



Do long-term camera trap sampling designs matter to estimate diel activity?

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Abstract

Effective long-term ecological monitoring (LTEM) is critical for monitoring wildlife activity, yet the consequences of the study design choices on its results are not well established. This study examines how camera trap sampling design influences activity estimates of roe deer and wild boar in Belgium's National Park Hoge Kempen. We compared two three-year designs: a systematic-random (SYS) and a stratified-random (STRAT) design, differing in camera trap (CT) number, deployment duration, and number of sampled locations. While activity levels were largely consistent across designs, diel activity patterns varied significantly, especially among years. This suggests that the use of different sampling designs in LTEM is not the main driver of differences in activity estimations. Hence, even when different camera trap study designs are applied over time within a long-term monitoring project, wildlife activity patterns can be analysed over the entire study period without loss of validity.

Keywords Activity patterns · Long-term ecological monitoring · Camera traps · Sampling design · Wildlife monitoring

Introduction

Wildlife camera traps (CTs) revolutionised wildlife monitoring by enabling cost-efficient, autonomous, non-invasive long-term data collection of wildlife in their natural habitats (Caravaggi et al. 2017, 2020). Although widely used, few CT studies are integrated into long-term ecological monitoring (LTEM) frameworks (Harmsen et al. 2017; Swanson et al. 2015; Twining et al. 2024; Zuleger et al. 2023), and guidelines for studying diel activity remain underdeveloped compared to other inferences (Frey et al. 2017; Kays et al. 2020; Rovero and Zimmermann 2016; Vazquez et al. 2019).

Accurate wildlife activity estimates require ≥ 100 detections (Lashley et al. 2018). Random CT placement relative to the diel patterns of movement, especially off-trail placement for ungulates, provide unbiased activity

estimations (Rowcliffe et al. 2014; Tanwar et al. 2021). Despite this, detailed sampling design guidelines remain limited in activity studies. CT number and deployment duration may both influence activity estimates as well. Increasing CT numbers improves sample size (spatial coverage or local sampling intensity) and precision but raises financial and labour costs (Duggan et al. 2021; Kays et al. 2020; Kissling et al. 2024). Similarly, decreasing deployment duration expands spatial coverage, while longer deployments improve detection rate estimations (Kays et al. 2021; Si et al. 2014). However, in contrast to abundance or occupancy, the influence of CT number and deployment length on activity estimates remains unknown (Kays et al. 2020, 2021; Si et al. 2014).

This study monitored roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) in the National Park Hoge Kempen (Belgium) (NPHK) over six years using two distinct CT sampling designs, each deployed for three years. These differed in CT number, deployment duration, and site selection. We analysed diel activity levels (proportion of time animals are active over a 24-hour period) and activity patterns (distribution of that activity across the 24 h). In order to determine the interchangeability for LTEM, we tested for differences in the outcomes of the two sampling designs.

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Methods & materials

Two consecutive CT surveys (May 2017–2020, May 2020–2023) were used to study medium-sized mammals in the NPHK, a human-dominated protected area in Belgium. Reconyx Hyperfire HC600 CTs were mounted 50 cm high, facing north (Wevers et al. 2020). Upon motion trigger, 10 consecutive images were taken without delay. No bait/lure was used and opportunistic sampling of trails was avoided.

The first survey employed a systematic-random sampling (SYS) design (Wevers et al. 2020), dividing the area into 40 compartments (1.5 km² each, respecting inaccessible areas, Fig. S1), each overlaid with a 300 × 300 m grid. Every three to four weeks, one randomly selected grid cell centroid per compartment was selected for CT placement, resulting in 520 locations each year. Since the third sampling year was a replicate of the second sampling year, a total of 1040 locations were visited (Fig. S2A). The second survey used a stratified-random sampling (STRAT) design. Sixty sampling locations were selected taking into account the proportional abundances of the main habitats (heathland, coniferous forest, deciduous forest, mixed forest, scrubland). These were divided into two subsets of 30 locations, which were sampled on an alternating basis every two months (Fig. S2B; Table S1).

Images were processed in Agouti (*agouti.eu*), grouped into events, and classified (Wevers et al. 2020). Roe deer and wild boar activity were analysed using the R-package ‘activity’ (Rowcliffe et al. 2014) and daily variation in daylength was corrected for using double anchoring (Nouvellet et al. 2012). Detection frequencies were compared using Poisson tests, accounting for trap days. Activity levels were compared using Wald tests, overlap in activity patterns using both Watson-Wheeler-tests and

a randomisation test based on overlap indices (Ridout and Linkie 2009). The Watson-Wheeler-test evaluates differences in either variance or means of two samples, whereas the randomisation test determines statistical significance by comparing the observed overlap indices to a randomized distribution (Ridout and Linkie 2009). Both tests were applied, as the Watson-Wheeler-test is commonly used in wildlife activity studies but has a tendency to detect significance more readily (Landler et al. 2021). Activity was compared between sampling designs seasonally (following the astronomical calendar), and between all sampling years. A significance level of 0.05 was used, and the Bonferroni correction adjusted for multiple comparisons (Dunn 1961). Analyses were conducted in R (R Core Team 2023) via Rstudio (RStudio team 2024).

Results

The SYS design resulted in 38,730 trap days across 1,013 sites, yielding 15,820 roe deer and 3,916 wild boar detections. The estimated 1,040 sampling locations were reduced to 1,013 throughout the period of three years due to CT malfunctions and theft. The STRAT design resulted in 25,305 trap days at 60 sites, recording 8,234 roe deer and 2,459 wild boar detections. Roe deer detection frequencies were significantly higher under the SYS design (rate ratio = 1.2553, CI = [1.2222; 1.2894], $p < 0.0001$), whereas wild boar showed no statistical difference (rate ratio = 1.0405, CI = [0.9891; 1.0948], $p = 0.1243$). Activity levels were similar across sampling designs for both species and every seasonal classification (Table 1). Between SYS and STRAT design, the only significant difference in activity level was for year-round wild boar data (Table 1). However, activity patterns differed significantly across

Table 1 Comparison of activity estimates derived from systematic-random sampling design (SYS) and stratified-random sampling design (STRAT) used sequentially in the National park Hoge Kempen (Belgium). Wald test p -value tests differences in activity levels. Watson-Wheeler test and randomisation test both assess differences in activity patterns inferred between sampling designs. Watson-Wheeler test is based on a difference in variance or means of two circular samples; the randomisation test is based on the probability of the overlap indices from a randomized distribution. Significant values are shown in bold

Species	Timeframe	Activity level difference (Wald test p -value)	Activity pattern difference (Watson-Wheeler test p -value)	Activity pattern difference (Randomisation test p -value)
Roe deer	Year-round	0.2522	<0.0001	<0.0001
	Spring	0.9198	<0.0001	<0.0001
	Summer	0.3618	<0.0001	<0.0001
	Autumn	0.5802	0.0028	<0.0001
	Winter	0.6323	<0.0001	<0.0001
Wild boar	Year-round	0.0160	<0.0001	<0.0001
	Spring	0.8287	0.0151	0.1061
	Summer	0.9386	<0.0001	<0.0001
	Autumn	0.0886	0.0725	0.0891
	Winter	0.5807	<0.0001	<0.0001

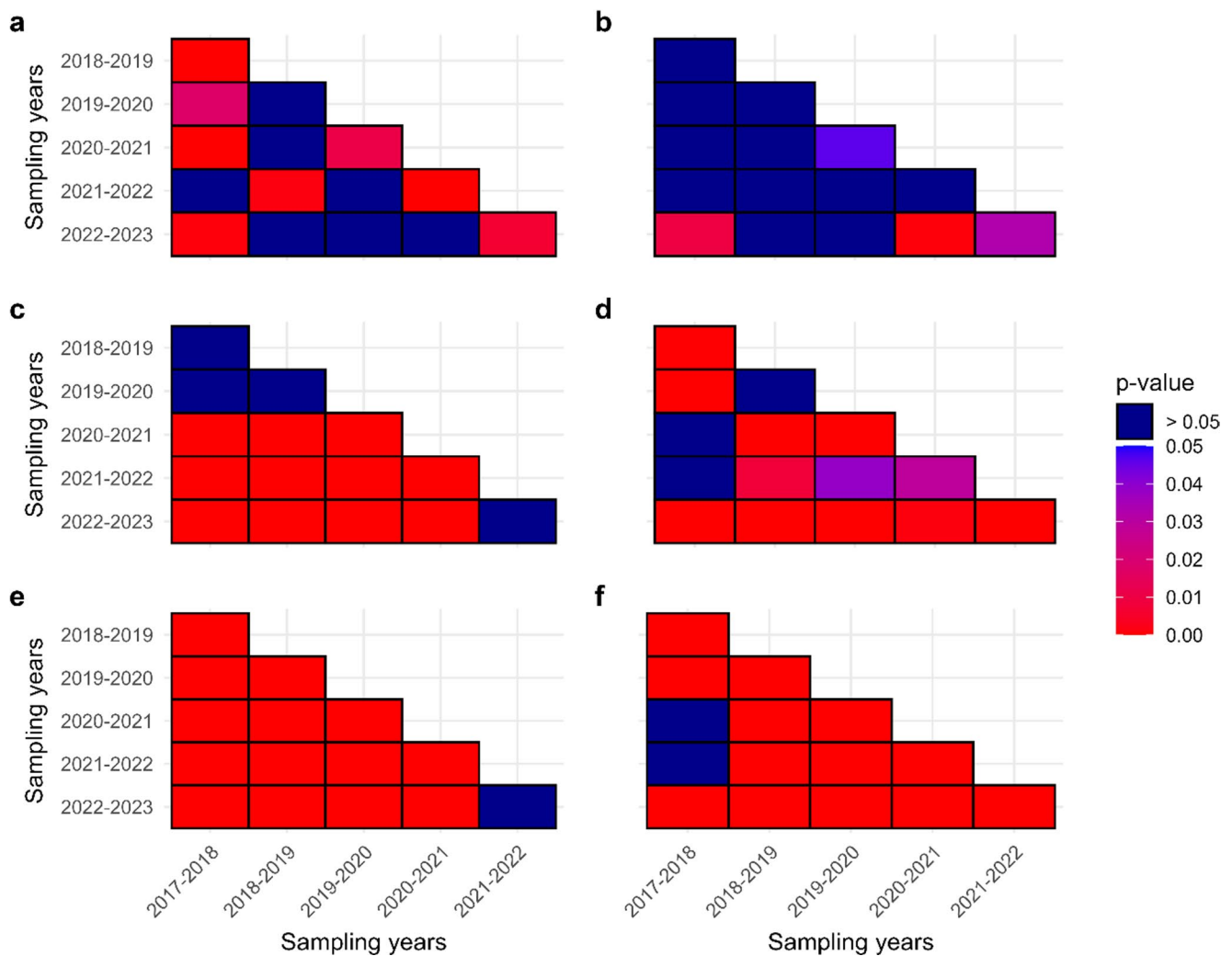


Fig. 1 Significances of pairwise comparison tests of year-round activity levels and patterns between sampling years. Sampling years 2017–2018, 2018–2019, and 2019–2020 used the systematic-random sampling design (SYS); sampling years 2020–2021, 2021–2022, and 2022–2023 used the stratified-random sampling design (STRAT). Pairwise comparison significance is indicated using a gradient from highly significant to just significant, from red to blue respectively. Non-significant differences are indicated in dark-blue. **(a)** Activity lev-

els of roe deer (*Capreolus capreolus*), assessed using the Wald test. **(b)** Activity levels of wild boar (*Sus scrofa*), assessed using the Wald test. **(c)** Activity patterns of roe deer, assessed using the Watson-Wheeler test. **(d)** Activity patterns of wild boar, assessed using the Watson-Wheeler test. **(e)** Activity patterns of roe deer, assessed using the randomisation test. **(f)** Activity patterns for wild boar, assessed using the randomisation test

most comparisons using both statistical tests (Table S2, Fig. S3–5). Only the summer activity pattern of wild boar was not significant using the randomisation test, and wild boar activity pattern in autumn was not significant using both statistical tests (Table 1).

When comparing activity levels across all sampling years, roe deer exhibited considerable inter-annual variation (Fig. 1A, Fig. S6A), whereas wild boar activity levels remained relatively consistent throughout (Fig. 1B, Fig. S6B). Regarding diel activity patterns, most pairwise comparisons were statistically significant for both species. For roe deer, the Watson-Wheeler test showed significant differences between all sampling years,

except between 2017–2018 vs. 2018–2019, 2017–2018 vs. 2019–2020, 2018–2019 vs. 2019–2020, and 2021–2022 vs. 2022–2023 (Fig. 1C). In contrast, the randomisation test identified significant differences for all year-pairs, except 2021–2022 vs. 2022–2023 (Fig. 1E). For wild boar activity patterns, the Watson-Wheeler test detected significant differences in all but three comparisons: 2017–2018 vs. 2020–2021, 2017–2018 vs. 2021–2022, and 2018–2019 vs. 2019–2020 (Fig. 1D). However, the randomisation test yielded non-significant results between 2017–2018 vs. 2020–2021 and 2017–2018 vs. 2021–2022 only (Fig. 1F).

Discussion

Within the context of using data collected with different sampling designs as part of the same LTEM, we investigated the differences in estimated wildlife activity based on inferences made from two different sampling designs used consecutively in the same natural area. One sampling design (SYS) was specifically designed to study the drivers influencing the distribution and activity of medium-sized mammals, while the other (STRAT) was tailored towards long-term monitoring of medium-sized mammals in the NPHK. They differed in number of CTs used, number of locations sampled and deployment length. We found differences in inferred activity patterns between both sampling designs and within each sampling design.

Detection rates differed between sampling designs for roe deer but not wild boar, yet both species had sufficient detections (≥ 100) to ensure reliable activity estimates of the activity level and activity patterns, with associated confidence intervals from bootstrapping (Lashley et al. 2018). In general, activity levels were relatively constant across sampling years and designs, particularly for wild boar. However, activity patterns were remarkably different between both set-ups, indicating different sensitivities of activity level and pattern estimates to design differences. Although both designs sample the habitats proportionally, potential differences in local landscape features and resource availability – on a finer scale than habitat – in the microsite of the CT may introduce unknown species-specific detection biases, which could translate into variable activity estimations (Hofmeester et al. 2019). To our knowledge, this has not yet been shown in a LTEM study (Buchholz et al. 2021). Other estimates have shown similar temporal variation in LTEM (Barlow et al. 2009; Harmsen et al. 2017; Krebs et al. 2023; Lincoln et al. 2020).

However, since differences occur between and within sampling years and designs, it is unlikely that the observed differences can be attributed to the change of sampling design. Known sources of small-scale variation for activity analyses, such as individual- and day-level behavioural variations, are not expected to influence long-term population-level estimates (Cederlund 1989; Krop-Benesch et al. 2013). Ecological factors, such as behavioural and environmental variation, may have contributed to the observed patterns (Podgórski et al. 2013; Stache et al. 2013).

Yet, the sequential (and not parallel) implementation of the two sampling designs is a limiting factor. Since observations were not made simultaneously, all of our conclusions comprise inherent uncertainty as to whether observed differences reflect ecological or methodological

effects. Hence, future studies should evaluate ecological inferences from comparing two sampling designs that are implemented simultaneously and in the same study site. Furthermore, those studies should then verify whether other ecological estimators, such as species richness and population density, show comparable results, and ascertain how design characteristics can be considered as model covariates to allow incorporation of design differences in the models. In brief, our investigation on the consistency of wildlife activity estimates across two CT sampling designs supports the idea that data derived from projects with different sampling designs can be combined for LTEM.

Recommendations for practice

Practitioners deciding between designs or integrating multi-project data should take several recommendations at heart: (1) When studying activity levels, SYS and STRAT designs appear robust, hence resource availability and logistical feasibility can guide design choice; (2) When studying activity patterns, which show higher variability than activity levels, therefore one should avoid design alterations during the project (except when overlap/calibration is possible).

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10344-025-02013-3>.

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Author contributions S.I. drafted and wrote the main manuscript, as well as analysed the data and prepared figures and/or tables. M.B. performed the experiments, and supervised. J.C. and N.B. conceived and designed the experiments, performed the experiments, and supervised. All authors reviewed the manuscript.

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Data availability Camera trap observation data and the R-script processing, analysing, and visualizing the data can be provided by the authors upon request.

Declarations

Ethical approval This declaration is not applicable as data was gathered using camera traps, which are considered to be a non-invasive method for animal studies.

Competing interests The authors declare no competing interests.

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References

- Barlow ACD, McDougal C, Smith JLD, Gurung B, Bhatta SR, Kumal S, Mahato B, Tamang DB (2009) Temporal variation in tiger (*Panthera tigris*) populations and its implications for monitoring. *J Mammal* 90(2):472–478. <https://doi.org/10.1644/07-MAMM-A-415.1>
- Buchholz R, Stamm J, Neha SA (2021) Can camera traps be used to measure climate change induced alterations of the activity patterns of elusive terrestrial vertebrates? *Clim Change Ecol* 2:100020. <https://doi.org/10.1016/j.ecochg.2021.100020>
- Caravaggi A, Banks PB, Burton AC, Finlay CMV, Haswell PM, Hayward MW, Rowcliffe MJ, Wood MD (2017) A review of camera trapping for conservation behaviour research. *Remote Sens Ecol Conserv* 3(3):109–122. <https://doi.org/10.1002/rse2.48>
- Caravaggi A, Burton AC, Clark DA, Fisher JT, Grass A, Green S, Hobaiter C, Hofmeester TR, Kalan AK, Rabaiotti D, Rivet D (2020) A review of factors to consider when using camera traps to study animal behavior to inform wildlife ecology and conservation. *Conserv Sci Pract*. <https://doi.org/10.1111/csp2.239>
- Cederlund G (1989) Activity patterns in moose and roe deer in a North boreal forest. *Ecography* 12(1):39–45. <https://doi.org/10.1111/j.1600-0587.1989.tb00820.x>
- R Core Team (2023) R: A Language and environment for statistical computing (Version 4.3.1) [Computer software]. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Duggan MT, Groleau MF, Shealy EP, Self LS, Utter TE, Waller MM, Hall BC, Stone CG, Anderson LL, Mousseau TA (2021) An approach to rapid processing of camera trap images with minimal human input. *Ecol Evol* 11(17):12051–12063. <https://doi.org/10.1002/ece3.7970>
- Dunn OJ (1961) Multiple comparisons among means. *J Am Stat Assoc* 56(293):52–64. <https://doi.org/10.2307/2282330>
- Frey S, Fisher JT, Burton AC, Volpe JP (2017) Investigating animal activity patterns and temporal niche partitioning using camera-trap data: challenges and opportunities. *Remote Sens Ecol Conserv* 3(3):123–132. <https://doi.org/10.1002/rse2.60>
- Harmsen BJ, Foster RJ, Sanchez E, Gutierrez-González CE, Silver SC, Ostro LET, Kelly MJ, Kay E, Quigley H (2017) Long term monitoring of Jaguars in the Cockscomb Basin Wildlife Sanctuary, Belize; implications for camera trap studies of carnivores. *PLoS ONE* 12(6):e0179505. <https://doi.org/10.1371/journal.pone.0179505>
- Hofmeester TR, Crooms JPM, Odden J, Andrén H, Kindberg J, Linnell JDC (2019) Framing pictures: a conceptual framework to identify and correct for biases in detection probability of camera traps enabling multi-species comparison. *Ecol Evol* 9(4):2320–2336. <https://doi.org/10.1002/ece3.4878>
- Kays R, Arbogast BS, Baker-Whitton M, Beirne C, Boone HM, Bowler M, Burneo SF, Cove MV, Ding P, Espinosa S, Gonçalves ALS, Hansen CP, Jansen PA, Kolowski JM, Knowles TW, Lima MGM, Millspaugh J, McShea WJ, Pacifici K, Spironello WR (2020) An empirical evaluation of camera trap study design: how many, how long and when? *Methods Ecol Evol* 11(6):700–713. <https://doi.org/10.1111/2041-210X.13370>
- Kays R, Hody A, Jachowski DS, Parsons AW (2021) Empirical evaluation of the spatial scale and detection process of camera trap surveys. *Mov Ecol* 9(1):41. <https://doi.org/10.1186/s40462-021-00277-3>
- Kissling WD, Evans JC, Zilber R, Breeze TD, Shinneman S, Schneider LC, Chalmers C, Fergus P, Wich S, Geelen LH W. T (2024) Development of a cost-efficient automated wildlife camera network in a European natura 2000 site. *Basic Appl Ecol* 79:141–152. <https://doi.org/10.1016/j.baec.2024.06.006>
- Krebs CJ, Boutin S, Boonstra R, Murray DL, Jung TS, O'Donoghue M, Gilbert BS, Kukka PM, Taylor SD, Morgan T, Drummond R, Sinclair ARE, Kenney AJ (2023) Long-term monitoring in the boreal forest reveals high spatio-temporal variability among primary ecosystem constituents. *Front Ecol Evol*. <https://doi.org/10.3389/fevo.2023.1187222>
- Krop-Benesch A, Berger A, Hofer H, Heurich M (2013) Long-term measurement of roe deer (*Capreolus capreolus*) (Mammalia: Cervidae) activity using two-axis accelerometers in GPS-collars. *Ital J Zool* 80(1):69–81. <https://doi.org/10.1080/11250003.2012.725777>
- Landler L, Ruxton GD, Malkemper EP (2021) Advice on comparing two independent samples of circular data in biology. *Sci Rep* 11:20337. <https://doi.org/10.1038/s41598-021-99299-5>
- Lashley MA, Cove MV, Chitwood MC, Penido G, Gardner B, DePerno CS, Moorman CE (2018) Estimating wildlife activity curves: comparison of methods and sample size. *Sci Rep* 8(1):4173. <https://doi.org/10.1038/s41598-018-22638-6>
- Lincoln AE, Wirsing AJ, Quinn TP (2020) Long-term use of non-invasive sampling methods: does successful sampling of brown bears by hair snares and camera traps change over time? *Wildl Res* 47(6):499–508. <https://doi.org/10.1071/WR19156>
- Nouvellet P, Rasmussen GSA, Macdonald DW, Courchamp F (2012) Noisy clocks and silent sunrises: measurement methods of daily activity pattern. *J Zool* 286(3):179–184. <https://doi.org/10.1111/j.1469-7998.2011.00864.x>
- Podgórski T, Baś G, Jędrzejewska B, Sönnichsen L, Śnieżko S, Jędrzejewski W, Okarma H (2013) Spatiotemporal behavioral plasticity of wild boar (*Sus scrofa*) under contrasting conditions of human pressure: primeval forest and metropolitan area. *J Mammal* 94(1):109–119. <https://doi.org/10.1644/12-MAMM-A-038.1>
- Ridout MS, Linkie M (2009) Estimating overlap of daily activity patterns from camera trap data. *J Agric Biol Environ Stat* 14(3):322–337. <https://doi.org/10.1198/jabes.2009.08038>
- Rovero F, Zimmermann F (2016) Camera trapping for wildlife research. Pelagic Publishing, <http://www.pelagicpublishing.com>
- Rowcliffe JM, Kays R, Kranstauber B, Carbone C, Jansen PA (2014) Quantifying levels of animal activity using camera trap data. *Methods Ecol Evol* 5(11):1170–1179. <https://doi.org/10.1111/2041-210X.12278>

- RStudio team (2024) RStudio: Integrated Development Environment for R (Version 2023.12.1.402) [Computer software]. Posit Software, PBC. <http://www.posit.co/>
- Si X, Kays R, Ding P (2014) How long is enough to detect terrestrial animals? Estimating the minimum trapping effort on camera traps. *PeerJ* 2:e374. <https://doi.org/10.7717/peerj.374>
- Stache A, Heller E, Hothorn T, Heurich M (2013) Activity patterns of European roe deer (*Capreolus capreolus*) are strongly influenced by individual behaviour. *Folia Zool* 62(1):67–75. <https://doi.org/10.25225/fozo.v62.i1.a10.2013>
- Swanson A, Kosmala M, Lintott C, Simpson R, Smith A, Packer C (2015) Snapshot Serengeti, high-frequency annotated camera trap images of 40 mammalian species in an African savanna. *Sci Data* 2(1):150026. <https://doi.org/10.1038/sdata.2015.26>
- Tanwar KS, Sadhu A, Jhala YV (2021) Camera trap placement for evaluating species richness, abundance, and activity. *Sci Rep* 11(1):23050. <https://doi.org/10.1038/s41598-021-02459-w>
- Twining JP, Kramer D, Perkins KA, Fuller AK (2024) Landscape-scale population trends in the occurrence and abundance of wildlife populations using long term camera-trapping data. *Biol Conserv* 290:110398. <https://doi.org/10.1016/j.biocon.2023.110398>
- Vazquez C, Rowcliffe JM, Spoelstra K, Jansen PA (2019) Comparing diel activity patterns of wildlife across latitudes and seasons: time transformations using day length. *Methods Ecol Evol* 10(12):2057–2066. <https://doi.org/10.1111/2041-210X.13290>
- Wevers J, Fattebert J, Casaer J, Artois T, Beenaerts N (2020) Trading fear for food in the anthropocene: how ungulates cope with human disturbance in a multi-use, suburban ecosystem. *Sci Total Environ* 741:140369. <https://doi.org/10.1016/j.scitotenv.2020.140369>
- Zuleger AM, Perino A, Wolf F, Wheeler HC, Pereira HM (2023) Long-term monitoring of mammal communities in the Peneda-Gerês National park using camera-trap data. *Biodivers Data J* 11:e99588. <https://doi.org/10.3897/BDJ.11.e99588>

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