

ORIGINAL RESEARCH

Are camera traps a reliable method for estimating activity patterns? A case study comparing technologies for estimating brown hyaena activity curves

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Abstract

Camera traps and radio-tags are both frequently and widely used sampling methods for deriving wildlife activity patterns. While radio-tags continuously monitor a limited number of tagged individuals, camera traps have the potential to monitor all population members, albeit from spatially restricted, fixed points. Such differences might result in differing activity pattern estimates between the two sampling methods. However, few studies have compared the activity patterns derived from simultaneously employed sampling methods, or explored if using combinations of techniques might reveal greater insights into activity patterns. To address this, we compared the activity patterns derived from camera traps placed at latrines and den sites, both in combination and separately, to those from movement rates and the activity sensor collected by GPS collars on brown hyaena *Parahyaena brunnea*. The activity curve produced by combined camera traps showed a relatively high level of overlap with those produced by the movement rates and activity sensor; 0.88 (95% CI's 0.87–0.89) and 0.85 (95% CI's 0.83–0.86) respectively. However, camera traps reflected higher levels of activity from 00:00 to 06:00, than the radio-tag methods, with data from den sites alone producing this higher level of activity. The results suggest that although hyaenas were active during the 00:00 to 06:00 period, they were so mainly at small, localized den sites, which reflected as lower levels of activity as derived by movement rates and activity sensors. Although our results reflect data from a single species and season, they illustrate the value of using a combination of techniques to disentangle complex behavioural activity patterns.

Introduction

The activity patterns of wildlife result from both internal biological rhythms and adaptations to daily and seasonal variations in environmental factors (Kolowoski et al. 2007; Ordiz et al. 2017). These patterns develop in order for individuals to most efficiently exploit their environment whilst simultaneously decreasing potential risks, such as direct encounters with potential predators or dominant competitors (Kitchen et al. 2000). Documenting activity patterns has important implications for understanding niche theory, community assemblages and animal behaviour (Frey et al. 2017). Additionally, such knowledge can inform conservation management decisions; a number of studies have recorded wildlife

changing activity patterns in response to human presence (Ordiz et al. 2017; Gaynor et al. 2018), hunting pressure (Kitchen et al. 2000; van Doormaal et al. 2015) and the reintroduction of predators on the diel patterns of prey species (Tambling et al. 2015). Such shifts in activity patterns may be detrimental as they may leave the animal unable to utilize a spatial or temporal resource to its full potential (Kitchen et al. 2000).

Camera traps are now a well-established and widely utilized sampling method in the field of ecology, with several hundred published studies per year using them (Wearn and Glover-Kapfer 2019). The timestamps of camera trap records represent the timing of occurrences of wildlife in points in space, resulting in fine-scale temporal data which can be used to describe activity patterns

(Frey et al. 2017; Sollmann 2018). Recent analytical advances regarding the analysis of circular data collected by camera traps (e.g. Ridout and Linkie 2009; Rowcliffe et al. 2014) have significantly improved the level of detail which can be gained from camera traps regarding activity patterns beyond grouping observations into discrete categories (Frey et al. 2017). Such advances have resulted in a large number of studies using camera traps for recording the activity patterns of a range of species; warthog *Phacochoerus africanus*, kudu *Tragelaphus strepsiceros*, buffalo *Syncerus caffer* and elephant *Loxodonta africana* (Tambling et al. 2015), Asian wild cat species (Lynam et al. 2013), jaguar *Panthera onca* and puma *Puma concolor* (Foster et al. 2013) and several mammalian species in Jordan (Edwards et al. 2017).

The technological advances in radio-tags have simultaneously allowed for an alternative sampling method for constructing activity patterns from long-term and continuous time periods for a range of species. Calculating distances between consecutive spatial data points collected by radio-tags gives a measure of the movement rates of individuals throughout the day, which can then be used to describe activity patterns (e.g. Ordiz et al. 2017; Henderson et al. 2018). However, movement rates are calculated using the straight line, rather than actual, distance between points and therefore likely under sample real movement rates and are impacted by missed spatial data points (Brown et al. 2012). Alternatively, many modern global position satellite (GPS) collars and tags house a motion sensor or accelerometer which are constantly measuring the activity of the tagged animal independent from its spatial data (Ungar et al. 2005; Berger et al. 2013). Both motion sensors and accelerometers measure behaviour at a high temporal resolution and have been found to produce results comparable to direct observation (Brown et al. 2013). Such data often allows a finer-scale representation of activity patterns than other methods (Zhang et al. 2015). Studies using accelerometer and motion sensors are becoming increasingly frequent in the literature, and advances in the technology are now allowing even small bodied (<100 g) species to be monitored (Hammond et al. 2016).

Differences in the activity patterns constructed using camera trap and radio-tags might be expected due to a number of factors, including the section of the target population they represent. Camera traps have the potential to collect temporal data from the entire population within a restricted and fixed area, whereas each radio-tag collects data from a specific individual throughout its home range and thus can be considered a more complete description of individual activity (Frey et al. 2017). Depending on the camera trap set-up employed, that is, baited, at resources such as water, etc, temporal data may reflect the timing of specific behaviours such as foraging

(Lashley et al. 2018), or be influenced by the presence of competitor species (Edwards et al. 2014). Furthermore, the probability of detecting a species may be influenced by a number of factors including camera trap placement (Mann et al. 2014; Edwards et al. 2016; Kolowski and Forrester 2017), body size (Randler and Kalb 2018) and ambient temperature at the study site (Rovero et al. 2014). In contrast, individual variation in diel patterns has previously been recorded for a number of species (Thompson et al. 1989; Kolowski et al. 2007; Hertel et al. 2017), and may confound inferences made regarding activity patterns derived from a low number of radio-tagged individuals.

Despite the potential for differences in activity patterns derived from radio-tags and camera traps, few studies have made such comparisons (Frey et al. 2017, but see Lashley et al. 2018). To help fill this data gap, we compared activity curves and circular datasets produced for brown hyaena *Parahyaena brunnea*, using three sampling methods applied simultaneously; (1) camera traps placed at latrines and dens, both separately and in combination, (2) straight line distances travelled between consecutive spatial data points from GPS collars, referred to as movement rates, and (3) the motion sensor within GPS collars, referred to as activity sensor. Both activity sensor and movement rates were compared as the two methods measure activity in a different way; activity sensors measure movement of the collar/animal and may therefore include activity such as feeding or grooming. In contrast, movement rates correspond only to when the animal is travelling within its environment. We firstly asked if camera traps can be used as an accurate method for estimating activity patterns, and, secondly if deriving activity patterns from a variety of sampling methods can give greater insights into species ecology. Given that brown hyaena of both sexes have been recorded as regularly visiting latrines, and latrines being scattered throughout the territory (Mills 1990), it was hypothesized activity patterns derived from latrine camera trap data would show high overlap with those derived from movement rates and the activity sensor. However, den camera traps, which are likely to reflect activity at a small, localized area, would show differences to the activity curves produced by movement rates and activity sensors.

Materials and Methods

Study site

The study took place on the Okonjima Nature Reserve (ONR), a privately owned 200 km² nature reserve, located approximately 50 km south of Otjiwarongo, north-central Namibia. The reserve receives an average annual rainfall

of 450 mm, which falls during the hot wet season from October to March. The vegetation is predominantly tree and scrub savannah, interspersed with silver *Terminalia sericea* and several *Acacia* species. The ONR is fully enclosed by an electrified perimeter fence, erected in 2010, which is impenetrable to brown hyaena (Edwards et al. 2019), however, brown hyaenas do not preferentially select for areas adjacent to the fence line (Edwards et al. 2020). Tourism lodges and staff housing are situated in the south-east section of the reserve, and the 20 km² surrounding these buildings is also enclosed with an electric wildlife proof fence, resulting in a total of approximately 180 km² of the ONR over which a variety of wildlife occur. The brown hyaena population was recently estimated to occur at a density of 24.01 brown hyaena/100 km², the highest density recorded throughout its distribution (Edwards et al. 2019).

Camera traps

During the 60-day survey period, which ran from 3 July 2019 to 1 September 2019, a total of 32 brown hyaena

latrines were monitored by camera trap as a sampling method for collecting temporal data (Fig. 1). Latrines were monitored in two of the brown hyaena clan home ranges, as part of an ongoing larger study (Edwards et al. in prep), hence the non-uniform coverage of the ONR. Brown hyaena latrines, collections of faeces at which multiple individuals visit to scent mark and gather olfactory information (Mills 1990) represent predictable areas of brown hyaena activity. Although latrine cameras are likely to reflect activity curves relating to when individuals are performing territorial behaviours, this approach was chosen for comparison as it is a common method for surveying brown hyaenas and is known to result in higher detection rates than cameras placed along roads (Edwards et al. 2019). Latrines were located by driving roads within the study site, and were mostly found at conspicuous landmarks such as next to roads, especially at cross roads, river-road junctions and at entrance gates. Monitored latrines were distributed with a mean nearest neighbour distance of 1.11 km (± 0.82 km, range 0.79 km–2.35 km). Latrines with the highest number of faeces, which also gave a uniform spatial distribution across the home range

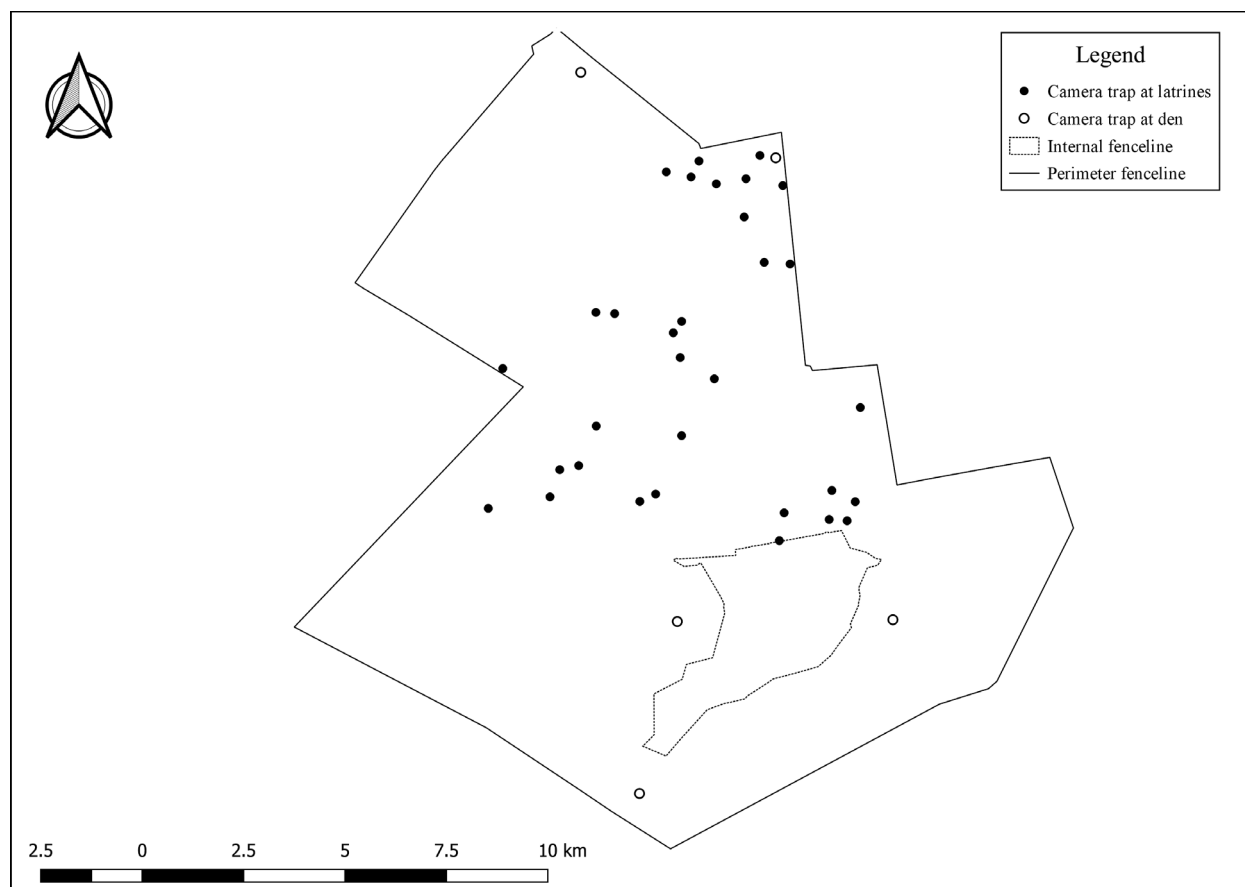


Figure 1. Locations of camera traps for brown hyaena latrine and den monitoring on ONR.

were chosen for monitoring, based on the assumption of a positive relationship between the number of faeces and the frequency of visits to latrines. Each latrine was monitored by a single Cuddeback X-change 11339 infra-red camera trap (Non Typical Inc., Wisconsin, USA), housed in a 'Cuddesafe' protective housing.

During the same 60-day survey period, five communal den sites were monitored by camera trap. Brown hyaenas utilize two types of dens; natal dens are those used only by the mother at which to give birth and raise the young for the first 3 months of their lives, and communal dens. Communal den sites are used by all clan members and cubs are brought there around 3 months of age (Mills 1990). Dens were located by plotting brown hyaena GPS data in QGIS 2.8.4 Wien (Quantum GIS Development Team 2005), and connecting consecutive GPS points by lines, using the 'Points to path' function. When points and lines are plotted in this way, dens reliably show up at clusters of points, with movement lines from all directions centering on the den site (Wiesel et al. 2019). Camera traps were focused on the main den burrow entrance at a distance of approximately two meters from the entrance. Only photographs showing adult individuals were included for analysis to be comparable to the latrine dataset which only contained adult individuals, and the GPS collar dataset which also only included adult individuals.

Camera traps were mounted approximately 50 m from the ground on a metal pole, and programmed to take five photos per trigger, with no delay between triggers and a photo quality of 20 mega-pixel. To produce activity curves, camera trap images of brown hyaenas at the latrines were first individually identified using the unique front leg stripe patterns by the lead author, and then classed into independent events using a criterion of a minimum of 30 min between consecutive photographs of the same individual. At the dens, adults often stayed for prolonged periods of time (maximum time 5 h 28 min), and thus to try and ensure time stamps were temporally independent, a random sub-sample of 50% of the records from each den were selected and included in the analysis. The time stamps of independent events were then used to produce activity curves.

GPS collars

During the study period, spatial datasets from five adult brown hyaena were available. These individuals consisted of one male and four females, which had been collared prior to the study period (Table 1), as part of an ongoing study. Brown hyaenas were either free darted ($n = 5$) or captured within a large (approx. 2×3 m) wire box trap internally lined with industrial grade conveyor belt rubber

Table 1. Summary of brown hyaenas monitored on Okonjima Nature Reserve.

ID	Sex	Monitoring start date
OHB04	Female	1 July 2019
OHB05	Male	3 July 2019
OHB06	Female	12 March 2019
OHB10	Female	14 November 2018
OHB11	Female	11 June 2019

to ensure hyaenas could not damage their teeth or foot pads by biting or digging at the wire ($n = 1$). The box trap was monitored with a live-feed camera and fitted with a remotely triggered door which ensured the capture team was able to dart the hyaena in less than 45 min after closing the door, minimizing stress on the animal. Brown hyaenas were darted using a Pseudart projector, using an average weight of 50 kg per animal for dose calculation. A combination of Ketamine (Intersana, Windhoek, Namibia) 125 mg, Medetomidine 2.50 mg (Kyron Laboratories, Johannesburg, RSA); Butorphanol 12.50 mg (Kyron Laboratories, Johannesburg, RSA) was used. If sedation was not deep enough, Ketamine at a dose of 0.50 mg/kg (approx. 20–25 mg) was intravenously injected via the saphenous vein. A minimum time lapse of 45 min was used before the antidote 'Antisedan' (Zoe-tis, Sandton, RSA) was given, at dose of 2.50 mg intravenously and 5 mg intramuscularly, and 'Trexonil' at 12.50 mg intravenously and 25 mg intramuscularly (Wildlife Pharmaceuticals, White River, RSA). Hyaenas were monitored using Wireless Wildlife (Potchefstroom, RSA) GPS collars, scheduled to take one fix per hour during the 24-h period. Data were remotely transferred via ultra-high frequency (UHF) connection base stations and repeaters.

Movement rates

Movement rates were used as a proxy for activity, based on the assumption of larger distances travelled equating to higher levels of activity throughout the diel period. Euclidean distances between consecutive spatial data points were calculated using the 'geosphere' package (Hijmans 2017) in statistical program R (R Core Development Team 2014). Such distances represent the minimum distances travelled between consecutive points rather than actual distances. Distances travelled were pooled over all individuals and the mean distance travelled per hour period calculated. The mean distances travelled were then converted into a continuous variable over a 24 time-period following (Lashley et al. 2018), where, if, for example, a mean distance of 350 m was calculated for the

period 03:00–04:00, 350 randomly distributed times between 03:00 and 04:00 were produced. This method allows the data to be continuous, but still representative of the observed activity curves based on motion sensor data (Lashley et al. 2018).

Activity sensor

The GPS collars contained a motion sensor, an omnidirectional tilt and vibration sensor, used to monitor the movement of the collar/animal. The sensor acts as a switch which chatters open and closed as it is tilted or vibrated, and is connected directly to one of the collar's central processing units and thus motion results in a higher count rate over a specified time period (O'Brien et al. 2013). To estimate activity curves, activity counts were pooled over all individuals and the mean count per hour period calculated. As with movement rates, the activity counts per hour throughout the 24-h period were pooled for all individuals and the mean activity count per hour calculated. Mean activity counts were then converted into a continuous variable following Lashley et al. (2018).

Data analysis

The package 'overlap' (Ridout and Linkie 2009) in statistical program R (R Core Development Team 2014) was used to non-parametrically estimate and plot the probability function of the distribution for each sampling method, plus a dataset which combined all camera trap (den and latrine) records, producing a visual representation of the activity pattern, referred to as the 'activity curve'. Here, events (time stamps from camera traps and the randomly distributed times produced from the distances travelled per hour and activity counts data), were viewed as a random sample taken from an underlying continuous temporal distribution, describing the probability of an event occurring at any given time (Ridout and Linkie 2009). The package was also used to calculate coefficients of overlap between the activity curves produced by each sampling method, using estimator Δ , a continuous variable between 0 and 1, where 0 indicates no overlap, and 1 indicates total overlap. The coefficient is defined as the area under the curve formed by taking the minimum of each density function of the two compared cycles at each time point (Monterroso et al. 2014). Confidence intervals for coefficients of overlap were calculated using 1000 bootstraps.

To statistically test for significant differences in the circular data produced by each sampling method, Watson's U^2 statistic was applied using package 'Circstats' (Lund and Agostinelli 2018), to test the null hypothesis of the

two samples coming from the same distribution. Descriptive statistics, such as the mean vector, were deemed unsuitable for the data produced, which showed bimodal activity peaks. For such data, Frey et al. (2017) noted the mean vector is likely to fall between the two peaks and therefore not biologically relevant.

Results

During the study period a total of 1878 camera trap nights were achieved by the latrine camera traps, with 586 independent brown hyaena events recorded, equating to a detection success of 0.31 events per trapping night. At the five dens a total of 300 camera trap nights were achieved, over which a total of 11121 photos of brown hyaenas were recorded. When taking a random sub-sample of 50% of these images, a total of 5560 images were used for analysis to try and ensure temporal independence. Therefore, 6146 camera traps images were included in the analysis. A total of 7200 spatial data points were collected from the five brown hyaena, and when converted into a continuous dataset, 14802 randomly distributed times were produced for movement rate dataset and 18 204 produced for the activity sensor dataset.

The density probability plots from all sampling methods showed brown hyaenas exhibited mainly nocturnal activity, with activity peaks around 23:00 for the activity and movement data sets and bimodal peaks at approximately 23:00 and 01:00 for the combined camera traps. The latrine camera traps showed a peak of activity around 19:00, whilst the den camera traps showed bimodal peaks at approximately 21:00 and 02:00. All sampling methods showed activity troughs around 15:00.

The overlap plots and coefficients of overlap indicated the activity curves produced by the movement rate and activity sensor sampling methods had the greatest degree of overlap with each other, with a coefficient of overlap of 0.95 (95% CI's 0.94–0.95) (Fig. 2). The movement rate and combined camera traps had a coefficient of overlap of 0.85 (95% CI's 0.83–0.86) (Fig. 2), and the activity sensor and combined camera traps showed a coefficient of overlap of 0.88 (95% CI's 0.87–0.89) (Fig. 2) (Table 2). The latrine camera traps and den camera traps showed a coefficient of overlap of 0.83 (95% CI's 0.79–0.86) (Fig. 2). The latrine and movement sampling methods showed a coefficient of overlap of 0.87 (95% CI's 0.85–0.88), whilst the latrine and activity sensor showed a coefficient of overlap of 0.84 (95% CI's 0.84–0.88) (Fig. 2). The den camera traps and movement sampling method showed a coefficient of overlap of 0.86 (95% CI's 0.85–0.88), whilst the den camera traps and activity sensors showed a coefficient of overlap of 0.87 (95% CI's 0.86–0.88) (Fig. 2). The Watson's U^2 test indicated significant

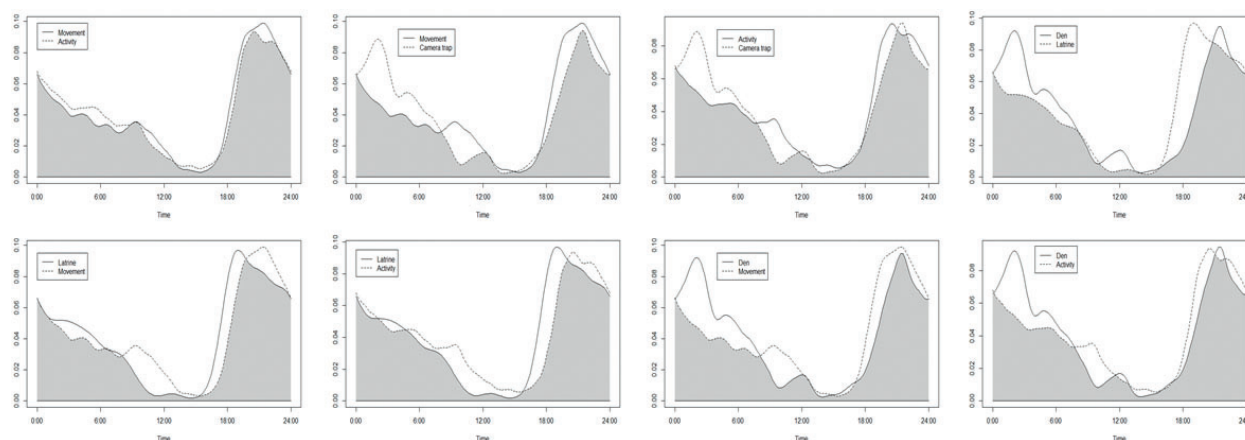


Figure 2. Overlap plots of the activity curves produced by different methods, with Δ ranging from 0.83 (95% CI's 0.79–0.86) for the den and latrine camera traps to 0.95 (95% CI's 0.94–0.95) for the activity sensor and movement rates.

differences between all pairwise comparisons of circular datasets (Table 2).

Discussion

With rapid advancements in wildlife monitoring technology, researchers are left with a variety of options for estimating species activity patterns. Relatively few studies have compared the activity patterns derived from simultaneously employed sampling methods utilizing different technologies (but see Lashley et al. 2018), nor explored how using combinations of techniques might reveal greater insights into activity patterns. By comparing the activity curves produced by three sampling methods; camera traps at latrines and dens, both separately and in combination, movement rates and activity sensors from GPS collars on brown hyaenas, we found the activity curves produced by activity sensor and movement rates showed a relatively high degree of overlap. In contrast, combined camera traps reflected higher levels of activity from 00:00 to 06:00 than activity sensor and movement rate methods. When comparing the activity patterns from den and latrine camera traps, data from den sites alone produced the higher level of activity from 00:00 to 06:00. The results suggest that although hyaenas were active during the 00:00 to 06:00 period, they were so mainly at the den sites, small localized areas, which reflected as lower levels of activity as derived by movement rates and activity sensors. Although our results reflect data from a single species and season, they illustrate the value of using a combination of techniques to disentangle complex behavioural activity patterns.

The activity curves produced by the combined camera traps overlapped those produced by the activity sensor

Table 2. Summary of the coefficients of overlap and Watson's U^2 statistics produced for each pairwise comparison of sampling methods.

Sampling methods	Overlap Δ (95% CI's)	Watson's U^2
Activity sensor vs. movement rate	0.95 (0.94–0.95)	0.35 ($P \leq 0.01$)
Activity sensor vs. combined camera traps	0.88 (0.87–0.89)	0.36 ($P \leq 0.01$)
Movement rate vs. combined camera traps	0.85 (0.83–0.86)	0.28 ($P \leq 0.01$)
Latrine camera traps vs. movement rate	0.87 (0.85–0.88)	0.31 ($P \leq 0.01$)
Latrine camera traps vs. activity sensor	0.84 (0.84–0.89)	0.33 ($P \leq 0.01$)
Den camera traps vs. movement rate	0.86 (0.85–0.88)	0.29 ($P \leq 0.01$)
Den camera traps vs. activity sensor	0.87 (0.86–0.88)	0.30 ($P \leq 0.01$)

and movement rates by 0.88 (95% CI's 0.87–0.89) and 0.85 (95% CI's 0.83–0.86) respectively, suggesting the combined camera trap sampling method produced a relatively accurate representation of activity curves. When comparing the activity curves produced by both active (food baited) and passive (set along game trails) camera traps to radio-tags in a range of species, Lashley et al. (2018) recorded overlap coefficients of 0.74 to 0.84 respectively, which were classed as relatively high. Despite the high levels of overlap estimated for the brown hyaena sampling methods, statistical tests indicated significant differences between all datasets produced by the different sampling methods. Furthermore, even an overlap coefficient of 0.95 (95% CI's 0.94–0.95) between the activity

curves produced by the activity sensor and movement rate sampling methods, produced a significant difference result. Such results may rather reflect a problem associated with the p -value of significance tests when using large sample sizes (Lin et al. 2013), in which, even very small differences in comparison datasets may result in a statistically significant difference. The movement rate and activity sensor datasets consisted of 14 802 and 18 204 times respectively and hence the statistical significances produced may not be a reflection of real differences in the datasets.

Despite the high degree of overlap between the combined camera traps with the activity sensor and movement rates, overlap plots highlighted a lower degree of activity between 00:00 and 06:00 recorded by the latter two methods. The reason for this difference between the sampling methods is revealed when the activity patterns from the latrine and den camera traps are compared. The activity pattern from the latrine camera traps follows closely that of the activity sensors and movement rates; a lower degree of activity from 00:00 to 06:00. However, the den camera traps show a higher level of activity for that period. Den sites are the central point of brown hyaena activity, and exist primarily to provide protection for cubs for the long period adults are away foraging (Mills 1990). At the study site, den sites typically consisted of a small area (approximately 5×5 m), of bare ground surrounding one or more den burrow entrances. All clan members visit communal den sites, to socialize and bring back food for the cubs (Mills 1990), and camera trap records from the study showed adults playing with cub and sub-adults, grooming and bringing back food to the den sites. Therefore, as the activity at den sites focuses around a relatively small area, both movement rates and activity sensor counts are likely to be lower than when hyaenas are travelling through the territories performing behaviours such as foraging and scent-marking, explaining the differences seen in the activity curves. These results suggest that using radio-tag methods alone, that is, movement rates and activity sensor counts, is unlikely to capture the full activity pattern of brown hyaena.

Data from den camera traps showed bimodal peaks in activity around 21:00 and 02:00, whereas latrine camera traps showed a single activity peak at approximately 19:00. Such results, give insights into how the active period of brown hyaena's diel period is constructed behaviourally at the study site; the first part of the night is likely spent performing territorial behaviours related to visiting latrines, whereas the second half is spent mainly at communal den sites. Although relatively few data are available on brown hyaena activity patterns, Mills (1990), estimated for individuals in the Kalahari, approximately

37.60% of their time was spent foraging/moving, in comparison to just 0.80% spent on social activities, as calculated from extended periods of directly following and observing individuals. Furthermore, Mills (1990) suggested brown hyaenas in the Kalahari were active for a higher portion of the diel cycle than spotted hyaenas, due to the habitat of foraging on one small item and then moving onto the next, rather than consuming larger food items as spotted hyaenas *Crocuta crocuta* do. Although the activity patterns from this study do not reveal when individuals might be actively foraging, it is most likely occurring during the first part of the night, as represented by higher movement rates and activity sensor counts. The time spent at the dens, and therefore, the percentage of the activity cycle spent engaged in social behaviours cannot be calculated from our dataset; the hourly GPS positions are unsuitable for fine scale temporal calculations and camera traps are only recording that den activity within their field of vision, individuals spending time at the den out of range of the camera will not be recorded. Setting GPS collars to record spatial data and activity counts at a higher temporal resolution, for example one reading taken every 5 min, would enable the time spent within the vicinity of the den to be calculated more accurately and compared to other study sites such as the Kalahari. However, such gains in data resolution must be weighed against the resulting decreased battery life on the radio-tag.

Although the activity curve produced by the combined camera traps showed relatively high levels of overlap with the activity curves produced by the movement rates and activity sensor sampling methods, camera traps reflected a lower level of late morning activity (i.e. 10:00 to 12:00). Such differences might reflect individuals moving away from the roads, where the latrine camera traps were located, as well as away from the communal den sites, into more secluded areas for use as daytime resting sites during that time. The opposite was found to be true for spotted hyaena in Hwange National Park (Kushata et al. 2017); spotted hyaena preferred resting sites close to the roads which was attributed to roads benefitting cursorial predators by allowing them to move faster through an area, and the lack of tourism activity on the roads during the study period. In contrast, brown hyaenas are predominantly scavengers (Mills 1990), and our study period coincided with the high peak of tourism activity on ONR. Alternatively, brown hyaenas may not rest in areas near latrines. Mills (1990) found that whilst latrines were scattered across the territory, they were more concentrated at the borders. Brown hyaenas may choose day time resting sites away from the territory border as a means of reducing potentially aggressive encounters with neighbouring clan members and if true, this could explain the lack of

late morning activity detected by camera traps. Additionally, within the study site communal den sites are rarely used as daytime resting sites (Edwards et al. in prep), although the reasons for this are unclear.

One limitation of our dataset is the female bias of individuals monitored with GPS collars. Four of the five monitored individuals were female, whereas the monitored male was a nomadic individual; no clan males were monitored during the study period. In contrast, the camera traps, having the potential to record all members of the population, undoubtedly recorded a higher proportion of male activity. Nomadic brown hyaenas are defined as those which move over large areas with an apparent disregard for territory boundaries, and do not form lasting relationships with conspecifics (Mills 1990). During the study period, the male, 'OHB05', was not recorded visiting the den site of any clan and thus this individual's activity pattern might be expected to differ from clan individuals on the basis of having little to no social interactions. Inter-sexual differences in activity patterns have previously been detected for large carnivores; Kolowski et al. (2007) found differences between the activity patterns and movement rates of male and female spotted hyaena with males tending to be more active than females, and more recently Havmøller et al. (2020), detected sexual segregation in the activity patterns of leopard *Panthera pardus*, with male leopards being more nocturnal than females. A larger sample of GPS monitored brown hyaenas, with a more equal ratio of male to female, would be needed to try and ascertain if differences between camera trap and GPS collar derived activity patterns might also be resulting from inter-sexual differences in activity patterns.

Placing camera traps along roads, is a frequently used method for surveying large carnivores; tiger *Panthera tigris* (Lynam et al. 2009), leopard *Panthera pardus* (Chapman and Balme 2010) and puma *Puma concolor* (Negrões et al. 2010), and has been found to result in a significantly higher detection success in comparison to off-road or random camera trap placements (Mann et al. 2014; Kolowski and Forrester 2017). Although brown hyaena are known to use roads whilst travelling (Welch et al. 2016), the placement of camera traps of roads resulted in a lower detection success in comparison to latrines at the study site (Edwards et al. 2019). Despite the potential lower capture success rates, activity curves derived from road camera traps may result in more accurate activity curves as they are not only reflecting activity patterns related to territorial behaviours as latrine camera traps do. As a result, we recommend future studies include camera traps placed along roads for comparisons of activity patterns. However, as dens at the study site were located away from roads (Edwards, pers. obs.), it is

unlikely that road camera traps would capture the period of activity between 00:00 and 06:00 detected by the den camera traps.

Although this study focuses on a single species and season, it adds to a limited number of studies comparing camera trap and radio-tag sampling methods for examining activity patterns of wildlife. Furthermore, it highlights how using novel combinations of sampling methods, and comparing the activity pattern each method produces, can give greater insight into the activity patterns of a species. Without including camera trap data from den sites, the high levels of activity during the second half of the night at den sites would have been not been revealed by either latrine camera traps, activity sensors or movement rates. While we advocate camera traps as a sampling method for estimating wildlife activity curves, we note that the influence of camera trap placement and the behavioural ecology of focal species must be taken into consideration when making inferences about resultant activity patterns. We therefore recommend, where possible, combinations of methods be used for estimating species activity curves, especially for those species which might frequently perform social or other behaviours at localized sites. Given the limited scope of this study, future studies should include higher sample sizes of radio-tagged individuals and be conducted across multiple seasons for a range of species.

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Data Availability Statement

Due to the 'Near threatened' status of brown hyaena and the exact spatial data showing den locations, data from this manuscript is not deposited in a public repository, but can be requested from the corresponding author.

References

- Berger, A., H. Hofer, and M. Heurich. 2013. Long-term measurement of roe deer (*Capreolus capreolus*) (Mammalia: Cervidae) activity using two-axis accelerometers in GPS-

- collars. *Ital. J. Zool.* **80**, 69–81. <https://doi.org/10.1080/11250003.2012.725777>
- Brown, D., S. LaPoint, R. Kays, W. Heidrich, F. Kummeth, and M. Wikelski. 2012. Accelerometer-informed GPS telemetry: reducing the trade-off between resolution and longevity. *Wildl. Soc. Bull.* **36**, 139–146.
- Brown, D., R. Kays, and R. Wilson. 2013. Observing the unwatchable through acceleration logging of animal behavior. *Anim. Biotelemetry* **1**, 1–16. <https://doi.org/10.1186/2050-3385-1-20>
- Chapman, S., and G. Balme. 2010. An estimate of leopard population density in a private reserve in KwaZulu-Natal, South Africa, using camera-traps and capture-recapture models. *S. Afr. J. Wildl. Res.* **40**, 114–120. <https://doi.org/10.3957/056.040.0202>
- van Doormaal, N., H. Ohashi, S. Koike, and K. Kaji. 2015. Influence of human activities on the activity patterns of Japanese sika deer (*Cervus nippon*) and wild boar (*Sus scrofa*) in Central Japan. *Eur. J. Wildl. Res.* **61**, 517–527. <https://doi.org/10.1007/s10344-015-0922-8>
- Edwards, S., A. C. Gange, and I. Wiesel. 2014. Spatiotemporal resource partitioning of water sources by African carnivores on Namibian commercial farmlands. *J. Zool.* **297**, 22–31. <https://doi.org/10.1111/jzo.12248>
- Edwards, S., A. C. Gange, and I. Wiesel. 2016. An oasis in the desert: the potential of water sources as camera trap sites in arid environments for surveying a carnivore guild. *J. Arid Environ.* **124**, 304–309. <https://doi.org/10.1016/j.jaridenv.2015.09.009>
- Edwards, S., M. Al Awaji, S. Edwards, M. Al, E. Eid, and O. Attum. 2017. Mammalian activity at artificial water sources in Dana Biosphere Reserve, southern Jordan. *J. Arid Environ.* **141**, 52–55. <https://doi.org/10.1016/j.jaridenv.2017.01.015>
- Edwards, S., J. Noack, L. Heyns, and D. Rodenwoldt. 2019. Evidence of a high-density brown hyena population within an enclosed reserve: the role of fenced systems in conservation. *Mammal Res.* <https://doi.org/10.1007/s13364-019-00432-7>
- Edwards, S., J. Noack, L. Heyns, D. Rodenwoldt, and L. M. Tarjan. 2020. Socioecology of a high-density brown hyaena population within an enclosed reserve. *Mammal Res.* **65**, 223–233.
- Foster, V. C., P. Sarmiento, R. Sollmann, N. Torres, A. T. A. Jacomo, N. Negroes, et al. 2013. Jaguar and puma activity patterns and predator-prey interactions in four Brazilian biomes. *Biotropica* **45**, 373–379.
- Frey, S., J. T. Fisher, A. C. Burton, and J. P. Volpe. 2017. Investigating animal activity patterns and temporal niche partitioning using camera-trap data: challenges and opportunities. *Remote Sens. Ecol. Conserv.* **3**, 123–132. <https://doi.org/10.1002/rse2.60>
- Gaynor, K. M., P. S. Branco, R. A. Long, D. D. Gonçalves, P. K. Granli, and J. H. Poole. 2018. Effects of human settlement and roads on diel activity patterns of elephants (*Loxodonta africana*). *Afr. J. Ecol.* **56**, 872–881. <https://doi.org/10.1111/aje.12552>
- Hammond, T. T., D. Springthorpe, R. E. Walsh, and T. Beg-Kirkpatrick. 2016. Using accelerometers to remotely and automatically characterize behaviour in small animals. *J. Exp. Biol.* **219**.
- Havmøller, R. W., N. S. Jacobsen, N. Scharff, F. Rovero, and F. Zimmermann. 2020. Assessing the activity pattern overlap among leopards (*Panthera pardus*), potential prey and competitors in a complex landscape in Tanzania. *J. Zool.* **311**, 1–8. <https://doi.org/10.1111/jzo.12774>
- Henderson, T., K. Vernes, and R. Rajaratnam. 2018. Using GPS technology to understand spatial and temporal activity of kangaroos in a peri-urban environment. *Animals* **8**, 97. <https://doi.org/10.3390/ani8060097>
- Hertel, A. G., J. E. Swenson, and R. Bischof. 2017. A case for considering individual variation in diel activity patterns. *Behav. Ecol.* **28**, 1524–1531. <https://doi.org/10.1093/beheco/arx122>
- Hijmans, R. J. 2017. geosphere: spherical trigonometry. R package, version 1.5-7. <https://CRAN.R-project.org/package=geosphere>
- Kitchen, A. M., E. M. Gese, and E. R. Schauster. 2000. Changes in coyote activity patterns due to reduced exposure to human persecution. *Can. J. Zool.* **78**, 853–857.
- Kolowski, J. M., and T. D. Forrester. 2017. Camera trap placement and the potential for bias due to trails and other features. *PLoS One* **12**, 1–20. <https://doi.org/10.1371/journal.pone.0186679>
- Kolowski, J. M., D. Katan, K. R. Theis, and K. E. Holekamp. 2007. Daily patterns of activity in the spotted hyena. *J. Mammal.* **88**, 1017–1028.
- Kushata, J. N., S. Periquet, T. Tarakini, M. Muzamba, B. Mafuwa, A. J. Loveridge, et al. 2017. Drivers of diurnal rest site selection by spotted hyaenas. *J. Zool.* **304**, 132–140. <https://doi.org/10.1111/jzo.12504>
- Lashley, M. A., M. V. Cove, M. C. Chitwood, G. Penido, and B. Gardner. 2018. Estimating wildlife activity curves: comparison of methods and sample size. *Sci. Rep.* **8**(1), <https://doi.org/10.1038/s41598-018-22638-6>
- Lin, M., H. C. Lucas, and G. Shmueli. 2013. Too big to fail: large samples and the *p*-value problem. *Inf. Syst. Res.* **24**, 883–1167.
- Lund, U., and C. Agostinelli. (2018). CircStats: circular statistics, from "Topics in Circular Statistics" (2001). R package version 0.2-6. <https://CRAN.R-project.org/package=CircStats>
- Lynam, A. J., A. Rabinowitz, T. Myint, M. Maung, K. T. Latt, and S. H. T. Po. 2009. Estimating abundance with sparse data: tigers in northern Myanmar. *Popul. Ecol.* **51**, 115–121. <https://doi.org/10.1007/s10144-008-0093-5>
- Lynam, A. J., K. E. Jenks, R. Steinmetz, and D. H. Reed. 2013. Terrestrial activity patterns of wild cats from camera-trapping. *Raffles B. Zool.* **61**, 407–415.

- Mann, G. K. H., M. J. O'Riain, and D. M. Parker. 2014. The road less travelled: assessing variation in mammal detection probabilities with camera traps in a semi-arid biodiversity hotspot. *Biodivers. Conserv.* **24**, 531–545. <https://doi.org/10.1007/s10531-014-0834-z>
- Mills, M. G. L. 1990. *Kalahari Hyenas Comparative behavioural ecology of two species*. Chapman and Hall, United Kingdom.
- Monterroso, P., P. C. Alves, and P. Ferreras. 2014. Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: implications for species coexistence. *Behav. Ecol. and Sociobiol.* **68**, 1403–1417.
- Negrões, N., P. Sarmiento, J. Cruz, C. Eira, E. Revilla, C. Fonseca, et al. 2010. Use of camera-trapping to estimate puma density and influencing factors in Central Brazil. *J. Wildl. Manage.* **74**, 1195–1203. <https://doi.org/10.2193/2009-256>
- O'Brien, G., F. Jacobs, M. Burnette, P. Kruger, I. F. Botha, and J. A. Cordier. 2013. Remote and manual radio telemetry methods to monitor and use fish behaviour in South Africa's inland waters. Report to the Water Research Commission, South Africa.
- Ordiz, A., S. Sæbø, J. Kindberg, J. E. Swenson, and O. Støen. 2017. Seasonality and human disturbance alter brown bear activity patterns: implications for circumpolar carnivore conservation? *Anim. Conserv.* **20**, 51–60. <https://doi.org/10.1111/acv.12284>
- Quantum GIS Development Team. 2015. QGIS. Retrieved from <http://www.qgis.org>. Accessed 1 Sept 2016.
- R Development Core Team. 2014. *R: a language and environment for statistical computing; Version 3.1.1*. R Foundation for Statistical Computing, Vienna, Austria.
- Randler, C., and N. Kalb. 2018. Distance and size matters: a comparison of six wildlife camera traps and their usefulness for wild birds. *Ecol. Evol.* **8**, 7151–7163.
- Ridout, M. S., and M. Linkie. 2009. Estimating overlap of daily activity patterns from camera trap data. *J. Agr. Biol. Environ. Stat.* **14**, 322–337.
- Rovero, F., F. Zimmermann, D. Berzi, and P. Meek. 2014. "Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. How do camera traps work? *Hydrobiologia* **24**, 148–156. <https://doi.org/10.4404/hystrix-24.2-6316>
- Rowcliffe, J. M., R. Kays, B. Kranstauber, C. Carbone, and P. A. Jansen. 2014. Quantifying levels of animal activity using camera trap data. *Methods Ecol. Evol.* **5**, 1170–1179. <https://doi.org/10.1111/2041-210X.12278>
- Sollmann, R. 2018. A gentle introduction to camera-trap data analysis. *Afr. J. Ecol.* **56**, 740–749. <https://doi.org/10.1111/aje.12557>
- Tambling, C. J., L. Minnie, J. Meyer, E. W. Freeman, R. M. Santymire, J. Adendorff, et al. 2015. Temporal shifts in activity of prey following large predator reintroductions. *Behav. Ecol. Sociobiol.* **69**, 1153–1161. <https://doi.org/10.1007/s00265-015-1929-6>
- Thompson, P. M., M. A. Fedak, B. J. McConnell, and K. S. Nichols. 1989. Seasonal and sex-related variation in the activity patterns of common seals (*Phoca vitulina*). *J. Appl. Ecol.* **26**, 521–535.
- Ungar, E. D., Z. Henkin, M. Gutman, A. Dolev, A. Genizi, S. R. Ecology, et al. 2005. Inference of animal activity from GPS collar data on free-ranging cattle. *Rangeland Ecol. Manag.* **58**, 256–266.
- Wearn, O. R., and P. Glover-Kapfer. 2019. Snap happy: camera traps are an effective sampling tool when compared with alternative methods. *R. Soc. Open Sci.* **6**, 181748.
- Wiesel, I., S. Karthun-Srijbos, and I. Jäneck. 2019. The use of GPS telemetry data to study parturition, den location and occupancy in the brown hyaena. *Afr. J. Wildl. Res.* **49**, 1–11.
- Zhang, J., V. Hull, J. Huang, S. Zhou, W. Xu, and H. Yang. 2015. Activity patterns of the giant panda (*Ailuropoda melanoleuca*). *J. Mammal.* **96**, 1116–1127. <https://doi.org/10.1093/jmammal/gyv118>