Complementing GPS cluster analysis with activity data for studies of leopard (*Panthera pardus*) diet

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Despite their wide distribution, feeding habits of leopards, *Panthera pardus,* outside savanna and forest habitats are poorly understood. We explored a novel approach of combining both GPS cluster and activity data analysis to study the hunting activity of a single female leopard in the Cederberg Mountains of the Western Cape, South Africa. Positions and acceleration data were obtained using a Vectronic GPS-PLUS collar. In total, 1760 GPS positions with a fix success of 87% were obtained between June 2008 and February 2009. Fifty-four of 78 potential kill sites identified from GPS data records were investigated 171 ± 91 days (mean ± S.D.) after the potential predation event which resulted in the detection of prey remains at 31 sites (success rate of 57.4%). Activity pattern was different at small-kill (rock hyrax; Hewitt's rock rabbit, *Pronolagus saundersiae*) sites compared to large-kill (antelope) sites, although data did not achieve significance ($P = 0.07$). Results of frequency analyses of activity data allowed the differentiation between feeding and non-feeding activity. The combination of different methods such as GPS telemetry and activity measurement provides a valuable means for detecting kill sites in rugged and largely inaccessible regions where direct observations and scat collection are difficult.

Key words: Cape leopard, *Panthera pardus*, GPS cluster analysis, feeding ecology, predation, activity, biological rhythm.

INTRODUCTION

The feeding ecology and activity patterns of leopards, *Panthera pardus,* have been studied intensively in savanna and forest habitats (*e.g.* Bailey 1993; Jenny & Zuberbühler 2005), but little information is available from rugged mountain areas such as the Cederberg Mountains of the Western Cape, South Africa (Norton *et al.* 1986; Martins *et al.* 2011). Most leopard diet studies in southern Africa have used faecal analysis or direct observations (Bothma & Le Riche 1984; Norton *et al.* 1986; Le Roux & Skinner 1989; Bailey 1993). However, direct observation and scat location of large carnivores in remote and mountainous regions are difficult, making studies of their feeding habits challenging (Knopff *et al.* 2009; Martins *et al.* 2011). In the past decade, the use of GPS location data has provided valuable insight into the diet and prey selection of elusive predators like cougars (*Puma concolor*, Anderson & Lindzey 2003; Knopff *et al.* 2010) and wolves (*Canis lupus*; Sand *et al.* 2005; Demma *et al.* 2007). Recent studies in sub-Saharan Africa, focusing on lions (*Panthera leo*;Tambling *et al.* 2010) and leopards (Martins *et al.* 2011) showed that these carnivores remain at kill sites for extended periods up to >24 hours. However, distinguishing non-kill sites from sites where small prey was killed remains an acknowledged challenge (Merrill *et al.* 2010). Although GPS cluster analysis as well as the use of acceleration data from GPS collars are well established in behavioural and ecological studies (*e.g.* Anderson & Lindzey 2003; Gervasi *et al.* 2006; Löttker *et al.* 2009; Merrill *et al.* 2010), both methods have never been combined to gain more detailed information on feeding behaviour of large predators despite the fact that both kinds of data are recorded simultaneously in modern collars (GPS collars from Lotek Engineering; *e.g.* Coulombe *et al.* 2006; GPS collars from Vectronic

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Table 1. Prey items found at kill sites of female leopard F10. Mean weights derived from Skinner & Chimimba (2005).

Prey species	Scientific name	*n*	Mean hours spent at kill site (range)	Mean weight (kg)	% of total biomass
Rock hyrax	*Procavia capensis*	17	7.7 (4–55)	3.66	29.3
Klipspringer	*Oreotragus oreotragus*	7	29 (10–48)	11.90	39.7
Common duiker	*Sylvicapra grimmia*	2	28 (24–32)	16.10	17.9
Cape grysbok	*Raphicerus melanotis*	1	6	10.25	4.5
Cape porcupine	*Hystrix africaeaustralis*	1	17	12.15	7.9
Hewitt's red rock rabbit	*Pronolagus saundersiae*	1	4	1.62	0.7

Aerospace, *e.g.* Löttker *et al.* 2009).

Within the scope of the Cape Leopard Trust Cederberg project, the study explored the possibilities of a combined use of both GPS and activity data in order to gain further insight into the behavioural ecology and feeding habits of leopards in the Cederberg Mountains. Our aims were (i) to describe leopard feeding habits by analysing GPS cluster locations, and (ii) to determine feeding patterns using activity data correlated with the GPS cluster analysis used to find kills.

METHODS

Study area

The rugged Cederberg Mountains, Western Cape, South Africa, (32°27′S; 19°25′E), are situated about 200 km north of Cape Town encompassing approximately 2000 km^2 of both Fynbos and Succulent Karoo biomes (Martins 2010).

Data collection

The adult female leopard F10 was trapped by the Cape Leopard Trust research team on 18 June 2008 and collared with a GPS radio-collar (Vectronic Aerospace GmbH, Berlin, Germany), weighing 2% of body weight. Capturing and collaring conformed to Western Cape Provincial Government's and American Society of Mammalogists' (Gannon *et al.* 2007) guidelines. Approval was provided by the provincial nature conservation authority Cape Nature (Ethics number of the University of Bristol: UB/08/025). The collar was programmed to record 8–24 GPS locations per day, to partly gain hourly and bi-hourly fixes for more intensive tracking. Apart from recording GPS locations, the collar was equipped with a dual-axis acceleration sensor, recording activity on two axes in 5-minute intervals (for a detailed technical description, see Krop-Benesch *et al.* 2010).

GPS cluster analysis

Location data were plotted in ArcGIS 9.2 (ESRI 2010) and sequentially inspected to identify location clusters. GPS location clusters that could signify potential feeding sites were defined as ≥ 2 locations within 100 m of each other over a minimum 4-hour period based on the used GPS schedule (Knopff *et al.* 2009, 2010). Because GPS locations are somewhat inaccurate (Webb *et al.* 2008), and because kill remains may be scattered around actual positions, a radius of 100 m within the selected positions was searched thoroughly for prey remains. Bones, hair, horns, feet and hooves were collected and used to identify prey species. If no prey remains were found after intensive search, a cluster was termed as non-kill cluster (Martins *et al.* 2011).

Statistical analyses

Activity data were broadly scattered and therefore averaged for the respective hours before and after cluster onset. Large kills (prey size >5 kg) were distinguished from small kills (prey size <5 kg, see Table 1). Generalized additive models (binomial GAM; package *mgcv*; Wood 2006) were used to investigate how activity was related to the probability of a binary response (kill = 1, no kill = 0 and small kill = 0, large kill = 1) occurring at a GPS cluster. In other words, we tested if activity differed significantly over time for kills or prey size (*P*-values <0.05 were read as significant). Subsequently, we used the fast Lomb-Scargle algorithm (Press & Rybicki 1989) to examine activity data for periodic components within each of eight confirmed kill clusters and eight 'normal activity' periods of at least 45 hours. Intervals of 'normal activity' were chosen as periods in which distances between consecutive GPS locations were >200 m. Sinusoidal components of activity data are uncovered by the algorithm and reflected as amplitudes (Ruf 1999). Consequently,

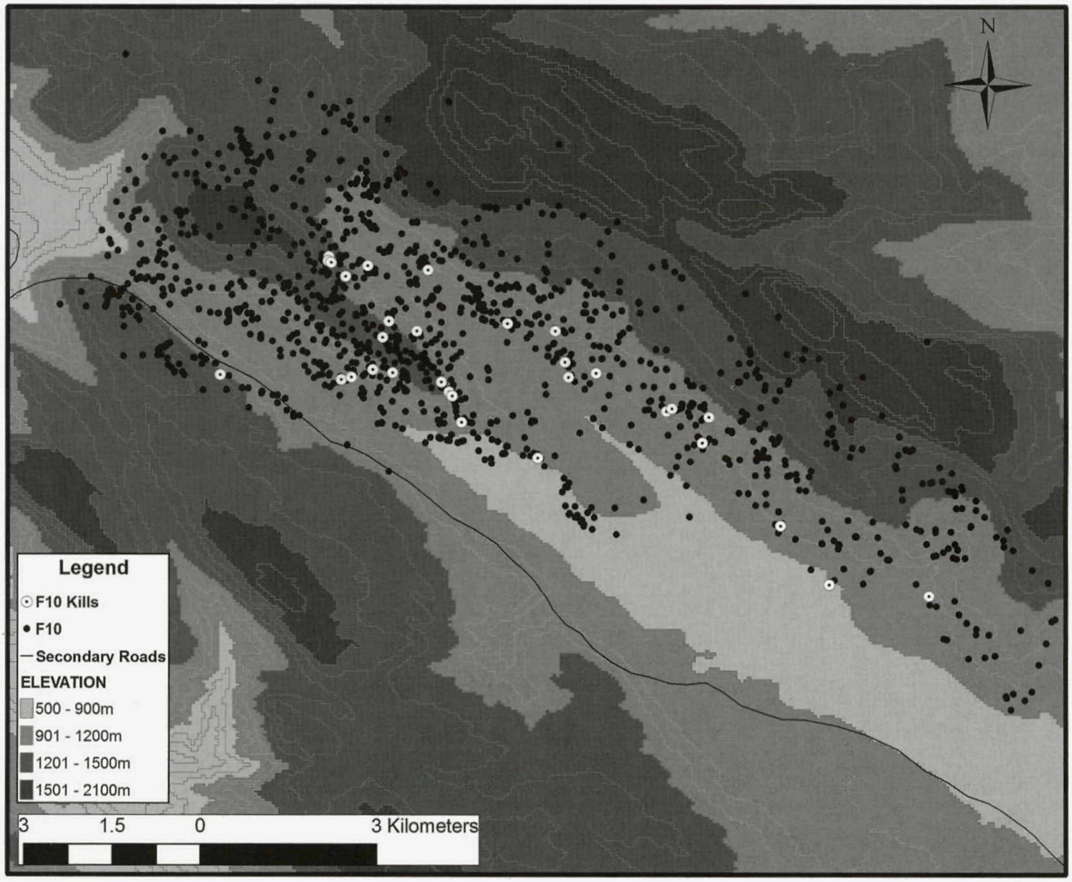

Fig. 1. GPS locations and confirmed kill sites of F10 in the period 18 June 2008–27 February 2009 (locations: $n = 1760$, kills: $n = 31$).

the Lomb-Scargle method calculates levels of statistical significance of peaks in the periodogram (Scargle 1982). For the frequency analyses, a source period of 24 hours was used. All statistical analyses were conducted using the open source programming language R (R developmental core team 2008).

RESULTS

Within the GPS-cluster study period from June 2008 to February 2009 (254 days), 1760 GPS positions and approximately 70 000 activity values were obtained. Seventy-eight potential kill sites from GPS data records of F10 were identified (Fig. 1). Fifty-four sites were investigated 171 ± 91 days (range = 22–302 d) after the potential predation event, which resulted in the detection of prey remains at 31 sites (confirmed kill sites). The success rate of finding kills using GPS cluster analysis was 57.4%. The majority of prey items killed by F10 consisted of klipspringers (22.6%) and rock hyraxes (55%), diurnal mammal species living in rocky, rugged terrain (Table 1). Other small antelope (common duiker and Cape grysbok) made up a further 9.7% of kills. All prey species were in the <20 kg class.

Activity recorded by the dual-axis accelerometer generally showed a decrease with the formation of a GPS location cluster. Comparison of activity within kill and non-kill clusters revealed no significant differences (GAM, $k = 7$, $P = 0.345$). We also did not find a significant difference (GAM, $k = 7$, $P = 0.07$) for mean activity when comparing clusters where larger prey (antelope) and smaller prey (rock hyraxes, rock rabbit) were found. However, activity levels at small-size and large-size kills were similar before the kills, but differed from each other after cluster onset. Activity decreased sharply at small-kills sites and stayed low for at least seven hours after the presumed time of kill,

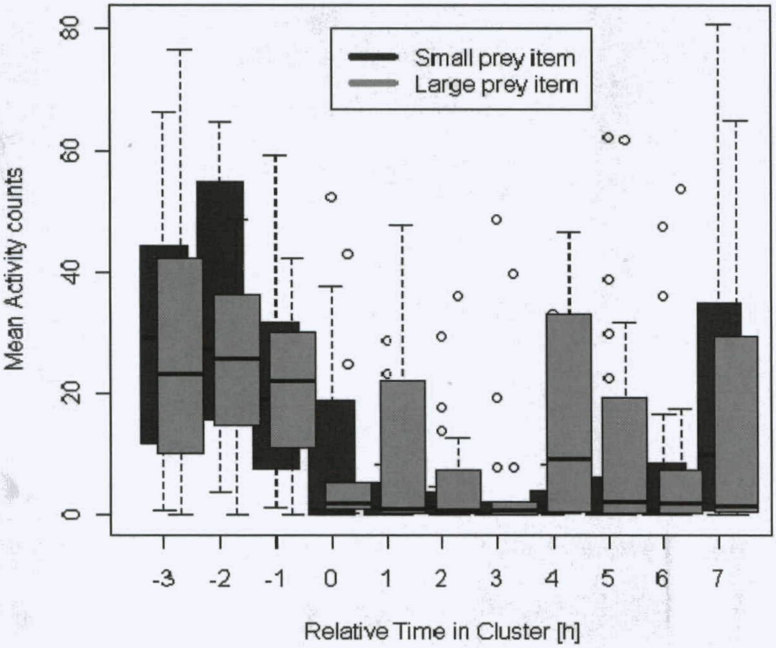

Fig. 2. Boxplot (median, upper and lower quartile, min and max) of activity counts from leopard F10 before and after cluster initiation, previously averaged over the particular hour relative to cluster onset. Black boxes indicate small prey items (rock hyrax, rock rabbit), grey boxes large kill items (antelope).

while activity at large-kill sites increased remarkably as soon as two hours after the kill – presumably as a result of eating motion (Fig. 2).

The Lomb-Scargle periodogram indicated that leopard activity at kill clusters and single positions differed remarkably in respect to the composition of their periodic components (Fig. 3). The algorithm revealed a circadian rhythm with a period length of 24 hours within most 'normal' activity, but not in feeding cluster intervals. In addition, the Lomb–Scargle periodogram detected ultradian rhythms with a period <24 hours (frequency >1).

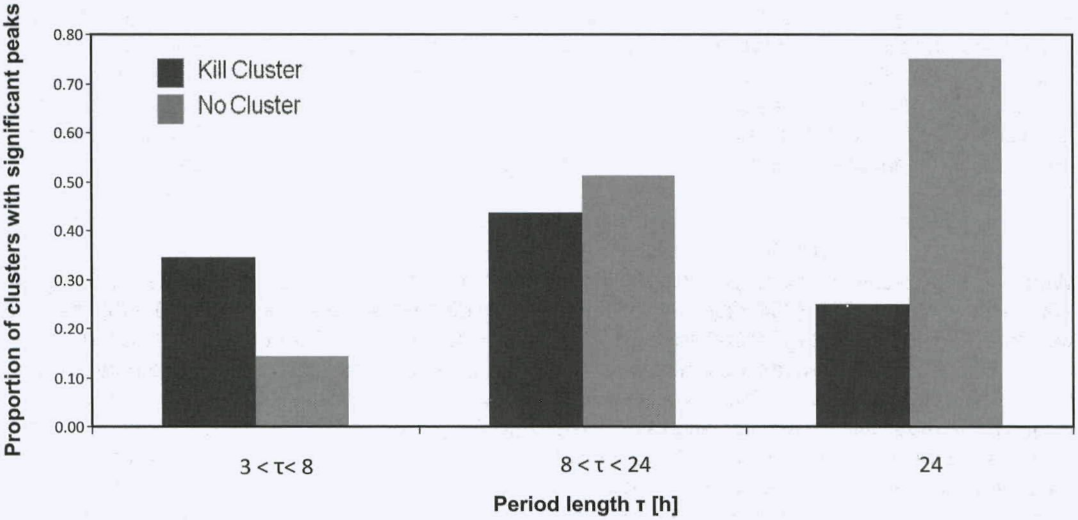

Fig. 3. Detection of significant periodic components within confirmed feeding cluster (black bars) and no-cluster (grey bars) sites computed by Lomb-Scargle algorithm.

Short-term rhythms were more frequent in feeding cluster activity than in normal activity. At frequencies of 4.5 and 5 (period lengths of 5.3 to 4.8 hours) the differences were significant ($P < 0.05$, binomial test), while highly significant ($P < 0.01$) for this sample at frequencies of 6.5, 8, 8.5 and 9 (period lengths of 3.7, 3, 2.8 and 2.7).

DISCUSSION

The use of GPS cluster analysis assumes that predators make a kill, stay for a certain amount of time, forming a cluster of GPS locations, and leave the cluster after the prey is consumed. It is also well understood that time spent at a kill site is dependent on size of the prey item (*e.g.* Tambling *et al.* 2010; Martins *et al.* 2011). We verified that cluster duration also affected success of locating kills, as demonstrated by Martins *et al.* (2011). Because there was a low probability of locating kills at sites occupied for less than 16 hours, these could have included resting sites as well as kill sites of smaller prey. We were therefore unable to determine an overall kill rate inclusive of all prey sizes. Generally, detection of smaller-bodied prey is crucial in avoiding kill-rate biases towards larger prey (Sand *et al.* 2005; Webb *et al.* 2008; Knopff *et al.* 2009). Small prey such as rodents or birds is likely to be consumed too quickly to be detected from GPS locations (however, see Tambling *et al.* (2012) for a method that supplements GPS methods with scat analyses, potentially reducing the bias towards larger prey). However, Martins *et al.* (2011) demonstrated that the importance of this type of prey in terms of biomass consumed was an insignificant part of the diet of leopards in the Cederberg.

In this study, we explored a new approach of combining GPS cluster analysis and activity data obtained from collar-integrated acceleration sensors in order to investigate the feeding ecology of leopards in the Cederberg Mountains, South Africa. At the time of our study, a sufficient GPS, acceleration and field survey data was only available for one leopard. Therefore, we did not aim to infer population level behaviour, but to present pilot data from a new methodological approach to current GPS cluster techniques. Although only a single female was monitored, our results are consistent with Martins *et al.* (2011), who found that klipspringers and rock hyraxes formed the majority of the leopard's diet in the Cederberg. Results were corroborated by previously conducted faecal analyses (Rautenbach 2010; Martins *et al.* 2011).

Combining the use of GPS locations and activity data allowed differentiation between certain behavioural categories (Krop-Benesch *et al.* 2010). An increase in leopard activity may be attributed to movement between two locations, or movement based at a cluster of locations where the animal is not in locomotion. Behaviour where the spatial activity of the animal cannot be deciphered due to close proximity of GPS locations, or length of time between locations, may be described using activity sensor data to include amongst others: hunting, pouncing, dragging of prey, rigorous feeding bouts when handling larger prey or resting (Krop-Benesch *et al.* 2010). No or very low recorded activity throughout the duration of clusters suggests these were probably resting sites (Anderson & Lindzey 2003). Thus, the integrated acceleration sensor provides a helpful means to reject non-kill clusters *a priori* in order to reduce field study efforts.

Using GAM, we were unable to differentiate between kill-clusters and non-kill clusters, either due to our small sample size and/or the high variety of activity at kill sites. However, there was a noticeable, although not statistically significant, interaction between the activity at small-kill sites where rock hyraxes were killed and the activity pattern at large-kill sites. As rock hyraxes provide only a fraction of the weight of antelope (Skinner & Chimimba 2005), carcasses are consumed effortlessly, with leopards remaining at kill site for intermediate periods of time. No distinct feeding activity pattern characteristic for small-kill sites was found. Killing and handling large prey animals such as klipspringers needs considerably more time and effort, resulting in distinct activity patterns at kills.

The frequency analyses (*i.e.* the Lomb-Scargle periodogram) demonstrated that large-kill clusters with a long duration were characterized by a specific activity pattern that consisted of resting intervals with low activity interrupted by feeding periods of variable length. Little is known about the activity and behaviour of leopards at a kill site (Bothma & Le Riche 1984; Bailey 1993). We can conclude that the Lomb-Scargle periodogram provides additional means to ascertain leopard activity while feeding on larger kills, as well, as differentiate kills from non-kills, given that the cluster duration is long enough (>24 hours). Therefore, the appropriate detection of kill sites using this approach is so far limited to larger kills. The method already has been recommended by Ruf (1999) for the study of biological rhythms in telemetrical time-series obtained from free-living animals. In this study, we showed that activity data can be used to provide insight into feeding activity patterns not understood before, and to determine duration and frequency of activities such as resting and feeding.

Studying leopards in mountainous regions is challenging (Martins *et al.* 2011) and requires a well-conceived implementation of suitable methods. Combining different techniques such as GPS/VHF telemetry and activity data from acceleration sensors provides helpful means in remote areas such as the Cederberg Mountains, where direct observation and scat collections are difficult. However, detection of kills by combination of activity and location analysis is laborious, as activity data need to be allocated to the corresponding location data. Due to their dissimilar impacts on the collar's battery life, GPS and activity data are obtained at different intervals. Analyses are further complicated when GPS fix schedules are irregularly changing as a consequence of collar success rate or schedule programming. Moreover, technical limitations of collars and time lags between event recording and field visits might have hampered the utility of GPS data in locating kills. For further study, observations of spatial use, activity and hunting behaviour on more individuals of each age and sex class should be performed to take into account intra-specific variability. Generally, it is advisable that clusters be investigated as soon as possible after they occur, because kills will be easier to locate (Tambling 2010), especially for smaller prey items. Increasing availability of real-time GPS data will assist in rapid investigation of clusters (Anderson & Lindzey 2003; Stotyn 2005). As acknowledged in Martins *et al.* (2011), kills in the Cederberg could have been washed away, covered by vegetation or burnt. In terms of scavengers in the area, there is currently no evidence of other large predators in the Fynbos part of the Cederberg where the home range of the monitored female was located. Densities of jackal in the Karoo part of our study area must be very low with fewer than five records since 2004 (Q. Martins, pers. comm.). Therefore, bone fragments would still remain. Despite possible biases, kills found still demonstrate diet based on clusters analysis. We were able to locate kill remains for up to 3.5 years after the kill event (Martins *et al.* 2011). In addition, the interval between the kill and searching for it was not significant in predicting whether a kill was found regardless of how this variable was included in the set of explanatory variables. However, in order to apply the method appropriately, smaller GPS fix intervals and a smaller time span between expected kills and surveys are required.

CONCLUSION

The purpose of this study was to present pilot data for using a novel approach of combining GPS and activity data in feeding ecology studies and to elucidate both advantages and disadvantages of using this method. We found that GPS clusters alone could provide one with certain parameters of predation (*e.g.* diet preferences, handling time). In combination with activity, one could predict kills from non-kills, particularly for larger prey. The method also gives further insight into feeding patterns when direct observation is improbable and might serve as a valuable addition to the classical GPS cluster investigation approach. Refining this technique with higher GPS fix rates, more efficient and timeous collection of kills will lead to an improved understanding of feeding patterns for wide-ranging and elusive predators in rugged terrain.

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