Feasibility of Using Proximity Tags to Locate Female Lion Panthera leo Kills

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Craig J. Tambling & Lydia E. Belton

Global positioning system (GPS) based telemetry studies are becoming more popular in large carnivore research. Recent advancements include detection and prediction of kill sites from GPS collar data. Thus far, the majority of models to detect kill sites focus on the patterns generated by a single focal individual. The prediction of kill sites helps increase sample sizes for diet studies of carnivores, especially when continuous observation methods cannot be employed. We propose and report on the feasibility of using the spatial association of multiple individuals from a social carnivore group to locate kill sites, using female lions *Panthera leo* in the Kruger National Park, South Africa, as an example. Our feasibility study suggests that lionesses cluster in space while at a GPS cluster with a kill. Clustering appeared most strongly in the first two hours of a kill, whereafter a more random association between individuals in space is observed. Additionally we found no difference in the initial spatial clustering pattern for kills of different sizes. When clusters are not associated with a kill (i.e. resting), female lions exhibit the random spatial association similar to the later hours found at kill sites. We feel that based on the initial results, association of social carnivores in space in combination with current spatio-temporal patterns of focal individuals can be used to improve kill-site models, but further research and larger sample sizes are required to validate our findings.

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Predation kill rates of carnivores on their principle prey provide insight into predator-prey dynamics and are important for the management of predator-prey communities (Franke et al. 2006). However, the determination of predator kill rates are often an elusive goal for researchers and managers alike (Laundré 2008). The adequate quantification of kill rates requires the location of all kill events made during a continuous time interval (Webb et al. 2008), best undertaken using continuous observation methods (Mills 1992). Methods employed for the continuous observation of carnivores, i.e. snow

tracking (Marucco et al. 2008) and continuous direct observations (Mills 1992), often result in small sample sizes of kills across different individuals or groups (Webb et al. 2008). Small sample sizes in predator-prey studies are often a leading criticism aimed at studies investigating observed kill rates (Franke et al. 2006). In light of limitations in collecting large quantities of kill data from direct observations, novel methods to assess and estimate kill rates are being developed and tested. These approaches are evolving as new technology is developed.

Advances in telemetry technology are providing an increasing quantity of fine-scale spatio and temporal data (Clark et al. 2006) which can be combined with statistical techniques to increase the probability of locating kill sites (Webb et al. 2008). This approach has been employed to estimate kill rates for wolves *Canis lupus* and mountain lions *Puma concolor* in North America and Europe (Anderson & Lindzey 2003, Sand et al. 2005, Franke et al. 2006, Webb et al. 2008) and lions *Panthera leo* and leopard *Panthera pardus* in South Africa (C.J. Tambling, unpubl. data, L.H. Swanepoel, unpubl. data). A common drawback in all the above mentioned studies is the failure to detect kill sites of small prey items that are characterised by short handling times (Sand et al. 2005, Webb et al. 2008). The lack of methods to identify kill sites of small prey items currently limits these approaches to detecting kill sites associated with large prey items (Franke et al. 2006). Wolves and lions coexist and hunt in social groups (Stander 1992, Adams et al. 2008), potentially allowing the incorporation of spatial interactions between members of the social group in models that could improve the current approaches in the identification of kill sites.

Proximity tags that record the association and distance between individual animals have been used and tested to detect contact rates (distances of < 40 cm) between brushtail possums *Trichosurus vulpecular* (Ji et al. 2005, Douglas et al. 2006) and contact distance and duration in racoons *Procyon lotor* (Prange et al. 2006). The main application of this technology has been the assessment of mating systems and associated close contact distances that could influence the spread of infectious diseases (Ji et al. 2005, Prange et al. 2006). Although these tags represent a valuable source of contact data which are hard to gather in the field other than by long-term observation, their wholesale and widespread use is often dependent on the saturation of detectors within a population, potentially limiting their use to readily captured and trapped species (Prange et al. 2006).

Female lions hunt and feed as part of a cohesive group (Packer & Ruttan 1988, Stander 1992). Consequently, proximity between individuals is a prospective variable that could be used to increase the predictive power of kill-site models developed using GPS collar data. The identification and monitoring of multiple lions within a single pride can be conducted using proximity tags, providing firstly presence or absence of individuals within the pride over

time, and secondly, a measure of the distance between individuals based on the strength of the signal between the tags. In this study, we investigate the relationship between proximity tags and a receiver built into a GPS collar, and the feasibility of using proximity tags to increase the ability to predict the state (kill or resting) of lions during stationary bouts from GPS movement data. We hypothesise that if lions make a kill, pride members will initially associate closely with each other at the carcass, followed by a loose random association of individuals as feeding declines. Additionally, periods with no kill will be characterized by the loose random association of lions whereby lions are spaced further apart than when feeding on a kill.

Material and methods

We conducted trial investigations on the relationship between proximity tags (hereafter referred to as tags) and the receiver in the Skukuza rest camp (31°59'E, 25°00'S) of the Kruger National Park (KNP), South Africa. As part of a larger investigation into the diet of lions in the central region of the KNP, we deployed a GPS collar and proximity tags on a pride of lions near the Satara rest camp of the KNP (31°77'E, 24°39'S). Our pilot study was conducted in open terrain with no vegetation between the receiver and the proximity tag.

For our study, we used GPS/GSM collars (African Wildlife Tracking) and associated proximity tags (African Wildlife Tracking), all built into collars. Proximity tags emitted a signal at a frequency of 866 MHz before being converted into a signal strength score depending on the strength of the signal when it reached the receiver. In order to assess the relationship between tag distance from the GPS receiver and the relative signal strength we placed the tags at a set of fixed points along a linear transect (400 m, 200 m, 150 m, 100 m, 50 m, 20 m and 5 m) away from a stationary receiver and recorded the relative signal strength at each distance. We converted the signal strength into a relative percentage based on the maximum signal strength obtained when the tag rests against the receiver. This allows an assessment of the general relationship between the signal strength and the active tag with the possibility of expanding this relationship to field observations.

On 19 May 2005, three female lions were immobilised using standard South African National

Park veterinary procedures (Smuts et al. 1977) and collared, one with a GPS collar and two with tags (Tag 21 and Tag 22). The tags remained on the lionesses for 182 (Tag 21) and 47 (Tag 22) days, respectively. The GPS collar was set to record a fix at every hour and we accessed the data remotely via the GSM service around the Satara rest camp. The GPS collar recorded the presence or absence of a signal from a tag as well as the relative signal strength. The GSM coverage around the Satara rest camp was limited, so lions often move out of GSM coverage for a period before returning and allowing data to be accessed. Using the remotely accessed data, GPS clusters (a cluster is defined as two or more consecutive GPS fixes that are < 100 m from the previous fix) were investigated for any possible indication that a kill was made at that cluster. Due to the limited GSM coverage and access to data, clusters were checked on average 7.5 days ($\pm$1.2) following the cluster occurrence. We searched an area of ~40 m in diameter around the GPS cluster as trials on the collars showed an average location error of ~10-20 m depending on the structure of the vegetation (C.J. Tambling, unpubl. data). We identified kills by the presence of stomach contents, teeth, bones, horns or hair at the GPS cluster, identifying the killed species to age and sex if possible.

For each cluster, we extracted the signal strength for seven hours following the start of the cluster. We used seven hours as this represents the average cluster duration for a kill while the tags were deployed. We used a factorial ANOVA to investigate the difference in signal strength between 1) clusters with kills and without kills, 2) the different hours following the start of the cluster, and 3) an interaction between the hour at the cluster and the state of the cluster (kill or no kill) for each individual tag. Factorial ANOVAs are generally robust and able to withstand non-normal data and departures from homogeneity of variance (Zar 1999). Additionally, for each hour we compared the size of the kill to the signal strength to ascertain if clustering was more prevalent with different size kills. All weights were obtained from Bothma et al. (2002) and any kill that had no age and sex was assigned an adult female weight. We categorised weights into the following three categories: a) small prey items of < 100 kg, b) medium-sized prey items between 100 and 500 kg and c) large prey items of > 500 kg. All statistical analyses were conducted using the statistical platform R (R Development Core Team 2008).
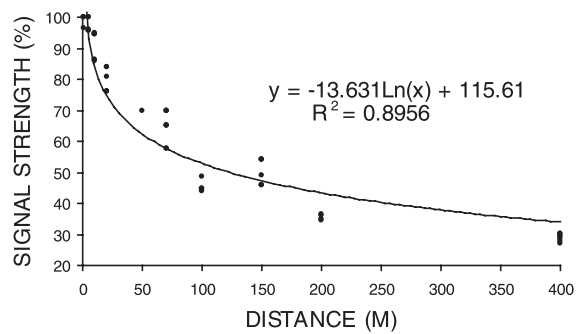
Figure 1. Relationship between the relative proximity tag signal strength and the distance between proximity tags and receivers (following a negative logistic curve) during a trial period in the Kruger National Park, South Africa.

Results

The relationship between signal strength and distance, independent of animals, can be represented by an inverse logistic curve ($R^2 = 0.9$). The observed signal strength (expressed as a percentage of the maximum signal strength) declined rapidly close to the receiver and followed a shallower decline further from the receiver (Fig. 1).

The lioness fitted with tag 21 was associated with the GPS collared lioness on 3,063 out of 3,504 (87%) recorded GPS locations. The lioness fitted with tag 22 was associated with the GPS collared lioness on 832 out of 887 (94%) recorded GPS locations prior to tag loss. During the time that tag 21 and tag 22 were deployed, we located 37 kills from 185 clusters and 10 kills from 57 clusters, respectively.

For tag 21, clusters with kills had significantly higher mean signal strength ($F_{1,2974} = 18.4$, P $\ll$ 0.001) than clusters without (Fig. 2). We found
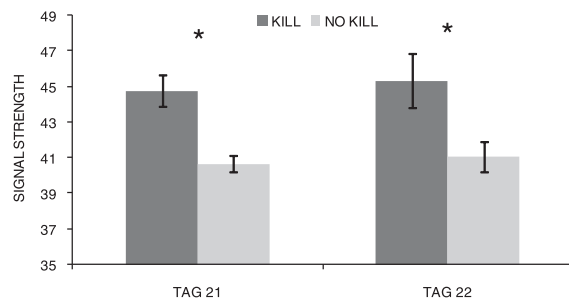

Figure 2. Mean signal strength (all hours combined) between the proximity tags of two female lions in relation to a global positioning system (GPS) collar (with proximity tag reader) fitted on the focal female lion at clusters with and without kills, from the Kruger National Park, South Africa. The asterisk signifies significant differences at a significance level of 0.05, and the maximum signal strength recorded for both tags was 72.
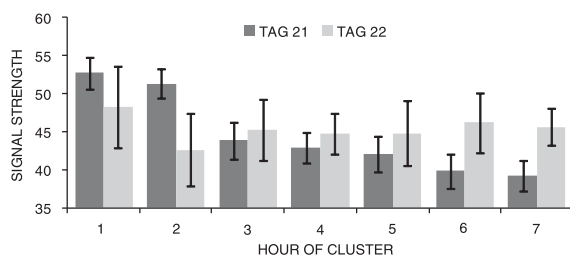
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Figure 3. Mean signal strength of two female lion proximity collars (Tag 21 and Tag 22) in relation to a GPS collar (fitted with a proximity tag reader) fitted on a focal female lion indicating the interaction between the cluster state (kill or no kill) and the hour of the cluster, in the Kruger National Park, South Africa.

significant variation in the signal strength observed across all hours following the start of a cluster ($F_{6,2593} = 2.67$, $P < 0.05$) with elevated signal strength observed during the first two hours of clusters (Fig. 3). We also witnessed a significant interaction between cluster state (kill, no kill) and hour of cluster for tag 21 ($F_{2,4409} = 4.45$, $P \ll 0.05$). Tukey's post hoc tests indicate that this difference was driven by elevated signal strength at the first and second hours of kill sites (see Fig. 3).

For tag 22, we similarly found a significantly higher signal strength at clusters with kills than at clusters without ($F_{1,971} = 5.27$, $P < 0.05$; see Fig. 2), although no differences in signal strength existed across the hours or between hours and cluster state (see Fig. 3).

For clusters at which a kill was confirmed, we found no difference in the signal strength associated with different sized prey categories for neither tag 21 nor tag 22. This result remained the same after investigating possible interactions between the size of prey and hour from the start of the cluster.

Discussion

Our results, although preliminary, show evidence that the use of the spatial association between members of a carnivore social group could potentially increase the predictive power of models used to locate kill sites. Our study represents a first effort at the use of proximity tags to locate kill sites in social carnivores and the results need to be viewed with caution due to the small sample size employed. Our signal strength results need to be validated with larger data sets before the application can be included in kill-site models. Additionally, due to the short time span that tag 22 was deployed, the sample

size of kills located with that tag is small, and differences in the signal strength at each hour between tag 21 and tag 22 may either reflect this small sample size or natural variation between animals. Future studies employing a greater number of tags will be needed to separate these two potential drivers of signal strength patterns across time at clusters.

Our initial testing of the relationship between distance and signal strength indicates a rapid decline in relative signal strength close to the receiver. With adequate calibration following the deployment of the tags on the animals, the estimated distance between individuals will be possible. The high sensitivity of signal strength close to the receiver could indicate small changes in mean distance between individuals. Multiple tags associated with a single collar would offer the greatest resolution of fine-scale spatial association between individuals (Prange et al. 2006), although the trade-off between applicability and logistical constraints will limit the deployment of multiple tags. In social carnivores of high tourism value (e.g. lions, wild dogs *Lycaon pictus* and spotted hyaena *Crocuta crocuta*), the trade-offs between research goals and tourism need to be considered, and this approach may only be applicable where tourism is low.

The spatial patterns observed among the females of the pride around the Satara rest camp are similar to previously studied lion prides in the KNP. Our proximity tags estimate an association with the GPS collar of 94 and 87% of time, respectively. Funston et al. (1998) showed that lionesses in the southern region of KNP spent 94% of the time with their full pride compliment or pride subgroup which they usually associate with. In Hwange National Park (HNP), Zimbabwe, pride female lions spent on average 89% of the time within the pride (Valeix et al. 2009). These levels of association for southern African lions are somewhat higher than the fission fusion driven systems of the Serengeti where pride females spend as little as 20-30% of the time together (Schaller 1972, Packer 1986). In cases such as KNP and HNP where pride fidelity is high, proximity tags will provide a valuable addition to any GPS based kill-site prediction model.

However, when pride fidelity is lower, such as in the Serengeti, a modification of the above approach will be needed if sequential commencement of feeding exists. Schaller (1972) noticed that on most occasions lions would begin feeding as soon as they arrived at a kill. In this situation, instead of using the proximity tag association at the beginning of a

cluster, using the proximity association between two individuals at the first hour that they are associated with each other may indicate the clustering effect of a carcass. This would, however, only be applicable for large kills, as smaller kills may be completely consumed prior to splinter groups of a pride arriving at a carcass.

The majority of kill-site models have identified the length of time that a cluster is occupied as a primary predictor of a kill (Anderson & Lindzey 2003, Sand et al. 2005, Franke et al. 2006, Laundré 2008). The use of the minimum length of time at a cluster has been shown to work well for larger kills; however, most authors still suggest limitations to predicting the location of small kills. In wolves, low success in locating small kills was assumed to be an artefact of the variation in time spent on small carcasses (Webb et al. 2008), thus limiting the applicability of cluster length to predict all kill sites. Our preliminary results suggest that in the absence of long cluster bouts (i.e. for small kills), a high degree of association of individuals at the start of a cluster could still indicate a kill. We found no difference in the association patterns between individuals at small and large kills suggesting that a similar initial feeding pattern may exist for all size kills. Although our preliminary results do suggest that the identification of clusters with small kills could be possible, we caution that further investigation may be needed to validate our initial observations.

Although not investigated in our study, the influence of the orientation of the collar, potential barriers (e.g. vegetation, other lions and carcasses) and topography will result in changes in the signal strength. The influence of these factors effecting GPS signal acquisition has been well documented in GPS collar studies (D'Eon et al. 2002, Di Orio et al. 2003, D'Eon & Delparte 2005, Lewis et al. 2007). Due to the nature of the UHF (ultra high frequency) signals used in the proximity tag, this impact will be unavoidable (Prange et al. 2006). However, even with this potential bias, the goal of kill-site prediction using GPS collars is to locate kills for wide-ranging and difficult-to-observe species where continuous observation approaches are not feasible. Unless continuous observation is done concurrently, the presence of potential barriers between proximity tags and receivers will not be known. However, calibration of the signal strength-distance relationship for different habitat types could allow adjustments of distance association relationships for each habitat type.

Apart from group fidelity and spatial association studies, further use of proximity tags exist for carnivore ecology. Proximity tags on individuals of solitary species can indicate contact periods and could be useful for the assessment of mating bouts and mating timing (see Ji et al. 2005). However, as pointed out by Prange et al. (2006), a saturation of proximity tags on all individuals in the study area will be needed for adequate mating system studies. Therefore, this approach will not be feasible for large carnivores in open systems where transitory individuals can associate with study individuals. During the course of our study, we obtained a single proximity reading for each hour at the same time as the GPS position was recorded. The increased storage capacity of collars (Clark et al. 2006) now allows for increased data capture, and proximity readings could be collected at a shorter frequency depending on the research-management question that is being addressed (Prange et al. 2006). A greater frequency of proximity readings could show potential contact networks within groups that could infer possible disease transmission routes (Ramsey et al. 2002, Ji et al. 2005, Bohm et al. 2008). Additionally, transmitters used in proximity tags vary in the frequency on which they operate (our study: 866 MHz; Ji et al. 2005: 160 MHz; Prange et al. 2006: 916.5 MHz), which then has implications for the distance that the proximity tag can be effective. Lower frequencies travel further than higher frequencies because they reflect less when travelling through dense vegetation or varying terrain (Mech 1983, Mech & Barber 2002). Therefore, if greater effective distances are required (detecting possible between-pride contacts), a tag with a lower frequency might be used, whereas a tag with a higher frequency would be best for detection of close-range distance variation (activity around a carcass). In some collars, the power (determining the UHF signal strength) can be adjusted allowing the detection distance of the proximity tags to be set by the user (Prange et al. 2006).

The amalgamation of GPS technology, which is becoming more popular for carnivore research, with additional technology will increase the data that can be collected, with the possibility of increasing sample sizes for research on elusive species. However, we do caution, along with many other GPS studies, that adequate calibration is needed and the biases inherent in GPS associated data need to be assessed and corrected if possible when planning a GPS telemetry study.

References

Adams, L.G., Stephenson, R.O., Dale, B.W., Ahgook, R.T. & Demma, D.J. 2008: Population Dynamics and Harvest Characteristics of Wolves in the Central Brooks Range, Alaska. - Wildlife Monographs 170: 1-25.

Anderson, C.R. & Lindzey, F.G. 2003: Estimating cougar predation rates from GPS location clusters. - Journal of Wildlife Management 67: 307-316.

Bohm, M., Palphramand, K.L., Newton-Cross, G., Hutchings, M.R. & White, P.C.L. 2008: Dynamic interactions among badgers: implications for sociality and disease transmission. - Journal of Animal Ecology 77: 735-745.

Bothma, J.d.P., Van Rooyan, N. & du Toit, J.G. 2002: Antelope and other smaller herbivores. - In: Bothma, J.d.P. (Ed.); Game Ranch Management. Van Schaik Publishers, Pretoria, South Africa, pp. 149-175.

Clark, P.E., Johnson, D.E., Kniep, M.A., Jermann, P., Huttash, B., Wood, A., Johnson, M., McGillivan, C. & Titus, K. 2006: An advanced, low cost, GPS-based animal tracking system. - Rangeland Ecology and Management 59: 334-340.

D'Eon, R.G. & Delparte, D. 2005: Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. - Journal of Applied Ecology 42: 383-388.

D'Eon, R.G., Serrouya, R., Smith, G. & Kochanny, C.O. 2002: GPS radiotelemetry error and bias in mountenous terrain. - Wildlife Society Bulletin 30: 430-439.

Di Orio, P., Callas, R. & Schaefer, R.J. 2003: Performance of two GPS telemetry collars under different habitat conditions. - Wildlife Society Bulletin 31: 372-379.

Douglas, M.E., Ji, W. & Clout, M.N. 2006: MateID: Design and testing of a noval device for recording contacts between free-ranging animals. - Wildlife Society Bulletin 34: 203-207.

Franke, A., Caelli, T., Kuzyk, G. & Hudson, R.J. 2006: Prediction of wolf (*Canis lupus*) kill-sites using hidden Markov models. - Ecological Modelling 197: 237-246.

Funston, P.J., Mills, M.G.L., Biggs, H.C. & Richardson, P.R.K. 1998: Hunting by male lions: ecological influences and socioecological implications. - Animal Behaviour 56: 1333-1345.

Ji, W., White, P.C.L. & Clout, M.N. 2005: Contact rates between possums revealed by proximity data loggers. - Journal of Applied Ecology 42: 595-604.

Laundré, J.W. 2008: Summer predation rates on ungulate prey by a large keystone predator: how many ungulates does a large predator kill? - Journal of Zoology 275: 341-348.

Lewis, J.S., Rachlow, L., Garton, E.O. & Vierling, L.A. 2007: Effects of habitat on GPS collar performance: using data screening to reduce location error. - Journal of Applied Ecology 44: 663-671.

Marucco, F., Pletscher, D.H. & Boitani, L. 2008: Accuracy of scat samples for carnivore diet analysis: wolves in the Alps as a case study. - Journal of Mammalogy 89: 665-673.

Mech, L.D. 1983: A Handbook Of Animal Radio-tracking. - University of Minnesota Press. Minneapolis, USA, 108 pp.

Mech, L.D. & Barber, S.M. 2002: A critique of wildlife radio-tracking and its use in national parks. - A report to the U.S. National Parks Service, 83 pp.

Mills, M.G.L. 1992: A comparison of methods used to study food habits of large African carnivores. - In: McCullough, D.R. & Barrett, R.H. (Eds.); Wildlife 2001: Populations. Elsevier Science Publishers LTD, London, England, pp. 1112-1123.

Packer, C. 1986: The Ecology of Sociality in Felids. - In: Rubenstein, D.I. & Wrangham, R.W. (Eds.); Ecological Aspects of Social Evolution. Princeton University Press. Princeton, USA, pp. 429-451.

Packer, C. & Ruttan, L. 1988: The evolution of cooperative hunting. - The American Naturalist 132: 159-198.

Prange, S., Jordan, T., Hunter, C. & Gehrt, S.D. 2006: New radiocollars for the detection of proximity among individuals. - Wildlife Society Bulletin 34: 1333-1344.

Ramsey, D., Spencer, N., Caley, P., Efford, M., Hansen, K., Lam, M. & Cooper, D. 2002: The effects of reducing population density on contact rates between brushtail possums: implications for transmission of bovine tuberculosis. - Journal of Applied Ecology 39: 806-818.

R Development Core Team 2008: R: A Language and Environment for Statistical Computing. - R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org

Sand, H., Zimmermann, B., Wabakken, P., Andrén, H. & Pedersen, H.C. 2005: Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. - Wildlife Society Bulletin 33: 914-925.

Schaller, G.B. 1972: The Serengeti Lion: A Study of Predator-Prey Relations. - The University of Chicago Press. Chicago, USA, 480 pp.

Smuts, G.L., Whyte, I.J. & Dearlove, T.W. 1977: A mass capture technique for lions. - East African Wildlife Journal 15: 81-87.

Stander, P.E. 1992: Cooperative hunting in lions: the role of the individual. - Behavioural Ecology and Socio-biology 29: 445-454.

Valeix, M., Loveridge, A.J., Chamaille-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. & MacDonald, D.W. 2009: Behavioural adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. - Ecology 90: 23-30.

Webb, N.F., Hebblewhite, M. & Merrill, E.H. 2008: Statistical methods for identifying wolf kill sites using global positioning system locations. - Journal of Wildlife Management 72: 798-807.

Zar, J.H. 1999: Biostatistical Analysis. - Prentice Hall. New Jersey, USA, 663 pp.