NATURAL SCIENCES *Indago*, Vol. 37, 2021, pp. 67– 76

Ranging behaviour of a territorial male Black-Backed Jackal in a small stock farming area in the Southern Free State

Alistair Green[1*] Nico L. Avenant[2] & Haemish I.A.S. Melville[1]

[1] 0-41 Calabash Building, Unisa Science Campus, cnr Pioneer Avenue and Christiaan de Wet Road, Florida 1710, Gauteng.
ORCID: Green, A: https://orcid.org/0000-0001-8960-2427
ORCID: Melville, H.I.A.S: https://orcid.org/0000-0003-3331-2273
[2] Department of Mammalogy, National Museum, PO Box 266, Bloemfontein, 9300, and Centre for Environmental Management, University of the Free State, Bloemfontein, South Africa.
ORCID: Avenant, N.L: https://orcid.org/0000-0002-5390-9010
**Corresponding author: alistairskipgreen@gmail.com*

Abstract

Damage causing predators are globally the most common source of human wildlife conflict and involve a broad spectrum of taxa. Black-backed jackals are considered damage-causing mesopredators and are perceived to have a considerable effect on live-stock production in South Africa. However, information regarding the ecology of black-backed jackals on South African farmlands is limited. This study provides additional insight into jackal activity and space use patterns on small stock farmlands. A single jackal was collared as part of a larger study investigating the spatial and temporal interactions between caracals and jackals on a small stock farming area in the southern Free State, South Africa. The home range was estimated as 45.47 km^2 (95% OUF AKDEc) with a core area of 1.59 km^2 (50% OUF AKDEc). Activity varied throughout the night with peaks occurring at 01:00, 05:00, and 18:00. The average velocity was estimated at 0.6 ± 1.0 km per hour with a maximum of 5.0 km per hour. The mean distance travelled per day was 9.71 ± 2.45 km. The jackal displayed residency behaviour which represents an insight into the movements and activity of a territorial male jackal in a farmland environment. Habitat selection analysis suggests that the Besemkaree Koppies Shrubland was used for denning while the open Xhariep Karroid Grassland was the jackal's main foraging ground.

KEYWORDS: Black-Backed Jackal; *Lupullella mesomelas*; Damage causing; Mesopredator; Home range; Activity pattern; Territoriality; South Africa.

INTRODUCTION

In South Africa, human-wildlife conflict and the attempts to manage such conflict are ubiquitous (Stadler 2006). Wild animals regularly damage and destroy crops, grazing lands and livestock (Woodroffe *et al.* 2005). Consequently, damage-causing animals have been subjected to both non-lethal and lethal control across much of their historic range. Large predators have been extirpated from farmlands to reduce incidents of predation on stock, and to protect people from possible threat (Van Sittert 1998). The removal of apex predators results in cascading effects on animals at lower trophic levels (Ritchie & Johnson 2009, Sinclair *et al.* 2010, Atkins *et al.* 2019). Influences that apex predators have on species regulation and habitat structure are pivotal in maintaining healthy natural ecosystems (Hayward *et al.* 2019). In the absence of top-down regulation, lower-level predators are thought to proliferate through a mechanism termed mesopredator release (Prugh *et al.* 2009; Tambling *et al.* 2018).

The black-backed jackal (*Lupulella mesomelas* Von Schreber 1775) (hereafter jackals) are known to prey on livestock and may thus negatively impact farmers' livelihoods. Jackals are mesopredators that are widely distributed throughout southern and eastern Africa. These predators are natural prey for martial eagles *Polemaetus bellicosus* (Daudin 1800), spotted hyenas, *Crocuta crocuta* (Erxleben 1777), leopards, *Panthera pardus* (Linnaeus 1758), and lions *Panthera leo* (Linnaeus 1758) (Loveridge & Nel 2013). In addition, there are several records of intraguild interactions between jackals and caracals (*Caracal caracal* Von Schreber 1776) (Melville *et al.* 2004; Loveridge & Nel 2013).

In the Free State, predation and disease are recognised as having considerable adverse effects on production of small stock (Van Niekerk 2010; Spies 2011), particularly Merino and Dorper sheep (*Ovis aries* Linnaeus 1758) (Strauss 2009). These circumstances are fuelling concerns about the future economic viability of small stock farming (Van Niekerk 2010; Turpie & Babatopie 2018). Furthermore, such sentiment has been exacerbated by recent socio-economic changes (Conradie *et al.* 2019). The combination of reduced profitability and socio-economic uncertainty may, amongst others, lead to increased unemployment and higher food prices (Knowlton *et al.* 1999).

Manuscript processed and edited by Gimo Daniel.
https://doi.org/10.38140/00679208/indago.v37.a5

Understanding animal movements is important to interpreting spatio-temporal patterns of many ecological processes at an individual, population and ecosystem level (Schick *et al.* 2008; Tomkiewicz 2010). These processes include territoriality and home range dynamics, predator-prey dynamics, intraguild interactions, habitat selection, disease spread and resource use (Gehrt *et al.* 2009; Broekhuis *et al.* 2013). Animal movement is influenced by both intrinsic physiological and extrinsic factors. Many demographic parameters, including foraging success, breeding success, migration and dispersal, can be directly related to patterns of space use (Gurarie *et al.* 2009). Habitat heterogeneity and composition affects movement patterns of individuals while they search for resources and while they are responding to intraspecific and interspecific interactions. Behavioural mechanisms that allow animals to exploit their temporally variable and spatially heterogeneous resources can be determined from the analysis of telemetry data (Schick *et al.* 2008).

There is a paucity of information in the available literature regarding jackal spatio-temporal ecology in farmland environments (Minnie *et al.* 2018) as the majority of the research, to date, on jackals has been carried out within nature reserves (Avenant & du Plessis 2008; Du Plessis *et al.* 2015). To formulate effective human–predator conflict management strategies there needs to be a fundamental understanding of context specific behaviour. This note presents a summary of the movement patterns of a territorial male jackal in a predominantly small stock farming area in the southern Free State.

MATERIALS AND METHODS

Study Area

The study was carried out in the southern Free State (30◦30'S, 26◦07'E) within a matrix of predominantly small livestock and game farms (Figure 1.). The broader area is comprised of a heterogeneous, undulating landscape within the Grassland and Karoo Biomes (Mucina *et al.* 2006). Two distinct vegetation regions are present in the study area, viz., open grassland that spans the majority of the steppe (Xhariep Karroid Grassland) and thick shrubland covering the slopes and valleys (Besemkaree Koppies Shrubland) (Mucina *et al.* 2006).

The altitude ranges between 1200 m and 1600 m above sea level. The area has a yearly average temperature of 18 ˚C and is described as a cold semi-arid climate. Mean minimum and maximum monthly temperatures vary between seasons, with extremes of -2 and 19˚C in July (winter), and 15 and 33˚C in January (summer). The dry season is from May to November and the wet summer rainfall season extends from December to April, with an average annual precipitation of 420 mm.

Capture and monitoring

From the 15th of May 2019 to the 10th of June 2019, padded foot-hold traps (Victor #3 Softcatch, Lititz, PA) were deployed by a certified trapper to capture jackals. To ensure maximum capture efficiency and to minimize stress and possible injuries to the animals, traps were checked twice daily, at sunrise and sunset, and rebaited when necessary. Upon capture, the jackal was anaesthetised using a pole syringe and fitted with a GPS collar. The sex, weight, morphometrics and body condition were all recorded. The jackal's age was estimated using growth curves derived from body mass and morphometric variables (Lombaard 1971). Body condition was determined through a physical exam onsite by the attending veterinarian. The veterinarian also noted health indicators including dehydration, parasitic load, scar tissue, tooth wear and eruption, and disease symptoms. Once both the collar fitment and the health check had been completed, the jackal was moved to a recovery cage where it was monitored until all signs of narcosis were absent. The jackal was then released at the capture site upon the veterinarian's approval.

A Tellus GPS telemetry/tracking collar (Followit AB, Lindesberg, Sweden) was fitted to the captured jackal. The collar weighed 240 g conforming to the prescribed maximum weight for fitment to research animals (Kenward 2000; Sikes 2016). The GPS collar included a digital VHF transmitter to allow for active tracking and a remote drop-off function so the collar can be removed without needing to recapture the animal. The collar was programmed to acquire locations at 4-hour intervals for six consecutive days and then hourly for 24-hours on the seventh day, every week. The hourly intervals on the seventh day were subsampled to provide a continuous 4-hour interval GPS data throughout the study. This sampling strategy was chosen to allow for an assessment of broad and fine scale movement patterns.

Capture and handling methods were reviewed and approved by the University of South Africa's Animal Research Ethics Committee (application number 2018/CAES/i16).

Data processing

The data recorded from the GPS collar at each positional fix included the date, time, longitude, latitude, number of satellites, battery voltage, and the horizontal dilution of precision (HDOP). To reduce the error in spatial fixes the data were initially screened to remove all points that had an HDOP of > 2 (Dussault *et al.* 2001). In addition, the first week of data was removed to reduce the possible affect that the trapping-collar-release procedure may have on behaviour. Displacement velocity and activity patterns were calculated from the hourly location fixes (Kaunda 2001). Distances travelled per hour

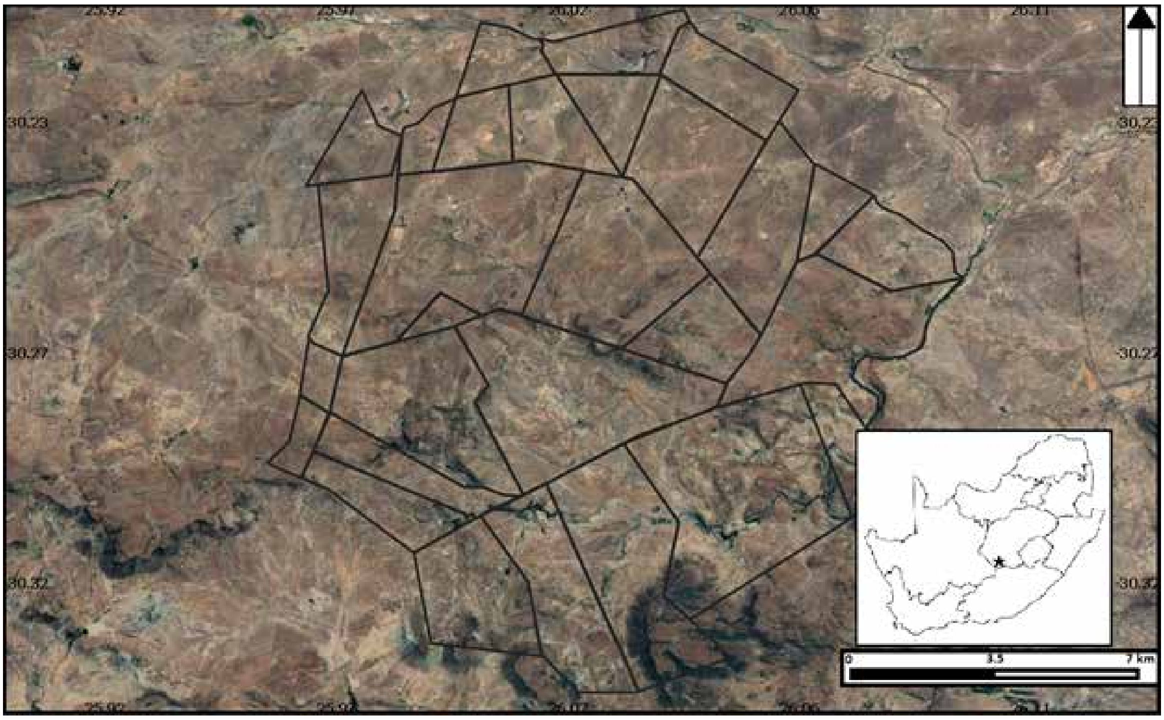

Figure 1. Location of the study area with farm borders demarcated, c. 20 km north of Bethulie in the southern Free State.

was assessed using a one-way ANOVA, Kruskal-Wallis H (McKnight & Najab 2010). To test between the different temporal scales, the days that coincided with the hourly fixes were collated and analysed separately to those days with 4-hour fixes. The hourly fixes were concatenated into four-hour intervals and the distance between the start and end points was calculated. This facilitated the comparison of the linear displacement over four hours to the additive effect of analysing hourly movements.

The home range was calculated at 95% and the core area at 50% using the minimum convex polygon (MCP) method and area corrected by an autocorrelated kernel density estimate (AKDEc) (Mohr 1947; Worton 1989; Fleming *et al.* 2015). The AKDEc estimate required selecting an autocorrelated movement model prior to bandwidth optimization (Flemming & Calabrese 2017). The monthly home range analysis excluded October 2019 due to the animal being removed on the 9th resulting in a low number of positional fixes.

Three continuous-time stochastic candidate movement models were considered and selected for using Aikake information criterion (AIC) (Akaike 1974). The standard model of free random movement is based on Brownian motion (IID). This model was then adjusted to include autocorrelation of time to indicate the animal's home range, Ornstein-Uhlenbeck motion (OU). The final model, Ornstein-Uhlenbeck-F (OUF), introduced an additional autocorrelation factor to account for the animal's velocity. This OUF model described the Brownian motion of the individual within a home range with random foraging periods (Fleming *et al.* 2015).

To assess habitat preference, animal locations within the home range generated by 95% OUF AKDEc were compared to the availability of different habitat types. The habitat type cover was transformed into a percentage of available area. A chi-squared test was then performed on the expected locations and observed locations with the expected locations as the number of fixes in proportion to the available habitat (Loveridge & Macdonald 2003).

RESULTS

On the 30th of May 2019 a male jackal was captured and monitored for a total of a 133 days until it was legally shot by a landowner on the 9th of October 2019 (Figure 2).

At capture, the jackal was estimated to be three years old, weighed 9.15 kg, and was in good body condition at the time of release. A < 5 cm cut was found on the trapped foot and treated with a topical wound spray. Upon recovery of the animal following its shooting it weighed 9.06 kg, suggesting that the animal suffered no adverse effects from the satellite collar. The study animal and seven pups were culled at its den site. A necropsy was performed on the collared jackal to determine whether it had preyed on sheep, however its stomach was empty.

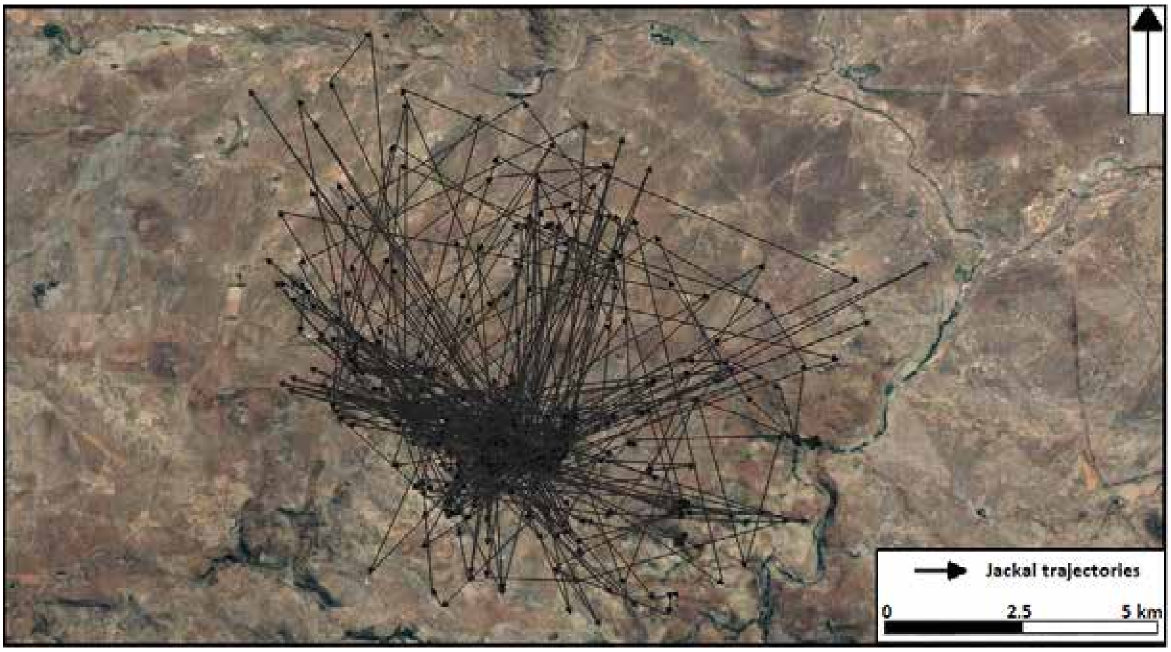

Figure 2. Movement pathways of a collared, territorial male jackal in the southern Free State, tracked between the 6th of June and the 9th of October 2019. Consecutive locations are joined with arrows indicating the directional linear displacement.

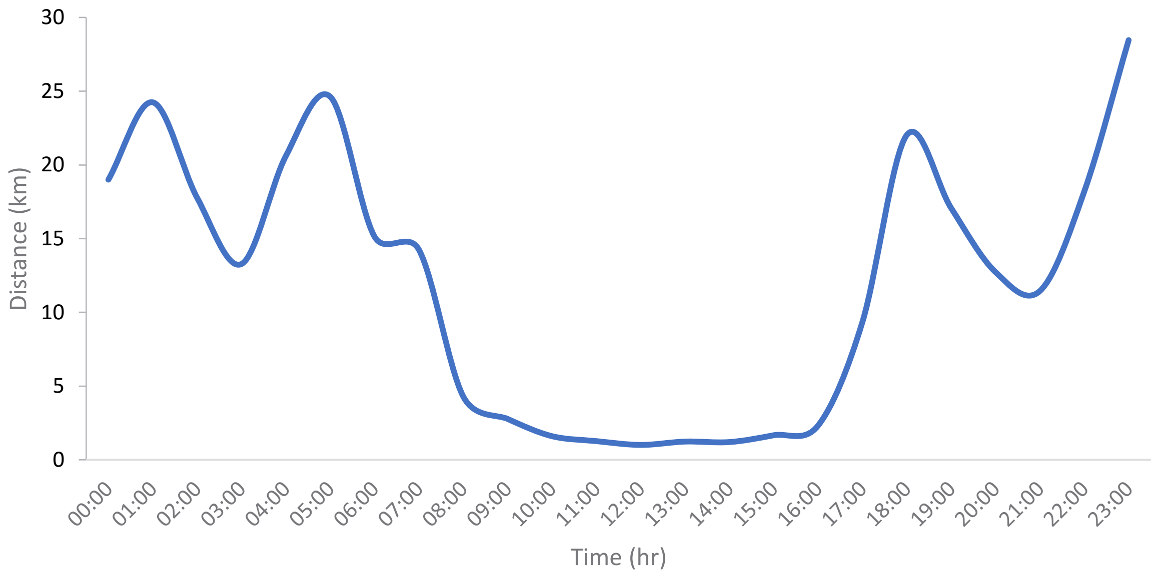

Figure 3. Estimation of the activity patterns of an adult male black-backed jackal *(Lupulella mesomelas)* on a small stock farming area in the southern Free State between the 6th of June 2019 and the 9th of October 2019. Activity patterns recorded as total linear distance travelled during each hour.

We recorded 1126 GPS fixes from the collared jackal from the 6th June 2019 to the 9th of October 2019. Only 16 attempts at obtaining a GPS fix were unsuccessful resulting in a 98.7% fix acquisition success rate. To reduce error, 24 positions which had an HDOP of > 2 were removed, reducing the sample data to 1102 locations.

The average distance travelled per month was 278.97 ± 41.36 km (N=4) and ranged between 326.87 km in June 2019 and 244.06 km in July 2019. The mean distance travelled per day was 9.71 ± 2.45 km (N=125). The farthest distance travelled in one day was 26.86 km and the shortest was 0.44 km, on the 21st of September and the 2nd of August respectively. The mean distance travelled per day from the hourly fixes was 14.28 ± 5.99 km with a range from 4.25 to 26.86 km. The average velocity was estimated at 0.6 ± 1.0 km/h with a maximum of 5.00 km/h. The time of day influenced the activity pattern of the jackal

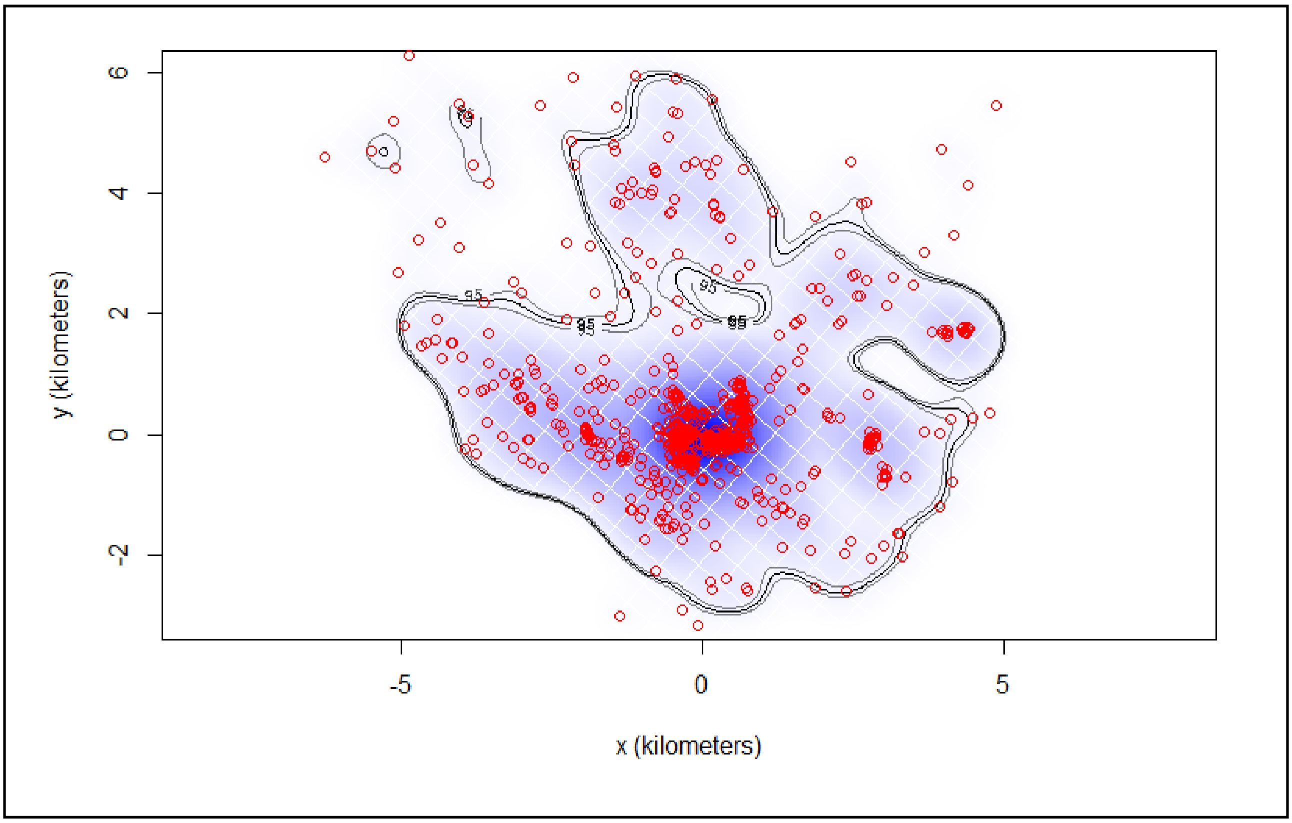

Figure 4. The area-corrected 95% autocorrelated kernel density estimation ($AKDE_C$) home range of the collared jackal including lower and upper confidence limits. GPS data points used for analysis are shown as red dots.

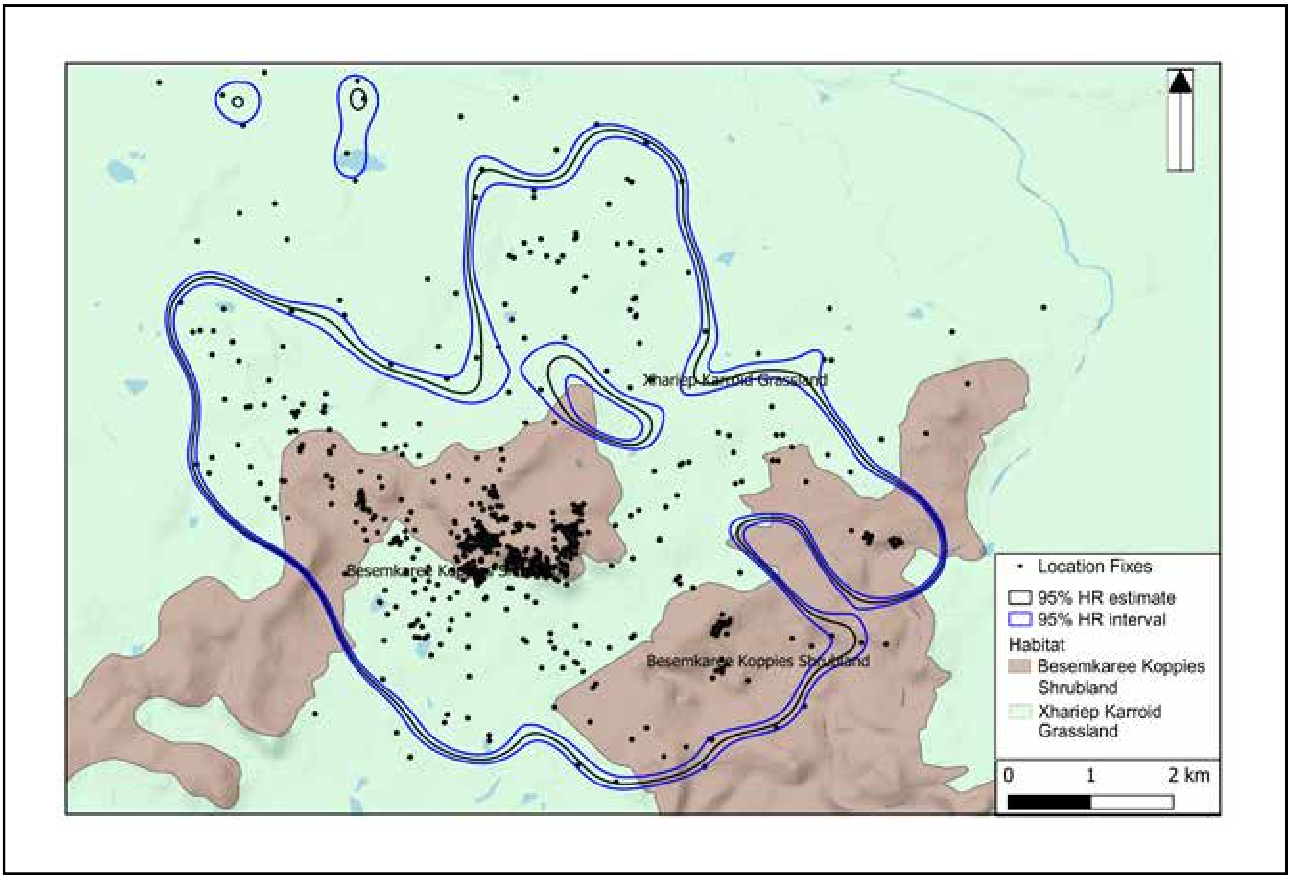

Figure 5. The AKDEc was overlaid onto the two identified habitat types. The GPS data points are shown as black dots. The cluster of locations portrays the jackal's preference for the Besemkaree Koppies shrubland habitat. Data collected on a small stock farming area in the southern Free State between the 6th of June 2019 and the 9th of October 2019.

Table 1. The continuous-time movement models for the area-corrected autocorrelated kernel density estimation ($AKDE_C$), using data collected on a small stock farming area in the southern Free State between the 6th of June 2019 and the 9th of October 2019*

Model	**ΔAICc**
OU + foraging (OUF)	0
BM + home range (OU)	10.35
Brownian motion (IID)	1164.20

*The three candidate models are the three models IID, OU and OUF. They are selected for by using the finite sample size corrected Akaike information criterion(ΔAICc)

Table 2. Home range and core area of use estimates for a territorial adult male black-backed jackal (*Lupulella mesomelas*) in a small stock farming area in the southern Free State from 6th June to 9th October 2019.

Month	N	95% home range km²			50% home range km²		
		MCP*1	$AKDE_c$*2	OUF $AKDE_c$*3	MCP	$AKDE_c$	OUF $AKDE_c$
June	218	47.40	61.70	65.39	9.28	11.03	11.48
July	243	32.79	39.16	40.83	1.41	4.13	4.59
August	248	23.43	23.72	27.62	0.19	1.19	1.43
September	324	23.34	21.81	23.30	0.36	1.57	1.59
Total	1102	45.99	43.06	45.47	1.24	2.47	2.57

*1 The minimum convex polygon (MCP)
*2 Area-corrected autocorrelated kernel density estimation ($AKDE_C$)
*3 Autocorrelated kernel density with foraging (OUF $AKDE_C$)

with movement peaks during the evening and early morning (H = 130.04, df=23, p<0.001) and resting for the eight-hour period centralised at midday (Figure 3).

The OUF model provided the best fit model to jackal movements using the 4-hour interval data (Table 1). The weighted OUF AKDEc indicated areas of high use with 95% confidence intervals (Figure 4). The jackal's home range across the entire period was 45.99 km² (95% MCP) and the core range was 1.24 km² (50% MCP), with the area-corrected autocorrelated kernel density estimate home range being 43.06 km² (95% AKDEc) and the core being 2.57 km² (50% AKDEc) (Table 2). The weighted OUF estimated the home range at 45.47 km² (95%) and the core at 2.57 km² (50%) (Table 2). The home range contained 30.4 km² of Xhariep Karroid Grassland (66.86%) and 15.07 km² of Besemkaree shrubland (33.14%) (Figure 5). The collared jackal was estimated to prefer the Besemkaree shrubland (x2= 887.79, P<0.001). This further emphasised when looking at the habitat composition relative to the study area where the Xhariep Karroid Grassland accounts for 91.4km² (69.3%) while the Besemkaree shrubland is only 40.5km² (30.7%).

DISCUSSION

This home range estimate of 45.47 km² is consistent with those from previous studies, with territory sizes ranging from 2.1 km² to 91.5 km² (Ferguson *et al.* 1983; Kaunda 2001; Kalmer *et al.* 2012). Although studies on farmlands are limited, Humphries *et al.* (2016) found that the home range of a male jackal in the more mesic KwaZulu-Natal was 11.4 ± 4.3 km². This is considerably smaller than the home range estimated for this study in the Free State and may be explained by differences in hunting pressure, prey availability, and varying environmental conditions (Kaunda 2001; Minnie *et al.* 2015).

The jackal in this study was predominantly active throughout the night, but it displayed clear peaks in activity at 0500 and 1800. This pattern is consistent with jackal living in areas with high levels of human persecution (Rowe-Rowe 1982; Ferguson *et al.* 1988) that typifies the study area. This behaviour is also exhibited in other wild canids that alter their activity on response to hunting pressures. In protected areas jackals may be active at any time during the day (Kaunda 2000; Humphries *et al.* 2016, Walton &

Joly 2003) or when their prey show peaks in activity (Ferguson *et al.* 1988; Kaunda 2000; Minnie *et al.* 2018).

The space use and Utilization Distribution demonstrated that the jackal concentrated its movements in the shrubland habitat which may be linked to denning areas (Kaunda 2001). This coincides with low hourly linear spatial displacement during the day. Excursions to the grassland habitat were typically associated with evening movements when activity peaked and hence is more likely linked to foraging behaviour. Jackals are known to be cursorial hunters (Kok & Nel 2004), and the flat open grassland could provide an ideal landscape for hunting.

The study period coincided with the August – November sheep lambing and jackal pup-rearing period in the southern Free State. Farm owners generally report peak stock losses during the lambing seasons, especially when this coincides with the period when jackals have their young (Bingham & Purchase 2002; Pohl 2015). The relatively high levels of stock predation by jackals, during this period, are probably related to the increased energy demand linked to pup-rearing especially in the case of lactating females, while young lambs are expected to be an easier prey than larger sheep.

The landowners in the study area reported stock losses in excess of 100 animals while the collared jackal was being monitored. Livestock predation reports were requested to contain the date and location of the animal carcass, including photographs. However, the data generated was haphazard and lacked any spatial references. Consequently, it was not possible to determine whether the study animal was responsible for any of these losses. Unfortunately, the collared jackal was culled prior to the end of the collar's lifespan, due to the perceived damage that it was causing to livestock. When the collared individual was removed, the den site was also located where seven grown pups were found (these animals were also culled).

Any inference from this analysis is highly restricted due to the single sample and the short monitoring period. However, this evidence is noteworthy because information regarding the temporal and spatial patterns of black-backed jackals in southern Africa is limited, with studies generally being restricted to protected areas (du Plessis *et al.* 2015). To better understand the spatial ecology of jackals, and their potential impact on small stock farming, it is essential that further studies, comprising larger samples, over longer periods are conducted. This will only be achieved through the collaboration with, and the understanding of, farming communities.

ACKNOWLEDGEMENTS

We thank the farmers of the Bethulie district who allowed us access to the area and permitted the loss of livestock from damage causing predators. In particular, we would like to thank H. & L. Grobbelaar, M. Le Roux, and F. & H. Jansen who provided their assistance and helped coordinate the work in the area. We would also like to thank N. Viljoen (nielviljoen.co.za) for his ongoing support and expertise. Mr. Viljoen was instrumental to the success of the project through his knowledge of trapping potentially damage-causing predators. We would also like to thank the National Research Foundation for the provided funding (TTK180416321416). Lastly, we would like to thank staff members from the University of South Africa and the National Museum, Bloemfontein, who aided in the development and execution of the project.

REFERENCES

AKAIKE, H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* **19**(6): 716–723.

ALPRU. 2008. Canis-Caracal Programme. *African Large Predator Research Unit*, University of the Free State (Project 3).

ATKINS, J.L., LONG, R.A., PANSU, J., DASKIN, J.H., POTTER, A.B., STALMANS, M.E., TARNITA, C.E. & PRINGLE, R.M., 2019. Cascading impacts of large-carnivore extirpation in an African ecosystem. *Science* **364**(6436): 173–177.

AVENANT, N.L. & DU PLESSIS, J.J. 2008. Sustainable small stock farming and ecosystem conservation in southern Africa: a role for small mammals? *Mammalia* **72**(3): 58–263.

BERGMAN, D.L., DE WAAL, H.O., AVENANT, N.L., BODENCHUK, M. & MARLOW, M.C. 2013. The Need to Address Black-backed Jackal and Caracal Predation in South Africa. *Wildlife Damage Management Conferences - Proceedings*, 165, 86–94.

BINGHAM, J. & PURCHASE, G.K. 2002. Reproduction in the jackals *Canis adustus* Sundevall, 1846, and *Canis mesomelas* Schreber, 1778 (Carnivora: Canidae). *Zimbabwe. African Zoology* **37**(1): 21–26.

BROEKHUIS, F., COZZI, G., VALEIX, M., MCNUTT, J.W. & MACDONALD, D.W. 2013. Risk avoidance in sympatric large carnivores: reactive or predictive? *Journal of Animal Ecology* **82**(5): 1098–1105.

CONRADIE, B., PIESSE, J. & STEPHENS, J. 2019. The changing environment: Efficiency, vulnerability and changes in land use in the South African Karoo, 2012–2014. *Environmental Development* **32(**4): 1–12.

DU PLESSIS, J.J., AVENANT, N.L. & DE WAAL, H.O. 2015. Quality and quantity of the scientific information available on Black-backed jackals and Caracals: Contributing to Human–Predator Conflict Management*? African Journal of Wildlife Research* **45**(2): 138–157.

DUSSAULT, C., REHAUME, C., JEAN-PIERRE, O. & JEAN, H. 2001. Influence of satellite geometry and differential correction on GPS location accuracy. *Wildlife Society Bulletin* **29**(1): 171–179.

FERGUSON, J.W.H., GALPIN, J.S. & DE WET, M.J. 1988. Factors affecting the activity patterns of black-backed jackals *Canis mesomelas. Journal of Zoology* **214**(1): 55–69.

FERGUSON, J.W.H., NEL, J.A.J. & DE WET, M.J. 1983. Social organization and movement patterns of Black-backed jackals *Canis mesomelas* in South Africa. *Journal of Zoology* **199**: 487–502.

FLEMING, C., FAGAN, W., MUELLER, T., OLSON, K., LEIMGRUBER, P. & CALABRESE, J. 2015. Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. *Ecology* **96**(5): 1182–118.

FLEMING, C. & CALABRESE, J. 2017. A new kernel-density estimator for accurate home-range and species-range area estimation. *Methods in Ecology and Evolution* **8**: 571–579.

GEHRT, S.D., ANCHOR, C. & WHITE, L.A. 2009. Home range and landscape use of coyotes in a metropolitan landscape: conflict or coexistence? *Journal of Mammalogy* **90**(5): 1045–1057.

GURARIE, E., ANDREWS, R. D. & LAIDRE, K. L. 2009. A novel method for identifying behavioural changes in animal movement data. *Ecology Letter* **12**(5): 359–408.

HAYWARD, M.W., EDWARDS, S., FANCOURT, B.A., LINNELL, J.D. & NILSEN, E.B., 2019. Top-down control of ecosystems and the case for rewilding: Does it all add up?, pp. 325–354. **In:** Pettorelli, N., Durant, S.M., du Toit, J.T. (Eds.) *Rewilding*. Cambridge University Press.

HISCOCKS, K. & PERRIN, M. 1988. Home range and movements of Black-backed jackals at Cape Cross Seal Reserve, Namibia. *South African Journal of Wildlife Research* **18**(3): 97–100.

HUMPHRIES, B.D., RAMESH, T., HILL, T.R. & DOWNS, C.T. 2016. Habitat use and home range of Blackbacked jackals (*Canis mesomelas*). *African Zoology* **51**(1): 37–45.

KALMER, J.F., STENKEWITZ, U., KLARE, U., JACOBSEN, N.F. & MACDONALD, D.W. 2012. Resource partitioning among cape foxes, bat-eared foxes, and black-backed jackals in South Africa. *Journal of Wildlife Management* **76**(6): 1241–1253.

KAUNDA, S.K.K. 2000. Activity patterns of lack-backed jackals at Mokolodi Nature Reserve, Botswana. *South African Journal of Wildlife Research* **30**(4): 157–162.

KAUNDA, S. 2001. Spatial utilization by Black-backed jackals in southeastern Botswana. *African Zoology* **26**(2): 113–152.

KENWARD, R.E. 2000. *A manual for wildlife radio tagging*. London: Academic Press.

KLARE, U.N.N., KAMLER, J.F., STENKEWITZ, U.T.E. & MACDONALD, D.W. 2010. Diet, prey selection, and predation impact of Black-backed jackals in South Africa. *The Journal of Wildlife Management* **74**(5): 1030–1041.

KNOWLTON, F.F., GESE, E.M. & JAEGER, M.M. 1999. Coyote depredation control: an interface between biology and management. *Journal of Rangeland Management* **52**(5): 398–412.

KOK, O.B. & NEL, J.A.J. 2004. Convergence and divergence in prey of sympatric canids and felids: opportunism or phylogenetic constraint? *Biological Journal of the Linnean Society* **83**(4): 527–538.

LOMBAARD, L.J. 1971. Age determination and growth curves in the Black-backed jackal, *Canis mesomelas* Schreber, 1775 (Carnivora: Canidae). *Annals of the Transvaal Museum* **27**(7): 135–169.

LOVERIDGE, A. & NEL, J. 2013. *Canis mesomelas*, pp. 173–179. **In**: Kingdon, J. & Hoffmann, M. (Eds.). *Mammals of Africa Volume V: Carnivores, Pangolins, Equids and Rhinoceroses*. London: Bloomsbury Natural History.

LOVERIDGE, A.J. & MACDONALD, D.W. 2003. Niche separation in sympatric jackals (*Canis mesomelas* and *Canis adustus*). *Journal of Zoology* **259**(2): 143–153.

MCKIGHT, P.E. & NAJAB, J. 2010. Kruskal-Wallis Test, pp. 1–1 **In**: Weiner, I.B. and Craighead W.E. (eds). *The Corsini Encyclopedia of Psychology*. Wiley, Hoboken, New Jersey

MELVILLE, H.I., BOTHMA, J.D. & MILLS, M.G. 2004. Prey selection by caracal in the Kgalagadi Transfrontier Park. *South African Journal of Wildlife Research* **34**(1): 67–75.

MINNIE, L., GAYLARD, A. & KERLEY, G. 2015. Compensatory life-history responses of a mesopredator may undermine carnivore management efforts. *Journal of Applied Ecology* **53**(2): 379–387.

MINNIE, L., AVENANT, N.L., DROUILLY, M. & SAMUELS, I. 2018. Biology and ecology of the black-backed jackal and the caracal, pp. 178–204. **In**: Kerley, G.I.H., Wilson, S.L. & Balfour, D. (Eds.). *Livestock predation and its management in South Africa: a scientific assessment.* Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth.

MOHR, C. 1947. Table of equivalent populations of North American small mammals. *American Midland Naturalist* **37**(1): 223–249.

MUCINA, L., HOARE, D.B., LÖTTER, M.C., PREEZ, J., RUTHERFORD, M.C., SCOTT-SHAW, C.R., BREDENKAMP, G.J., POWRIE, L., SCOTT, L., CAMP, K.G.T., BEZUIDENHOUT, H., MOSTERT, T.H., SIEBERT, S., WINTER, P., BURROWS, J.E., DOBSON, L., WARD, R.A., STALMANS, M. & SELETENG K.L. 2006. Grassland Biome. **In**: Mucina, L. & Rutherford, M.C. *The Vegetation of South Africa, Lesotho and Swaziland.* Pretoria.

POHL, C.F. 2015. *The diet of caracal (*Caracal caracal*) in the Southern Free State*. M.Sc. thesis, Department of Zoology and Entomology, University of the Free State.

PRUGH, L.R., STONER, C.J., EPPS, C.W., BEAN, W.T., RIPPLE, W.J., LALIBERTE, A.S. & BRASHARES, J.S. 2009. The Rise of the Mesopredator. *BioScience* **59**(9): 779–791.

RITCHIE, E.G. & JOHNSON, C.N. 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* **2**(9): 982–998.

ROWE-ROWE, D.T. 1982. Home range and movements of Black-backed jackals in an African montane region. *South African Journal of Wildlife Research* **12**(3): 79–84.

SCHICK, R.S., LOARIE, S.R., COLCERO, F., BEST, B.D., BOUSTANY, A., CONDE, D.A., HALPIN, P.N., JOPPA, L.N., MCCLELLAN, C.M. & CLARK, J. S. 2008. Understanding movement data and movement processes: current and emerging directions. *Ecology Letters* **11**(12): 1338–1350.

SIKES, R.S. & THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2016. Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* **97**(3): 663–688.

SINCLAIR, A.R.E., METZGER, K., BRASHARES, J.S., NKWABI, A., SHARAM, G. & FRYXELL, J.M. 2010. Trophic cascades in African savanna: Serengeti as a case study. *Trophic cascades: predators, prey and the changing dynamics of nature* **20:** 255–274.

SPIES, D.C. 2011. *Analysis and quantification of the South African red meat value chain*. Ph.D. Thesis. Bloemfontein: University of the Free State.

STADLER, H. 2006. Historical perspective on the development of problem animal management in the Cape Province. Pretoria: *Proceedings of a workshop on holistic management of human-wildlife conflict in the agricultural sector of South Africa*.

STRAUSS, A.J. 2009. *The impact of predation on a sheep enterprise in the Free State Province*. Ph.D. Thesis. Bloemfontein: University of the Free State.

TAMBLING, C.J., AVENANT, N.L., DROUILLY, M. & MELVILLE, H.I.A.S. 2018. The role of mesopredators in ecosystems: potential effects of managing their populations on ecosystem processes and biodiversity, pp. 205–254. **In**: Kerley, G.I.H., Wilson, S.L. & Balfour, D. (Eds.). *Livestock predation and its management in South Africa: a scientific assessment.* Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth.

TOMKIEWICZ, S.M. 2010. Global positioning system and associated technologies, pp. 2163–2176. **In**: *Animal behaviour and ecological research*. London: Philosophical Transactions of the Royal Society of London B: Biological Sciences.

TURPIE, J.K. & BABATOPIE, A. 2018. The socio-economic impacts of livestock predation and its prevention in South Africa, pp. 53–81. **In**: Kerley, G.I.H., Wilson, S.L. & Balfour, D. (Eds.). *Livestock predation and its management in South Africa: a scientific assessment.* Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth.

VAN NIEKERK, H.N. 2010. *The cost of predation on small livestock in South Africa by medium sized predators*. MSc thesis. Bloemfontein: University of the Free State.

VAN SITTERT, L. 1998. Keeping the enemy at bay: the extermination of wild carnivora in the Cape Colony. *Environmental History* **3**(3): 333–356.

WALTON, L.R. & JOLY, D.O. 2003. *Canis mesomelas*. *Mammalian Species* **715**, 1–9.

WOODROFFE, R., THIRGOOD, S. & RABINOWITZ, A. 2005. The impact of human-wildlife conflict on natural systems, pp. 1–12. **In**: Woodroffe, R., Thirgood, S., Rabinowitz, A. (Eds.) *People and Wildlife, Conflict or Co-existence?* Cambridge, Cambridge University Press.

WORTON, B. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**(1): 164–168.