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METHODS PAPERS

An empirical assessment of the role of independence filters in temporal activity analyses using camera trapping data

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Abstract

Independence filters are commonly applied to camera trapping data when determining the temporal activity patterns of species or populations. However, recent research challenges the validity of independence filters, stating that it leads to flawed inferences of temporal activity patterns and a substantial reduction in sample sizes, and should not be used. This study presents an empirical counter-argument using data from Snapshot Serengeti. By manually applying 60-minute independence filters, common behaviours influencing the reliability of activity patterns derived from density-based analyses in African savanna species were identified. Results showed that applying independence filters primarily leads to decreased midday activity densities, mainly due to herding behaviour and the prevalent use of shade in a tree-sparse savanna. Idle herds or individuals that feed or rest in front of camera traps also influenced derived activity patterns. Furthermore, it is confirmed that adequate sample sizes are generally maintained after applying independence filters. The findings from this study highlight the shortcomings of the recent research disputing the use of independence filters in temporal activity analyses and underscore the importance of a comprehensive approach of inspecting data, understanding species behaviour, and considering regional environmental characteristics. This will ensure more accurate representations of species' true temporal activity patterns.

Significance statement

Most studies that use camera-trapping data to examine when a species population is active will discard any subsequent photos of the same species taken at the same camera-trap within a certain time frame. This approach aims to prevent potential bias introduced by interdependent sequences of photos in activity analyses. A recent study, however, concluded that the use of these data filters is flawed and should be avoided. In response, a counter-argument backed by the first empirical evidence supporting the necessity of these data filters is presented. Through proper data inspection, examination of behaviours captured in discarded images and considering habitat characteristics, this study demonstrates how these filters help to provide a more accurate depiction of a species' true activity pattern.

Keywords Camera traps · Pseudoreplication · Serengeti · Shade-use · Temporal overlap · Time-to-independence

Introduction

Understanding the temporal activity patterns of populations or species provides valuable insights into their ecology, physiology, and ethology. These patterns shed light on various aspects, including evolutionary adaptations (Hall et al. 2012; Gerkema et al. 2013), responses and resilience to climate change (Levy et al. 2019), energy balance (Weyer et al. 2020), competition (Hayward and Hayward 2006), and predator avoidance (Tambling et al. 2015). Commonly, data used to determine temporal activity patterns are collected through camera trapping surveys (Frey et al. 2017), and

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density-based analyses, such as probability density functions, are employed to statistically measure and compare the data (Ridout and Linkie 2009; Sollmann 2018; Niedballa et al. 2019). However, processing data for temporal activity analyses using point-based sampling requires careful consideration of event independence and potential pseudoreplication (Overdorff 1996; Ridout and Linkie 2009; Meek et al. 2014; Colgrave and Ruxton 2018; Niedballa et al. 2019). This is usually accounted for through independence filters which entails retaining one detection within the dataset and discarding subsequent detections of the same species from the same camera trap within a specified independence interval. Although the duration of this interval varies considerably among studies, a length of 30–60 min is most prevalent (Peral et al. 2022).

Peral et al. (2022) put forth a contrasting perspective on the use of independence filters in temporal activity analyses. According to their study, applying independence filters leads to substantial losses in sample sizes and introduces erroneous changes in diel activity patterns, ultimately resulting in flawed inferences (Peral et al. 2022). However, the common method used to analyse these temporal activity patterns, i.e., kernel density estimates, assumes that data are independent (Silverman 1986; Fleming et al. 2015). The aim of the current study is to challenge the viewpoint proposed by Peral et al. (2022) by conducting a comparative study using data from the same camera trapping survey, Snapshot Serengeti (Swanson et al. 2015), and employing similar methods to analyse the diel activity patterns of species populations. Moreover, the study seeks to underscore the importance of independence filtering and the associated assumptions of commonly used methods, raw data inspection, and a comprehensive understanding of species' behaviour and environmental characteristics specific to the study region. By doing so, the study aims to demonstrate the critical role these factors play in influencing the outcomes of temporal activity analyses.

Methods

Data collection and study site

To compare the current study's findings with those of Peral et al. (2022), data from the same camera trapping network were analysed, albeit at later dates. The analyses focussed on season 8 of the Snapshot Serengeti project, which encompasses the period from October 2013 to within July 2014. Snapshot Serengeti comprises a grid network of 225 camera traps placed within Tanzania's Serengeti National Park, where each camera is placed within the centre of a 5 km^2 grid unit (Swanson et al. 2015). The camera traps are triggered by movement whereafter a burst of three photos is taken in quick succession during daylight or a single photo at night given camera-flash limitations. A trigger delay of 1-minute was set between successive capture events (see Swanson et al. 2015 for a more detailed description of the Snapshot Serengeti project). The raw data was processed by Zooniverse (https://www.zooniverse.org/) whereby a citizen-science approach was used to identify the animals in each capture event. Consequently, the data received from Snapshot Serengeti were already processed in capture events, with each data record containing information such as the identified species, time, date, camera station, and links to the specific photos from the capture event. Each data record for daytime captures, therefore, contains the three images from the burst setting, while night-time captures feature a single photo.

Species selection

Five species were included in the analysis: Thomson's gazelle *Eudorcas thomsonii*, Cape buffalo *Syncerus caffer caffer*, spotted hyaena *Corcuta crocuta*, lion *Panthera leo*, and cheetah *Acinonyx jubatus*. Thomson's gazelle were included as they showed the greatest response to applied independence intervals in Peral et al. (2022). Buffalo were included as they are a large-bodied herbivorous species that form large herds and also showed a considerable response to the application of independence intervals in Peral et al. (2022). Among the carnivores studied by Peral et al. (2022), only spotted hyaenas exhibited a significant change in their diel activity patterns according to the Watson U^2 test and displayed a noticeable change in their peak activity periods. Hence, spotted hyaenas were included in the analysis. Although cheetahs and lions were not part of Peral et al.'s (2022) analyses, it was decided to include them in the current study as they are both attracted to isolated shade trees as daytime resting sites in Serengeti's savanna (Swanson et al. 2016). Cheetahs are primarily diurnal which contrasts with the nocturnal spotted hyaenas and they are more likely to have considerably fewer detections within the dataset.

Independence filtering and data inspection

Independence filtering was performed by manually removing the subsequent detections of the same species at the same camera station occurring within a 60-minute time period following a species detection. The same procedure was then applied to the next detection of the species that remained after the 60-minute mark. A 60-minute independence interval length was used as it had the greatest impact on the activity patterns analysed by Peral et al. (2022). Photos from each removed capture event were thoroughly inspected during the manual removal of detection records, taking note of the animals' behaviour. These behaviours were categorised into five groups: (1) the use of shade provided by trees, (2) herding behaviour or movement in groups, where multiple individuals could be identified in a photo or different individuals subsequently triggered a camera trap multiple times within the 60-minute independence period, (3) a single individual of a species that sequentially triggered a camera trap multiple times within the 60-minute independence period, (4) feeding behaviour, where single or multiple individuals of a species were observed feeding, and (5) resting behaviour, where single or multiple individuals of a species were lying down on the ground. These behaviours were examined as they would result in multiple subsequent capture events over a short period. Multiple or simultaneous behaviours observed in a camera-trap photograph were counted separately for each categorisation. It was not possible to record data blind because the method used to identify behaviours involved photographs of focal animals captured on camera-traps in the field.

Data analysis

The *overlap* package (Ridout and Linkie 2009) was utilised in R Statistical Software (v4.0.3; R Core Team 2023) using RStudio (v1.4.1103; RStudio Team 2023) to visualise the diel activity patterns of each species before and after the independence filtering process. These graphs depict the kernel density distributions of capture times of a species across the 24-hour diel period. A smoothing parameter, K = 3, was consistently applied throughout the analyses to produce smoothed activity curves that accounted for variation in the activity patterns of a population due to imperfect detection. Coefficients of overlap ($\widehat{\Delta}$) and their associated confidence intervals were calculated using the *overlap* package (Ridout and Linkie 2009) in R to assess the similarity in activity patterns for each species before and after the independence filtering process. The 95% smoothed bootstrapped confidence intervals were calculated using 1000 resamples of the data. The coefficient of overlap is a proportional value that ranges from 0 (no overlap) to 1 (complete overlap) and is derived from non-parametric kernel density estimates of two temporal activity distributions (Ridout and Linkie 2009). Lastly, the overlap in core activity periods, the highest 50% of the activity density distribution, for each species were determined before and after the filtering process using the *circular* package (Agostinelli and Lund 2017) in R. Core activity overlap allows for a more in-depth analysis and comparison of the temporal activity patterns of species and is particularly useful in species that display the same broad activity categorisations, i.e., nocturnal, diurnal, crepuscular, or cathemeral (Smith et al. 2023). The highest bandwidth value between the filtered and unfiltered data was used to calculate the overlap in core activity periods between the two data sets; optimal bandwidth for each sample was calculated using the *overlap* package in R and represents the concentration parameter that dictates the smoothness of the density distribution curve (Ridout and Linkie 2009).

Table 1 Comparison of detection records before and after filtering for independence using a 60-minute interval

Species	Number of detections		Detections removed (%)
	Unfiltered data	Filtered data	
Thomson's gazelle	11,601	2825	75.6%
Buffalo	2343	646	72.4%
Spotted hyaena	1026	830	19.1%
Lion	962	351	63.5%
Cheetah	138	110	20.3%

Results

The two herbivore species, Thomson's gazelle and buffalo, had noticeably more detections removed after the application of the 60-minute independence filter than the carnivore species (Table 1). The most detections removed within a single 60-minute period was 40 of Thomson's gazelle. Furthermore, the herbivores showed a considerable decline in activity density during the mid-day period after the filtering process (Fig. 1). This resulted in an increase in activity density during other periods of the day and a prolongation of core activity periods. A similar trend, albeit less pronounced, was observed for cheetah (Fig. 1). The lions exhibited an atypical diurnal activity pattern with a prominent peak around noon. This diurnal behaviour persisted even after applying the independence filter, but with a diminished peak that led to an increase in activity density during night-time (Fig. 1). These visual changes in activity patterns were reflected in the temporal overlap coefficients before and after the filtering process, mainly affecting the core activity periods more than their overall diel activity patterns for each species (Table 2). In contrast, the diel activity patterns of spotted hyaenas remained largely unaffected by the 60-minute independence filter (Fig. 1; Table 2).

The analysis of removed detection records revealed distinct behaviours for each species. Herding and shade-use were most prevalent in the removed detection records of Thomson's gazelle and buffalo (Figs. 2, 3, 4 and 5), with buffalo also frequently engaging in resting behaviour (Figs. 2 and 6). Spotted hyaena and cheetah had a higher proportion of removed detections involving single individuals

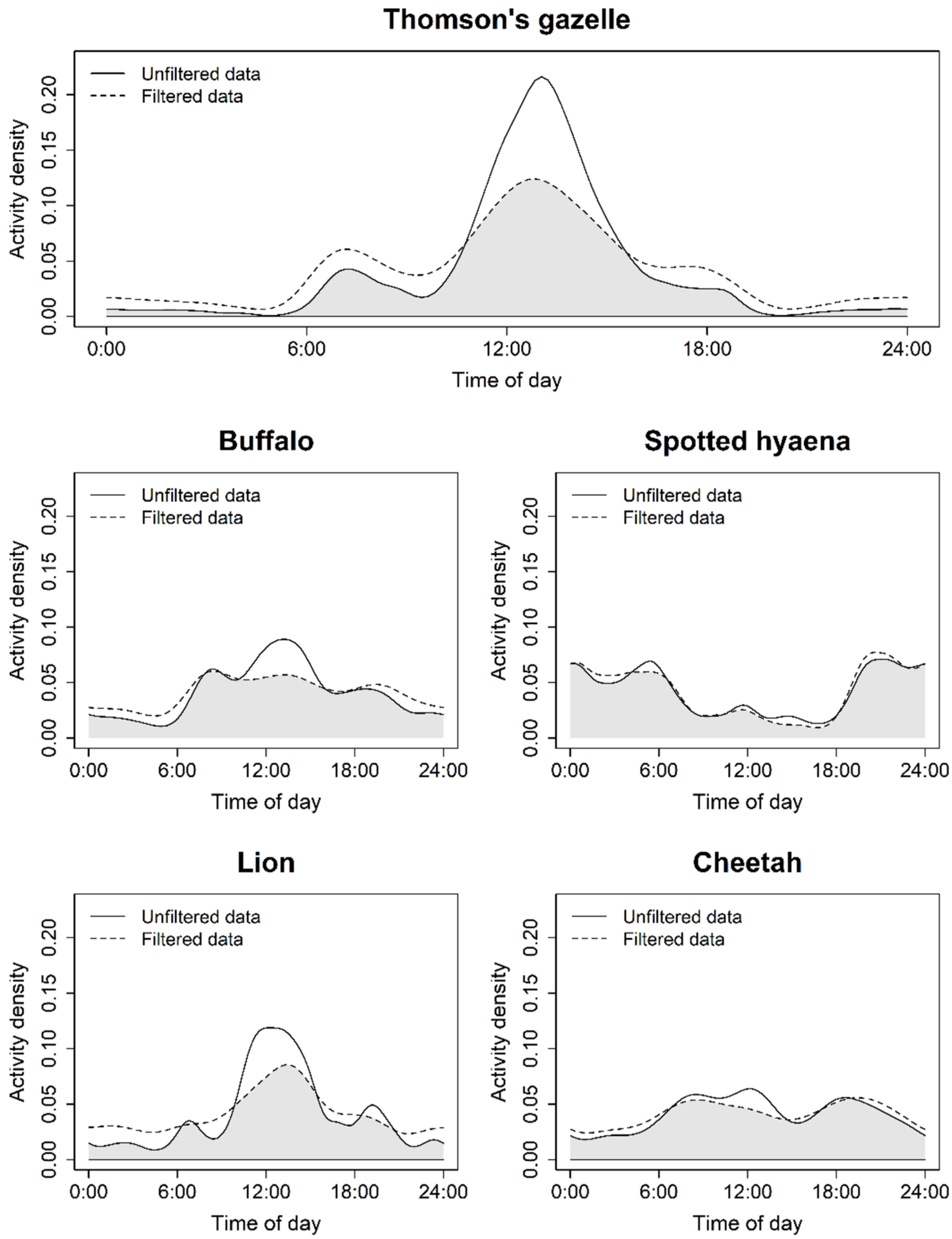

Fig. 1 Diel activity patterns of species before and after applying the 60-minute independence filter. The shaded area represents the overlapping activity periods between the two data sets

Table 2 The overlap in temporal activity patterns for each species before and after applying a 60-minute independence filter

Species	Coefficient of overlap (95% CI)	Overlap in core activity periods
Thomson's gazelle	0.78 (0.76–0.80)	0.64
Buffalo	0.88 (0.85–0.92)	0.72
Spotted hyaena	0.95 (0.93–0.98)	0.88
Lion	0.83 (0.77–0.87)	0.73
Cheetah	0.93 (0.85–0.99)	0.74

triggering the camera trap multiple times, along with a notable occurrence of shade-use (Figs. 2 and 7). Most of the removed lion detections were of single or multiple individuals resting in the shade of trees where camera traps were placed (Figs. 2 and 8). As expected, the removed detections of spotted hyaenas and lions often contained multiple individuals, reflecting their social nature (Fig. 2).

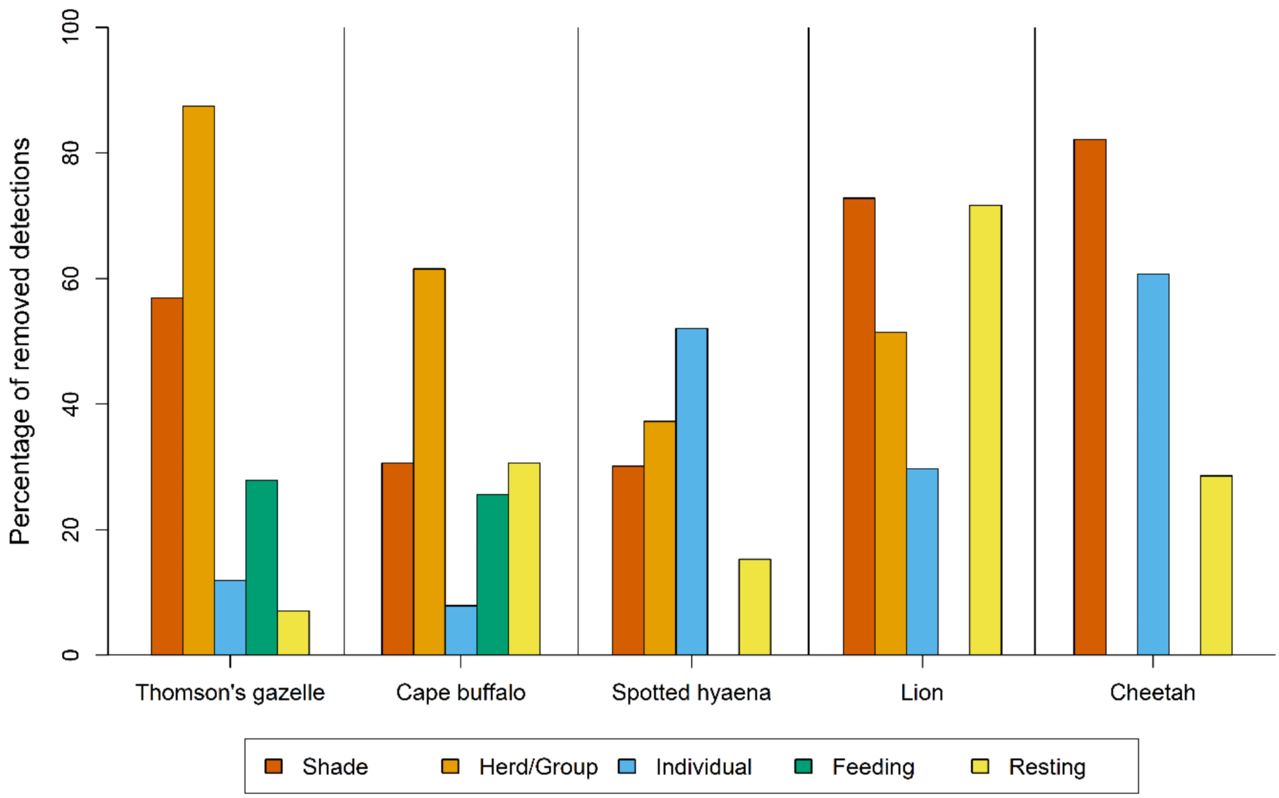

Fig. 2 The weight of each behaviour observed in the removed detections after applying the 60-minute independence filter. These behaviours include a member/members of the species observed within the shade of trees (Shade), within a herd or group structure (Herd/Group), as an individual repeatedly triggering the camera (Individual), engaged in grazing or feeding on a carcass (Feeding), or being inactive by lying down (Resting)

Discussion

Using thorough data inspection and an insight into the study region's environmental characteristics, this study demonstrates that independence filtering is a vital addition to temporal activity analyses. The findings contradict the notion put forward by Peral et al. (2022) that independence filtering is "not valid and should not be used" for temporal activity analyses based on camera trapping data. Omitting independence filters is a violation of the assumption of data independence with the application of kernel density estimation and distribution that can lead to inaccurate representations of species' diel activity patterns. Caution should be given to generalisation and the use of refuge sites by individuals of a studied species, where the solution would be to have a comprehensive understanding of the raw data collected during a study, environmental conditions like shade availability, species-specific behaviours such as the level of sociality, and the data collection protocol applied.

Although the application of independence filters could result in substantial reductions in sample sizes, it does not pose a threat to the outcome of temporal activity analyses in most cases. While a sample size of at least 100 detections has been recommended for camera trapping surveys (Lashley et al. 2018), reliable activity results can be obtained even with sample sizes as low as 10 records (Nakabayashi et al. 2021), depending on the species' activity patterns. Species with more specific activity periods require fewer detections to produce reliable activity curves compared to species with broad activity ranges (Niedballa et al. 2019). For example, lower sample sizes would be required to accurately display the diel activity patterns of highly crepuscular African wild dogs *Lycaon pictus* (Hayward and Slotow 2009; Veldhuis et al. 2020; Smith et al. 2023) compared to leopards *Panthera pardus* that exhibit broader and more variable diel activity patterns (Hayward and Slotow 2009; Havmøller et al. 2020; Smith et al. 2023). After applying independence filters, species with larger group sizes or higher sociality may experience greater sample size losses. In the current study and in Peral et al. (2022), herbivores (with large herd sizes) and social carnivores (lions in the current study and spotted hyaenas in Peral et al. 2022) showed the greatest reductions in sample size due to the filtering process. However, adequate sample sizes remained for all species after the filtering process, enabling reliable representations of their diel activity patterns (see supplementary Table S2 of Peral et al. 2022). Losses in sample size may have been substantial,

Fig. 3 A large herd of buffalo triggering a camera trap multiple times within a 60-minute period. The sequence was captured between 7:45 am and 8:45 am

but not significant enough to compromise adequacy or reliability.

It is insufficient to merely describe how a species' activity pattern changes after the application of independence filters without investigating the underlying reasons. The behaviours exhibited by species in the removed detections during periods of substantial change, such as mid-day, provide insight. Firstly, the current study shows that shade-use is a particularly important behaviour to consider in a tree-sparse semi-arid savanna ecosystem that experiences high daytime ambient temperatures. As most of the camera traps in the Snapshot Serengeti network are mounted on the trunks of shady trees (Swanson et al. 2015), any animals that seek shade under these trees to avoid thermal stress will be photo-captured multiple times until they move away when solar radiation intensity decreases and ambient

Fig. 4 A herd of Thomson's gazelle grazing in front of a camera trap between 7:06 am and 7:42 am. The complete sequence contained 22 detections within a 60-minute period

temperatures cool down. Another important factor to consider is herding behaviour and the degree of sociality of a species. For instance, as a herd moves past a camera trap, it will inevitably result in multiple subsequent detections if the herd remains within the camera's range. Feeding behaviour will be observed much more frequently for herbivores, particularly at camera stations overlooking grazing lawns where herds spend a considerable amount of time. Importantly, these behaviours are not mutually exclusive, as a herd of buffalo, for example, may utilize shade while some individuals feed or rest within the camera trap's view.

The observed trends in the results regarding changes in activity patterns before and after independence filtering align with those of Peral et al. (2022). These changes include a decrease in mid-day activity density and an expected density response of slightly increased activity during other periods of the day. The changes in peak activity density seen in Peral et al. (2022) are, therefore, related to a decrease in mid-day activity density. However, results from the current study demonstrate that for diurnal species, the core activity period lengthens after applying independence filters, which should reflect a more accurate representation of their core activity periods. For instance, considering its biology, the diurnal Thomson's gazelle is unlikely to allocate most of its activity budget to mid-day when high solar radiation and temperatures peak, resulting in substantial thermal stresses (Shrestha et al. 2014; Blank and Li 2022). Similarly, the unfiltered activity patterns of nocturnal spotted hyaenas

Fig. 5 A herd of Thomson's gazelle standing in the shade of a tree where a camera trap is mounted. This sequence was captured from 12:48 pm to 13:46 pm

presented by Peral et al. (2022) exemplify the significance of shade-use. They observed a spike in activity around midday, which is highly unusual (e.g., see Kolowski et al. 2007; Cusack et al. 2017; Veldhuis et al. 2020) as there is no biological reason for spotted hyaenas to have a spike in activity when ambient temperatures are high and solar radiation intensifies (Cooper 1990; Hayward and Slotow 2009). This anomaly is likely due to spotted hyaenas seeking shade provided by trees where cameras are mounted and is rectified through independence filtering. Changes in the species' diel activity patterns shown by Peral et al. (2022) occurred after the application of an independence filter, regardless of the length considered for the filter. This means that applying a 5-minute independence filter had nearly the same effect on the unfiltered data as a 60-minute independence filter. No noticeable change in activity patterns is observed between the filtered datasets of Peral et al. (2022). This shows that it is the application of an independence filter within the current data context that allows for more accurate interpretations of a species' activity patterns and not necessarily the length of the independence interval applied. However, considering that the application of an independence filter aids in removing detections where target species are at rest (e.g., shade use), applying a longer independence interval should be preferred over a shorter interval seeing that sufficient sample sizes are maintained. It is suggested with confidence that the only change in activity patterns with the application of independence filters seen in Peral et al. (2022) is due to the same behaviours identified in the current study, particularly social behaviour and shade-use.

Activity in animals is a dichotomous state, where they are either active or inactive at any given moment (Aschoff 1954; Altmann 1974). The basic definitions of activity presented by Aschoff (1954) and Altmann (1974) must be adapted for a more dynamic view of what activity entails and the characteristics of the data that are collected to determine activity patterns, respectively. Animal activity cannot only be limited to the definition by Aschoff (1954); an animal that is

Fig. 6 A herd of buffalo lying down in the shade of a tree where a camera trap is mounted. This sequence contained 23 detections between 12:05 pm and 13:05 pm

not performing functional actions associated with reproduction, resource acquisition or survival should be considered as inactive. For example, many predators, including lions, cheetahs, and predatory birds such as owls would wait in ambush or actively seek prey whilst in a stationary state, but would still be functionally active. Moreover, many species (e.g., lions) in a resting state will regularly move position over very short distances that will trigger camera traps; the animal moves which satisfies the definition by Aschoff (1954) but is functionally inactive. Unlike implanted accelerometers (Weyer et al. 2020) and direct observational recordings (Davies and Skinner 1986) that continuously record the activity of an individual or group of individuals, camera traps are stationary and only have a limited view of the landscape. Data collected through camera-trapping for activity analyses does not reflect the concept of a continuous

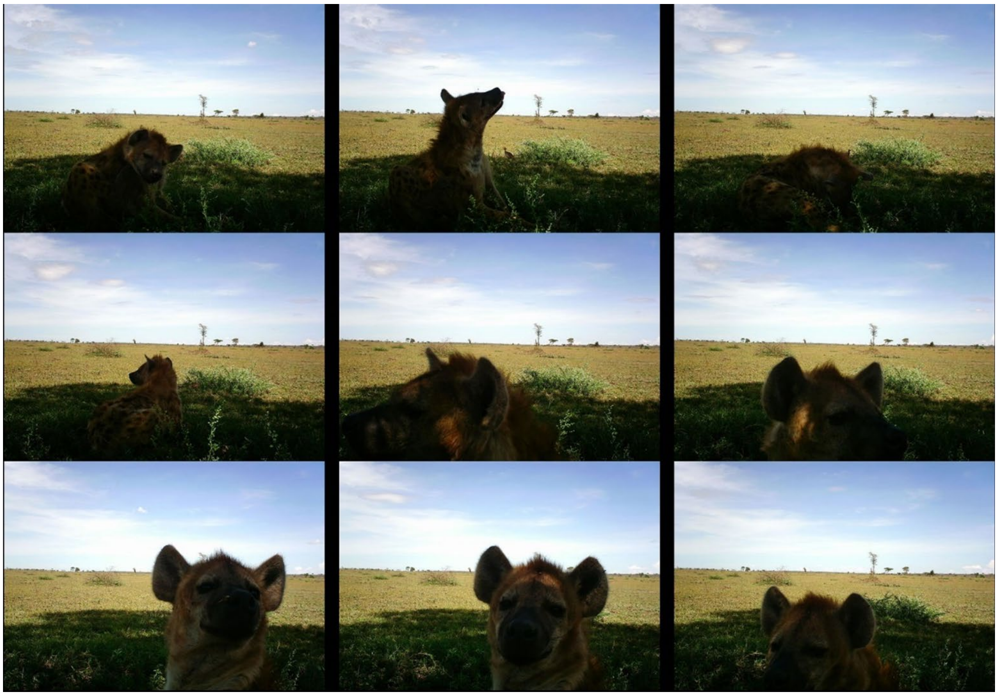

Fig. 7 A solitary spotted hyaena resting in the shade of a tree while triggering the camera trap multiple times. This sequence spanned from 14:29 pm to 15:18 pm

active or inactive state, but rather an event that must be processed and transformed by analytical procedures to reflect activity patterns. Researchers must adapt to the limitations of camera trapping by applying data processing measures that will result in as accurate a display of a species' activity patterns as possible. When combining the limitations of camera trapping and the dynamics of density distributions, independence filtering becomes crucial. For example, if event A records 40 detections (as seen in the current study) of a species moving past a camera trap within a 60-minute period, and event B records only one detection of the same species moving past the same camera trap within a 60-minute period, event A would have a 40 times higher density effect than event B. In other words, the individuals in event A would be 40 times more active at that particular time than the individuals in event B. This is unsound and incorporates aspects of detection frequencies rather than true activity. Independence filtering, thus, reduces this limitation to produce more accurate representations of a species' true activity patterns. Additionally, considering herds or groups of animals as single collective units that produce a single record of activity, rather than treating each individual as a potential record, can enhance the accuracy of activity analyses.

The apparent diurnal activity patterns of Serengeti's lions displayed in this study is a misrepresentation of their true activity patterns. Lions in the open, tree-sparse landscape of the Serengeti are attracted to shade trees as resting spots (Swanson et al. 2016). This was confirmed in the behaviours observed among removed lion detections due to independence filtering, and the substantial reduction in activity density during midday hours. Lions are predominantly nocturnal or crepuscular and typically become inactive during the daylight hours, particularly at midday when the risk of heat stress is highest (Schaller 1972; Hayward and Slotow 2009; Mogensen et al. Mogensen; Searle et al. 2011). Without thorough raw data inspection and an insight into the study site's environmental characteristics, an inaccurate conclusion of lion activity patterns would have been reported. This illustrates the importance of a careful review of the raw data and gaining insights into species behaviours and data collection procedures before analysing temporal activity patterns, particularly in desktop studies that rely on second-hand data, such as long-term camera trapping projects intended to serve broad study objectives like Snapshot Safari (Pardo et al. 2021). The definition of activity and the binary nature of data used in pertinent activity analyses may be compromised by camera traps positioned on or in the view of shade trees in a tree-sparse region like the Serengeti. This is because the cameras will record animals at rest while they are in thermal refuges, producing detections that are not suitable for use in activity analyses (Rowcliffe et al. 2014). Given that many temporal activity studies may still use less suitable camera-trapping data that was intended for disparate or broad objectives, independence filtering will transform the data to a state that allows for

Fig. 8 A pair of lions resting under a tree where a camera trap is mounted. This sequence contained 29 detections that spanned from 12:25 pm to 13:24 pm

more reliable representations of activity patterns. However, temporal activity studies of species with ambiguous refuge sites will benefit from camera traps being placed randomly in the area with respect to the target species' routine movements (e.g., endpoints of diel migrations) and behavioural patterns that will better match the perspectives of a binary state of activity or inactivity (Rowcliffe et al. 2014; Rovero and Zimmerman 2016). This will satisfy the fundamental assumption of independence of sampling sites relative to the movement of target species (Rowcliffe et al. 2014; Rovero and Zimmerman 2016), an assumption that is violated by Peral et al. (2022) when not applying independence filters and raw data inspection to reduce the impact of dependent sequences and detections of animals at rest.

In conclusion, this study challenges the broad statement by Peral et al. (2022) that independence filtering is "not valid and should not be used". It is demonstrated in the current study that consecutive detections of a species within a short period (e.g., 60-minutes) are empirically dependent based on species behaviour, leading to issues of pseudoreplication in density-based analyses. A comprehensive dismissal of the use of independence filtering in relevant analyses based on an erroneous study that states its invalidity (Peral et al. 2022), may discredit all the previous research that employed independence filters in temporal activity analyses. This includes seminal studies that helped to develop the relevant methods, like Ridout and Linkie (2009) and Rowcliffe et al. (2014). The use of independence filters is not flawless, but it contributes to more accurate and reliable results by supporting assumptions of data independence. Although the time-lag associated with independence filters is usually chosen arbitrarily or adopted from a previous study (Burton et al. 2015), consideration must be made for species-specific or study-specific context as the necessary time-lag for independence may differ due to sampling protocols and species behaviour; time-lag periods that will maximise independence can be determined using methods such as autocorrelation functions (Parsons et al. 2016) or lorelograms (Iannarilli et al. 2019). Future research should also aim to refine the method of independence filtering, such as by averaging the times of each detection falling within the chosen independence interval to produce a more accurate representation of the capture events, rather than relying solely on using the first detection in the capture sequence. Moreover, the development of an analytical framework or set of guidelines for relevant temporal activity analyses that can be universally applied to species and populations is encouraged. Therefore, the use of independence filters in temporal activity analyses is endorsed, provided that proper data investigation and knowledge of the study region's characteristics can support its use.

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Data availability The data analysed in the current study is publicly available on the LILA BC repository at https://lila.science/datasets/snapshot-serengeti.

Declarations

Ethics approval No ethical approval was required for conducting this study.

Conflict of interest There are no conflicts of interest to declare regarding this study.

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