on detailed knowledge of the area. These vector GIS layers were then used to create distance rasters for analyses.

We screened model covariates (Table 1) for collinearity at a level of $r > |0.7|$ using Pearson correlations (Nielsen *et al.,* 2004). Only uncorrelated variables were used in the same model structure. Slope was not included in the caracal movement models because it was highly correlated with terrain ruggedness. Due to multicollinearity between shrubland and open areas, we excluded open areas from the analyses. We preserved terrain ruggedness and shrubland in the models because we consider them to be the most biologically relevant covariates for our study species, which is a solitary felid that relies on cover for hunting and for caching large prey, as documented in our predation study of collared caracal (Teichman & Cristescu, unpublished data).

Caracal movement analyses

We used Step Selection Functions (Fortin *et al.*, 2005; Thurfjell *et al.*, 2014) to investigate movement choices of caracal in relation to habitat and human-related risk variables. Step Selection Functions identify habitat selection of a moving animal by comparing environmental parameters of observed steps with generated random steps that are derived from the same starting point (Fortin *et al.*, 2005). Step Selection Functions were built using GPS location data from 8 male caracal monitored from March 2014 to February 2015.

To generate random steps at each observation, we sampled turn angle and step length distributions derived from the observed turn angles and step lengths of collared individuals (Fortin *et al.,* 2005). A total of 6,135 actual steps were used in the analysis. We partitioned our data into wet and dry seasons based on rainfall (Davis *et al.*, 2016) because vegetation productivity, and presumably wildlife activity, are driven by precipitation. A total of 4,526 steps were analyzed in the wet season (March 2014-October 2014) and 1,609 steps in the dry season (November 2014-February 2015). If there was > 3.5 hours or < 2.5 hours between GPS fixes, these locations were excluded from the analyses. Therefore, 311 locations were not used in the analysis. Random step lengths ranged between 1 m and 4.5 km. Five random steps were calculated for each observed step (Squires *et al.*, 2013) and values of variables were contrasted for the observed and random steps (use/available data) (Roever, 2007).

To estimate the Step Selection Functions, we used conditional logistic regression (R package “mclogit”) with the independent variables as fixed effects. We did not apply a mixed-effects modelling approach but instead ran separate models for each individual, thereby keeping track of variable sample sizes (i.e. number of movement “steps”) between caracal (Gillies *et al.,* 2006). This framework also allowed us to implement a two-stage approach (Fieberg *et al.*, 2010), wherein we ran season-specific models for each individual caracal and then drew inferences across all caracal through model averaging (Grueber *et al.*, 2011, Symonds & Moussalli 2011). We derived top-ranked models from the candidate model set for each individual caracal and season based on the Akaike Information Criterion corrected for small sample size (AICc) (Anderson *et al.*, 1998), defining them as those models with ΔAICc < 2 (Burnham & Anderson, 2002). Although model averaging has recently been under scrutiny (Cade, 2015), it is commonly used to account for model selection uncertainty. We averaged across individuals the coefficients outputted from the top-ranked models provided their ΔAICc < ΔAICc of the null model. We compared the results of model averaging to the individual analyses.

RESULTS

Individual caracal differed substantially in their movement choices, with AICc support received for various model combinations of our competing three hypotheses (Tables 2, 3). For all analyses we report main patterns focusing on instances where confidence intervals for beta coefficients did not overlap zero for at least 25% of monitored individuals, regardless of the sign of the parameter (i.e., negative or positive). For example, for eight monitored caracal, a minimum of two caracal must have shown selection, avoidance or combinations thereof in order for the effect to be reported. We also include the results of model averaging for comparison with the individual analyses.

Wet season movement models

Of eight caracal monitored during the wet season, top-ranked model(s) of seven individuals had ΔAICc < 2 and ΔAICc < null model ΔAICc. Four caracal avoided plowed fields, two caracal avoided high elevations and two individuals selected rugged terrain (Table 3). Three caracal selected shrubland whereas one individual avoided it. With regard to anthropogenic features, two caracal avoided electric fences and two moved in the vicinity of buildings. Two individuals avoided main roads whereas one caracal selected for main roads.

Individual and population-level (averaged) models were most consistent for the plowed fields variable (mean ± SE, -1.052 ± 0.425), (Fig. 2), but even for this variable the avoidance pattern was detected for only four individuals (50%). Model averaging showed no significance of any other factors for movement, while the individual analyses showed significant variation among caracal in relation to movement decisions, for both natural habitat selection and anthropogenic features (Supplementary Material S3).

Dry season movement models

Of four caracal monitored during the dry season, models converged for tree individuals, which all had top-ranked model(s) with ΔAICc < 2 and ΔAICc < null model ΔAICc. One caracal avoided plowed fields, one caracal selected shrubland and one moved in rugged terrain. (Fig. 2). One caracal moved close to farm buildings and one avoided main roads.

There was no similarity in outputs of individual and population-level models. Individual models showed effects of plowed fields, shrubland, terrain ruggedness, as well as buildings and main roads. Whereas model averaging suggested that caracal moved close to electric fences ($-0.711\times10^{-4} \pm 0.359\times10^{-4}$), but revealed no effect of other variables on caracal movement choices (Supplementary Material S3).

DISCUSSION

We demonstrated how habitat variables and human-derived risk variables influence habitat selection of caracal along movement paths on livestock farms with carnivore persecution. Individual and population-level (model-averaged) analyses produced similar results when most of the individual caracal behaved similarly with respect to a habitat feature. However, the outcomes of individual and population analyses were only consistent for plowed fields, which were avoided by caracal. When individuals responded differently with regards to a given variable, such as some caracal in the wet season, model averaging was not able to detect an effect. Wildlife management decisions are typically based on population-level parameters and individual behavioural responses are rarely considered. In certain settings, particularly in wildlife-human conflict situations, the behaviour of specific individuals and not of the population is the appropriate level for management interventions, especially when these are lethal. Therefore, data collection and analysis tailored to individuals can be used to inform farmers on the most appropriate management interventions (individual or species specific) to mitigate livestock losses and the costs of predation management.

Although caracal are a widely distributed mesopredator, frequently in conflict with farmers over livestock predation (Drouilly *et al.,* 2018), current understanding of caracal habitat selection and movement patterns on farmland is poor. In our study area, plowed fields are open spaces where caracal and other carnivores are easily detected, which enables opportunistic shooting as well as targeted culls using spotlighting and call playbacks at night. Avoidance of plowed fields by caracal that we documented coincides with other studies of felid response to agricultural lands and might relate to the lack of cover and shelter from human disturbance (Dickson and Beier, 2002; Reed *et al.,* 2016; Ramesh *et al.,* 2016). Other studies emphasize the value of cover for stalking and catching prey by felids (Koehler & Hornocker, 1991; Williams *et al.,* 1995). Our findings differ from those of Ramesh *et al.,* (2017) who found that caracal in the more mesic KwaZulu-Natal province of South Africa selected human modified habitat including forestry land and cultivated areas. They attributed this result to increased abundance of domestic prey in these habitats, whereas in our study area, livestock feed on natural vegetation and therefore do not typically aggregate in agricultural fields, which may account for the discrepancy in findings. Many caracal in Namaqualand selected for shrubland, which we suggest is because this habitat provides cover for hunting and is used by both domestic and wild prey, including small mammals (van Deventer & Nel, 2006).

Caracal selection of rugged terrain matches other felid studies (Bouyer *et al.,* 2015; Drouilly *et al.*, 2018). A growing body of literature shows that terrain ruggedness is an important natural landscape characteristic that can facilitate predator use of human-dominated landscapes (Nellemann *et al.,* 2007) by hindering human access and providing adequate cover (Nielsen *et al.,* 2004). It follows that free-range livestock farming operations in rugged terrain might experience more depredation than do farms in flatter areas as was recently demonstrated by Drouilly *et al.* (2018) for both caracal and baboon (*Papio ursinus*) in the semi-arid Karoo regions of South Africa.

In our study area, electric fences were accompanied by large rocks placed on both sides of the fence base in an attempt to limit animals from digging underneath. Nonetheless, animals including ardvarks (*Orycteropus after*) and porcupines (*Hystrix cristata*) regularly dug holes large enough for caracal to pass through. Selection of electric fences may be a result of caracal walking along the fence lines until they came to a hole to pass through. Farmers patrolled fence lines to fill holes, however, some holes remained open for months on end. Electric fences can be lethal if the holes under them are used to trap mesocarnivores that attempt to cross underneath.

Although some carnivores avoid human developments (Smith *et al.,* 2019), our observations of caracal moving near rural housing adds to a body of literature demonstrating that felids may roam and feed around rural residential areas (Knopff *et al.,* 2014; Wilmers *et al.,* 2013). Predators may perceive some housing areas to have low human-derived risk because of infrequent human use. Movements of individual caracal close to buildings might be partially related to livestock availability. Some livestock, particularly lambs and their mothers, are kept close to farm buildings to facilitate care and reduce depredation, and some caracal might be exploring these areas when young livestock are present.

Mixed results of caracal response to roads are supported by other studies on felids. For example, Dickson & Beier (2002) demonstrated that although cougar home ranges tended to be far from 2-lane paved roads, cougars did not avoid smaller roads within their home range. Other studies have shown that leopards (Mann *et al.*, 2015) and bobcats (*Lynx rufus*, Lovallo & Anderson, 1996) were prevalent on roads while other felids avoid roads (Jafari *et al.*, 2018). In densely vegetated environments, roads can act as movement corridors and facilitate rapid travel when patrolling a territory or searching for prey. Our study system had limited areas with impenetrable vegetation, thus there may not have been a movement benefit for caracal to use roads.

IMPLICATIONS

Our study provides the first quantitative assessment of factors that influence caracal movement and habitat selection on livestock farms. We demonstrated that transformed landscapes (plowed fields) are avoided by caracal at the population level, whereas many other habitat and anthropogenic features are associated with variable movement choices by individual caracal that are further complicated by seasonality. Individual movement decisions by caracal (e.g., moving close to farm buildings) could predispose certain individuals to higher levels of conflict with farmers, suggesting that livestock predation may vary markedly with individual and therefore blanket control at the species level may be both costly to farmers and caracal. We recommend that more resources and emphasis are placed on understanding the ecology of individual carnivores on livestock farms with the goal of reducing livestock depredation, and not simply predator numbers. Removing predators that do not prey upon livestock is costly, includes welfare harms to predators, and may have unintended consequences that exacerbate rather than mitigate livestock losses to wildlife.

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Table 1 Ecologically relevant variables used in *a priori* candidate models to identify movement choices of caracal on livestock farms. Negative expected relationships imply an inverse relationship with observed “steps” (dependent variable), whereas a positive expected relationship implies a direct relationship with observed “steps”. Note that for distance variables ‘–’ implies selection of areas close to the respective feature.

Variable	Unit	Variable Type	Expected relationship	Reference	Species
Natural habitat features					
Elevation	m	continuous	–	Bouyer *et al.,* 2015; Ramesh *et al.,* 2017	Eurasian lynx, caracal
Terrain ruggedness	m	continuous	+	Bouyer *et al.,* 2015	cougar, Eurasian lynx
Distance to rock	m	continuous	+	Teichman & Cristescu, unpublished data	caracal
Shrubland	m	categorical	+	Reed *et al.,* 2016	bobcat
Treed areas	m	categorical	+	Reed *et al.,* 2016	bobcat
Human-derived risk					
Distance to electric fence	m	continuous	–	Cavalcanti *et al.,* 2012	jaguar
Distance to farm buildings	m	continuous	+	Knopff *et al.,* 2014	leopard, Eurasian lynx, cougar
Distance to main road	m	continuous	+	Dickson & Beier, 2002	cougar
Distance to 4WD road	m	continuous	–	Haverland & Veech, 2017	bobcat
Plowed field	m	categorical	+	Ramesh *et al.,* 2017	caracal

Table 2 Top models (ΔAICc < 2) for individual male caracal (n = 7) movements during the wet season on farmlands in South Africa.

CARACAL ID & MODEL CODE	MODEL DESCRIPTION	K	LL	AICc	ΔAICc	w
NCM1						
NULL	null model (USE)	1	-200.70	403.5	0.0	0.23
HABMOD1	distance to rock	2	-200.13	404.6	1.1	0.13
HUMOD1	plowed field	2	-200.59	405.5	2.0	0.08
NCM2						
huHABMOD21	distance to buildings + distance to main road + distance to 4WD + distance to electric fence + plowed field + treed + shrub + terrain ruggedness + elevation	10	-1385.60	2798.5	0.0	0.88
NCM3						
HUMOD2	distance to electric fence + plowed field	3	-751.39	1509.4	0.0	0.24
HUMOD1	plowed field	2	-753.04	1510.4	1.0	0.15
huHABMOD5	distance to electric fence + plowed field + treed + terrain ruggedness	5	-749.72	1511.2	1.7	0.10

huHABMOD15	distance to electric fence + plowed field + elevation	4	-751.16	1511.4	2.0	0.09
NCM4						
HABMOD1	distance to rock	2	-1435.89	2876.1	0.0	0.83
NCM5						
huHABMOD21	distance to buildings + distance to main road + distance to 4WD + distance to electric fence + plowed field + treed + shrub + terrain ruggedness + elevation	10	-744.82	1517.0	0.0	0.31
huHABMOD18	distance to building + distance to main road + shrub + terrain ruggedness	5	-753.21	1518.1	1.1	0.18
huHABMOD1	plowed field + shrub + terrain ruggedness	4	-754.74	1518.6	1.6	0.14
huHABMOD4	distance to electric fence + plowed field + shrubland + terrain ruggedness	5	-753.57	1518.9	1.9	0.12
NCM6						
huHABMOD18	distance to building + distance to main road + shrub + terrain ruggedness	5	-696.94	1405.6	0.0	0.65
huHABMOD20	distance to building + distance to main road + treed + shrub + terrain ruggedness	6	-696.47	1407.4	1.8	0.26
NCM7						
huHABMOD1	plowed field + treed + shrub	4	-81.24	171.6	0.0	0.20
HABMOD1	distance to rock	2	-84.85	173.2	1.6	0.09
NCM8						
huHABMOD4	distance to electric fence + plowed field + shrub + terrain ruggedness	5	-279.02	569.7	0.0	0.30
HUMOD2	distance to electric fence + plowed	3	-281.79	570.2	0.5	0.23
huHABMOD15	distance to electric fence + plowed field + elevation	4	-280.66	570.4	0.7	0.21

Table 3 Top models (ΔAICc < 2) for individual male caracal (n = 3) movements during the dry season on farmlands in South Africa.

CARACAL ID & MODEL CODE	**MODEL DESCRIPTION**	**K**	**LL**	**AICc**	**ΔAICc**	**w**
NCM4						
huHABMOD1	plowed field + shrub + terrain ruggedness	4	-1179.98	2369.1	0.0	0.22
huHABMOD3	plowed field + treed + shrub + terrain ruggedness	5	-1178.72	2369.1	0.1	0.21
huHABMOD4	distance to electric fence + plowed field + treed + shrub	5	-1178.76	2369.2	0.2	0.20

huHABMOD6	distance to electric fence + plowed field + treed + shrub + terrain ruggedness	6	-1177.52	2369.5	0.4	0.18
NCM5						
HUMOD5	distance to building + distance to main road	3	-144.31	295.3	0.0	0.33
HUMOD6	distance to building + distance to main road + plowed field + distance to electric fence + distance to 4WD	6	-140.53	295.5	0.3	0.29
NCM6						
huHABMOD18	distance to building + distance to main road + shrub + terrain ruggedness	5	-170.77	353.2	0.0	0.39
huHABMOD19	distance to building + distance to main road + treed + terrain ruggedness	5	-171.27	354.3	1.0	0.24
HUMOD5	distance to building + distance to main road	3	-174.12	354.9	1.6	0.17

Figure 1 Study area in the Namaqualand region, Northern Cape, South Africa. The extent of the study areas is denoted by the thick black line around the individual farm boundaries of commercial livestock farms (thin black lines). The gray filled area shows a portion of the Namaqua National Park that borders the farms included in the study.

Figure 2 Relative importance of variables influencing movement choices of caracal on South African farmlands in the a) wet season (March 2014 - October 2014) and b) dry season (November 2014 - February 2015). Individual analysis of selection (S) and avoidance (A) (i.e., coefficients with confidence intervals that did not overlap zero) are represented by bars. Absence of bars denotes variable was not in top models.

Figure 1

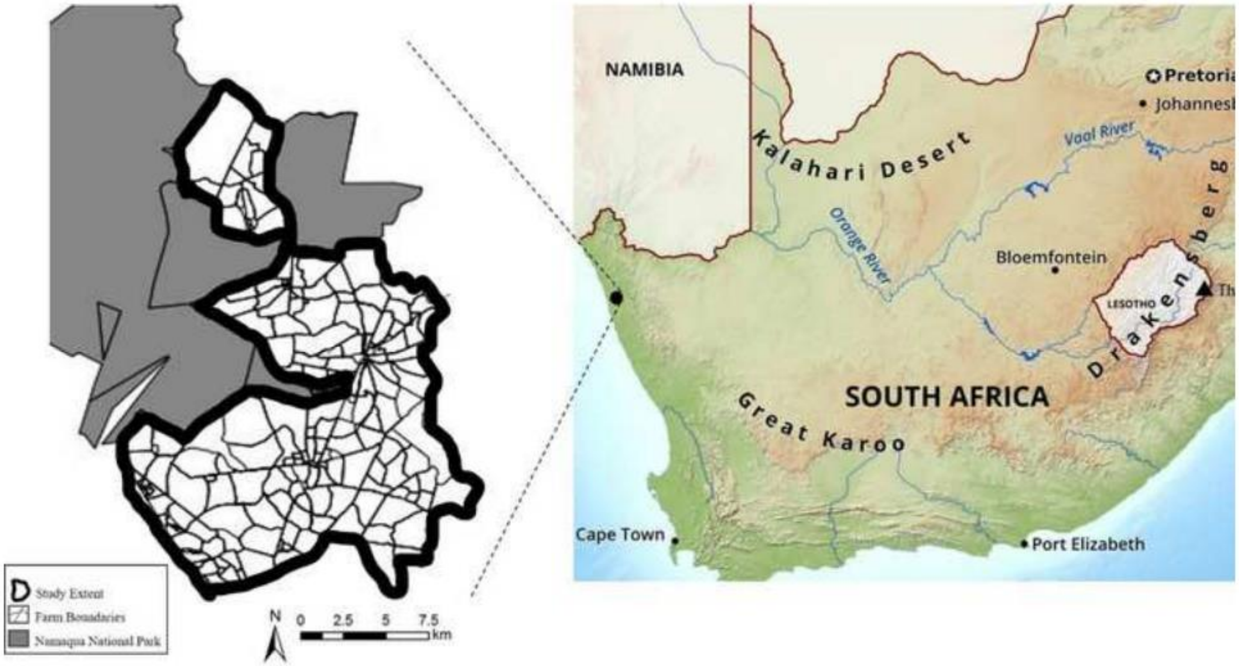
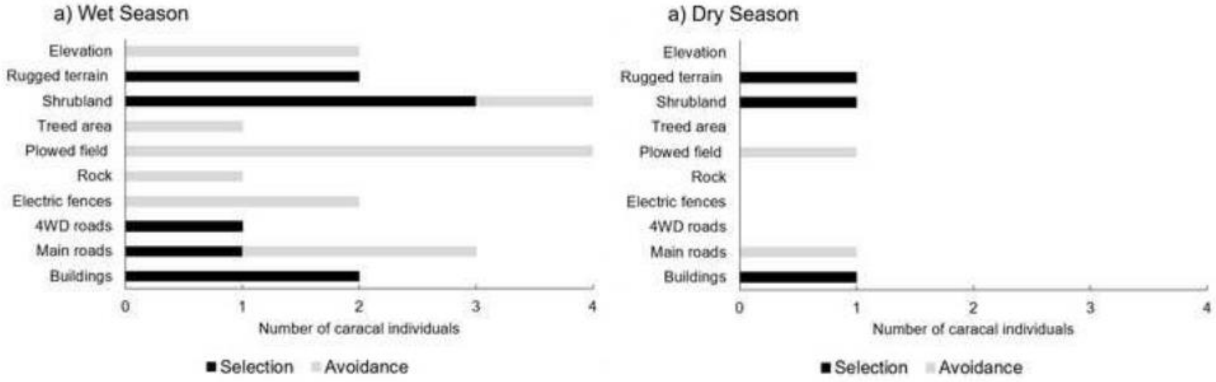

Study Extent
Farm Boundaries
Namaqua National Park
N
0
2.5
5
7.5
km
NAMIBIA
Pretoria
Johannesb
Kalahari Desert
Vaal River
Orange River
Bloemfontein
LESOTHO
Drakensberg
SOUTH AFRICA
Great Karoo
Cape Town
Port Elizabeth

Figure 2


a) Wet Season
Elevation
Rugged terrain
Shrubland
Treed area
Plowed field
Rock
Electric fences
4WD roads
Main roads
Buildings
0
1
2
3
4
Number of caracal individuals
■ Selection
Avoidance
a) Dry Season
Elevation
Rugged terrain
Shrubland
Treed area
Plowed field
Rock
Electric fences
4WD roads
Main roads
Buildings
0
1
2
3
4
Number of caracal individuals
■ Selection
Avoidance