Mammalian Biology 89 (2018) 90–94

Contents lists available at ScienceDirect

Mammalian Biology

journal homepage: www.elsevier.com/locate/mambio

Short communication

No respect for apex carnivores: Distribution and activity patterns of honey badgers in the Serengeti

Maximilian L. Allen[a,*], Brittany Peterson[a], Miha Krofel[b]

[a] Department of Forest and Wildlife Ecology, University of Wisconsin, 1630 Linden Drive, Madison, WI 53706, United States
[b] Wildlife Ecology Research Group, Department of Forestry, Biotechnical Faculty, University of Ljubljana, Večna pot 83, SI-1000 Ljubljana, Slovenia

ARTICLE INFO

Article history:
Received 18 August 2017
Accepted 10 January 2018
Handled by Sabine Begall

Keywords:
Abundance
Activity patterns
Distribution
Honey badger
Interspecific interactions
Mellivora capensis

ABSTRACT

Honey badgers are cryptic carnivores that occur at low densities and range across large areas. The processes behind site-level honey badger abundance and detection rates are poorly understood, and there are conflicting results about their avoidance of larger carnivores from different regions. We used data from 224 camera traps set up in the Serengeti National Park, Tanzania to evaluate patterns in detection rates, spatial distribution, and activity patterns of honey badgers. Our top models showed that the relative abundance of larger carnivores (e.g., African lions, *Panthera leo*, and spotted hyenas, *Crocuta crocuta*) was important, but surprisingly was positively related to honey badger distribution. These results suggest that honey badgers were not avoiding larger carnivores, but were instead potentially seeking out similar habitats and niches. We also found no temporal avoidance of larger carnivores. Honey badgers exhibited seasonal variation in activity patterns, being active at all times during the wet season with peaks during crepuscular hours, but having a strong nocturnal peak during the dry season. Our detection rates of honey badgers at individual camera traps were low (3402 trap nights/detection), but our study shows that with adequate effort camera traps can be used successfully as a research tool for this elusive mustelid.

© 2018 Deutsche Gesellschaft für Säugetierkunde. Published by Elsevier GmbH. All rights reserved.

The geographical patterns of a species' abundance affect range limits, gene flow and population dynamics (Brown, 1984; Sagarin et al., 2006). The geographical range and abundance of species, however, can be highly variable: a species can be widespread but have low abundance throughout the range or only be found in a small geographic range but have high abundance (Rabinowitz et al., 1986). The former likely best describes honey badgers (*Mellivora capensis*), which are large, solitary mustelids with extensive home ranges (Johnson et al., 2000; Begg et al., 2005). Honey badgers exist at low densities across the majority of their range, which includes most of sub-Saharan Africa and portions of the Arabian and Indian peninsulas (Do Linh San et al., 2016). Despite their extensive distribution, honey badgers have not been well studied (Begg et al., 2003; Proulx et al., 2016), and there is a need to better understand their distribution, abundance, habitats and ecology to help define local and overall population status (Do Linh San et al., 2016) and develop proper conservation programs (Proulx et al., 2016).

Detection rates and abundance estimates for carnivores can be affected by many factors. Detection rates are affected by survey intensity (Rovero and Marshall, 2009) and how well surveys account for the habitat use of the species (Meek et al., 2014), and may also be influenced by species behavior and activity patterns. For example, seasonal patterns in distribution and activity are often based on breeding behavior (Vogt et al., 2014; Allen et al., 2015) or prey activity (Sinclair, 1979; Durant et al., 2010) and modulated by the light regime (Heurich et al., 2014). The distribution of smaller carnivores can also be affected by the presence, abundance and activity of larger carnivores (Durant, 1998; Wang et al., 2015; Newsome et al., 2017). Honey badgers are sometimes killed by large carnivores (Begg, 2001), but previous studies have given conflicting results regarding honey badger reactions to larger carnivores (e.g., Ramesh et al., 2017; Rich et al., 2017), making it unclear whether potential intraguild predation results in spatial and/or temporal avoidance.

The main difficulties in obtaining accurate estimates of honey badger abundance are their large home ranges, cryptic behavior, and low densities. Mean sizes of home ranges in Kalahari semi-desert were estimated as 541 km^2 for adult males, 151 km^2 for young males, and 126 km^2 for adult females (Begg et al., 2005). These relatively large home ranges compared to body size were attributed to low prey availability and a long period of cub dependence (12–16 months). Honey badgers have been documented in a variety of habitats from rain forests (Bahaa-el-din et al., 2013, Greengrass, 2013) to woodlands (Bird and Mateke, 2013) and

* Corresponding author.
E-mail address: maximilian.allen@wisc.edu (M.L. Allen).

https://doi.org/10.1016/j.mambio.2018.01.001
1616-5047/© 2018 Deutsche Gesellschaft für Säugetierkunde. Published by Elsevier GmbH. All rights reserved.

deserts (Begg et al., 2003), but preferences and selection of specific habitats, as well as effects of habitat characteristics on local abundance are largely unknown. Honey badgers are often nocturnal (Bird and Mateke, 2013), but activity in South Africa appears to shift to diurnal during the cool season (Begg et al., 2016).

Camera traps are being increasingly used to understand the populations (Chandler and Royle, 2013; Parsons et al., 2017) and behaviors of cryptic wildlife (Vogt et al., 2014; Allen et al., 2016). The use of systematic grid sampling with camera traps allows for continuous surveying across large spatial and temporal scales. We used this approach in a National Park in Tanzania to understand patterns in detection rates of honey badgers. Our objectives were to 1) calculate detection rates and determine the viability of using camera traps for studying honey badgers, 2) determine whether honey badger activity varied between seasons, and 3) determine the variables that are driving the distribution of detections for honey badgers, for which we used an *a-priori* modeling framework to test a series of model hypotheses composed of 10 variables explaining honey badger distribution.

Camera trap surveys were conducted in the Serengeti National Park (hereafter referred to as Serengeti), Tanzania. The Serengeti is characterized by open woodlands in the northern portions, with treeless grass plains in the south (Grant et al., 2005). Rocky outcrops or 'kopjes' support trees and shrubs and are found throughout the Serengeti, often providing the only cover on the plains (Durant, 1998). Mean annual rainfall ranges from 350 mm in the southeast to 1200 mm in the northwest (Norton-Griffiths et al., 1975) and is concentrated in the wet season (November to May) with very little rain in the dry season (June to October) and temperatures remaining consistent across seasons (Sinclair, 1979; Durant, 1998).

We used data collected as part of the Snapshot Serengeti Project (see Swanson et al., 2015, 2016) for monitoring the carnivore community. The project systematically deployed 224 camera traps in a randomly distributed grid using 5 km^2 intervals, with camera traps placed in strategic locations within 250 m of the center of each grid to maximize wildlife detection. We used the data from July 2010 to May 2013 for this study. The date, time, and camera trap site ID was recorded for each photograph, and the project used citizen scientists to determine the species and behavior (standing, resting, moving or eating) in the photographs (Swanson et al., 2016). We then proofed each of the photos that were tagged as honey badgers, and subsequently removed 5 events that had been misidentified as honey badgers. To reduce pseudoreplication, we considered photos of a species at a camera trap site within 30 min of a previous photo to be the same event (Wang et al., 2015; Rich et al., 2017). Events with multiple individuals were treated as a single event with the highest number of individuals documented. We then collected habitat variables (Appendix A in Supplementary material) for each camera trap using available layers in Arc GIS (Environmental Systems Research Institute, Redlands, CA).

We used program R version 3.3.1 (R Core Team, 2016) for all statistical analyses. We first calculated summary statistics for our data and then tested our series of hypotheses and models.

We calculated our detection rate as the 'number of detections per trap night' for each camera trap, and reported overall detection rates, and the range and mean for individual camera trap sites. We then totaled the number of independent events (E) for each species, and determined their relative abundance (RA) at each camera trap as:

$$RA = (E/TN) \times 100$$

where TN is the total number of trap nights that the camera trap was operational. We used relative abundance as our measure because they are often an accurate index of abundance (Parsons et al., 2017), and our limited sample sizes precluded us from using occupancy.

To understand the activity patterns of honey badgers we first changed the time of each event to radians and then fit the data to a circular kernel density and used its distribution to estimate the activity level using the *overlap* package (Ridout and Linkie, 2009). To determine whether honey badger activity varied by season we used the *overlapEst* function to test whether activity patterns varied between the wet and dry season, where we considered $\Delta_1 > 0.80$ to be strong overlap and 0.50–0.79 to be medium overlap (Lynam et al., 2013). We then used the *overlapEst* function to test whether honey badgers varied in activity patterns from larger carnivores (spotted hyena, *Crocuta crocuta*, and leopard, *Panthera pardus*). We did not test for African lions because their activity data was biased in favor of mid-day activity, because several camera traps were located at location regularly used as a daybed (A. Swanson, Personal Comm.), and therefore we believe that the records do not reflect true circadian activity for this species.

To understand our detection patterns for honey badgers we tested among the 14 *a-priori* models (Table 1). We fitted our models using Generalized Linear Models (GLMs) with a binomial logit link indicating whether a honey badger was detected or not at a camera trap. We compared our models using AIC weight (AIC_w) (Burnham and Anderson, 2002), and considered each of the models until a cumulative $AIC_w = 0.90$ to be our top models.

We had a total of 98,644 trap nights at 224 camera traps. We detected 29 honey badger events at 23 individual camera traps, among which 6 events included 2 honey badgers. In 86% of events the honey badgers were moving, but we also documented standing (10%) and eating (4%).

Our overall detection rate among all camera traps was 3402 trap nights/detection. Our detection rates for the 23 individual camera traps with detections ranged from 94 to 720 trap nights/detection, with a mean rate for individual camera traps of 404.4 ($\pm$40.6 SE) trap nights/detection. October had the highest number of detections ($n = 5$), followed by 3 detections in each of February, March, and June. No detections were recorded in July or August.

We found that honey badger activity was generally similar among seasons with a medium overlap ($\Delta_1 = 0.69$). The main difference being that during the wet season ($n = 15$) honey badgers were active during all times, with peaks during crepuscular hours, but during the dry season ($n = 14$) they showed a strong nocturnal peak (Fig. 1). Honey badgers had strong temporal overlap with both spotted hyenas ($\Delta_1 = 0.85$) and leopards ($\Delta_1 = 0.82$) (Fig. 1).

Our best model 'Lion Abundance' had 2 times more explanatory value ($AIC_w = 0.57$) as the next best model 'Apex Carnivore Avoidance' ($AIC_w = 0.27$). These two were our top models (Table 2), however, the variables in the models did not always affect honey badger abundance in the way we predicted. In 'Lion Abundance', African lions had a positive relationship ($ß_{lion} = 0.009$), and in 'Apex Carnivore Avoidance', both African lions and spotted hyenas had positive relationships ($ß_{lion} = 0.009$, $ß_{hyena} = 0.001$).

The small number of studies focused on honey badgers in the published literature may be directly related to the difficulty of finding and detecting this elusive mustelid. In our study, we documented 29 honey badger events across 98,644 trap nights (an average of 3402 trap nights needed for each detection). Some of the camera traps had notably higher success, but even our most frequently visited camera trap still needed on average 94 nights per detection. These detection rates appear to be much lower than those found with nocturnal vehicle surveys (e.g., 0.1 honey badgers/km; Waser 1980), or those of other carnivores (e.g., Ramesh et al., 2017; Rich et al., 2017). The low detection rate limited our ability to detect differences in behaviors and detections by month or time of day, and also precluded us from using occupancy modeling for our analyses.

Our top models suggest that honey badger distribution is not negatively affected by interspecific interactions with larger car-

Table 1
Our *a-priori* models to explain honey badger distribution at camera sites in Serengeti National Park. We provide the name of the model, the variables included and the hypothesis behind the model together with references used to develop it.

Name	Variables	Hypothesis
Habitat Preference	HABT*GRHT	Distribution of honey badgers will be dictated by their preferred habitat (Durant et al., 2010; Vanderhaar and Hwang, 2003).
Water Availability	RIVR	The distribution of honey badgers will be dictated by the proximity to water and riparian habitats (Durant et al., 2010).
Habitat and Water Availability	HABT * GRHT + RIVR	The distribution of honey badgers will be dictated by a combination of available habitat and water (Durant et al., 2010; Vanderhaar and Hwang, 2003).
Cover	COVR	The availability of cover will dictate the distribution of honey badgers (Durant et al., 2010).
Kopje	KOPJ	The availability of kopjes for cover, possible den sites, and habitat heterogeneity will dictate the distribution of honey badgers (Durant et al., 2010).
Cover and Kopje	COVR + KOPJ	The distribution of honey badgers will be dictated by areas that provide cover (Durant et al., 2010).
Human Abundance	HUAB	The distribution of honey badgers will be dictated by trying to avoid areas frequently used by humans (Proulx et al., 2016).
Leopard Abundance	LPAB	The distribution of honey badgers will be dictated by trying to avoid areas frequently used by leopards (Begg, 2001; Do Linh San et al., 2016; Ramesh et al., 2017).
Leopard Abundance and Cover	LPAB + COVR	The distribution of honey badgers will be dictated by avoiding leopards and cover to escape (Ramesh et al., 2017).
Lion Abundance		The distribution of honey badgers will be dictated by trying to avoid areas used by African lions (Begg, 2001; Do Linh San et al., 2016).
Cascading Carnivore Abundance	LPAB * LNAB	Honey badgers will be more frequently found where lions are abundant due to their deterring the leopards (Ramesh et al., 2017)
Apex Carnivore Abundance	LNAB + HYAB	The distribution of honey badgers will be dictated by trying to avoid areas frequently used by group-living apex carnivores (Begg, 2001; Do Linh San et al., 2016).
Trapping Effort	TRAP	The number of camera trap nights will have greater influence on the distribution of honey badgers than biological factors (Wegge et al., 2004).

Table 2
The results of our *a-priori* model selection for honey badger distribution in Serengeti National Park, with individual models ranked based on their AIC_w.

Name	Variables	AIC	ΔAIC	AIC_w	Cum AIC_w
Lion Abundance	LNAB	140.09	0.00	0.57	0.57
Apex Carnivore Avoidance	LNAB + HYAB	141.58	1.49	0.27	0.84
Cascading Predation	LPAB * LNAB	143.64	3.55	0.10	0.94
Cover and Kopje	COVR + KOPJ	146.82	6.73	0.02	0.96
Cover	COVR	146.94	6.85	0.02	0.98
Leopard Abundance and Cover	LPAB + COVR	148.89	8.80	0.01	0.99
Kopje	KOPJ	149.89	9.80	0.00	0.99
Human Avoidance	HUAB	150.18	10.09	0.00	0.99
Trapping Effort	TRAP	151.88	11.79	0.00	1.00
Water Availability	RIVR	152.13	12.04	0.00	1.00
Leopard Abundance	LPAB	152.53	12.44	0.00	1.00
Habitat and Water Availability	HABT * COVR + RIVR	152.62	12.53	0.00	1.00
Habitat Preference	HABT * GRHT	154.94	14.85	0.00	1.00

nivores, but instead honey badgers seek out similar habitats and niches as larger carnivores. In our top two models the interactions with African lions and spotted hyenas were important, while our third best model also included leopards, and presence of all three species coincided with higher detection of honey badgers at camera trap sites. Honey badgers also exhibited strong temporal overlap with spotted hyenas and leopards suggesting there was also no temporal avoidance of larger carnivores. It could be that our low sample size limited our ability to determine what drives site-level detection of honey badgers, but the data suggest that honey badgers are not avoiding larger carnivores in Serengeti, as was suggested by Ramesh et al. (2017) for badgers and leopards in South Africa. Instead, our results support the study by Rich et al. (2017) and Balme et al. (2017), who reported a lack of repulsion of carnivore guild species. Although it has been documented that large carnivores occasionally kill honey badgers (Begg, 2001), honey badgers are notorious for their aggressive behavior and high resource holding potential even when faced with much larger carnivores (Estes, 1992). Their aggressive threat display is often successful in preventing predation even against largest of carnivores, such as African lions, spotted hyenas, and leopards (Begg, 2001). Our results suggest that honey badgers may exhibit less avoidance of large carnivores in space and time than other, less aggressive mesocarnivores, which are often constrained by apex carnivores (Durant, 1998; Hayward and Slotow, 2009; Newsome et al., 2017).

The benefit of systematic grid sampling with camera traps is that it allows for continuous surveying across large spatial and temporal scales (Swanson et al., 2015; Rich et al., 2017) while not affecting the activity or behavior of wildlife (Vogt et al., 2014; Allen et al., 2016). We found that honey badgers exhibited seasonal variation in their activity, which is in accord with studies from other ecosystems (Begg et al., 2016; Bird and Mateke, 2013). During the wet season honey badgers were active throughout the 24-h cycle, but during the dry season honey badgers showed a strong nocturnal peak. Honey badgers avoid the hottest times of the day by staying in burrows in other systems (Begg et al., 2003; Bird and Mateke, 2013), but temperatures in the Serengeti stay similar throughout the year, suggesting that the circadian cycles are not dictated solely by temperatures. This could, however, be an artifact of our low sample sizes, or the placement of cameras as honey badgers may be seeking out shaded areas during day similar to African lions.

Adjustments to the systematic camera trap design used may allow for higher detection rates in the future. First, it is important to understand that these camera traps were placed in areas that would allow for detections of all wildlife species (Swanson et al., 2015), and not just honey badgers. A camera trap study target-

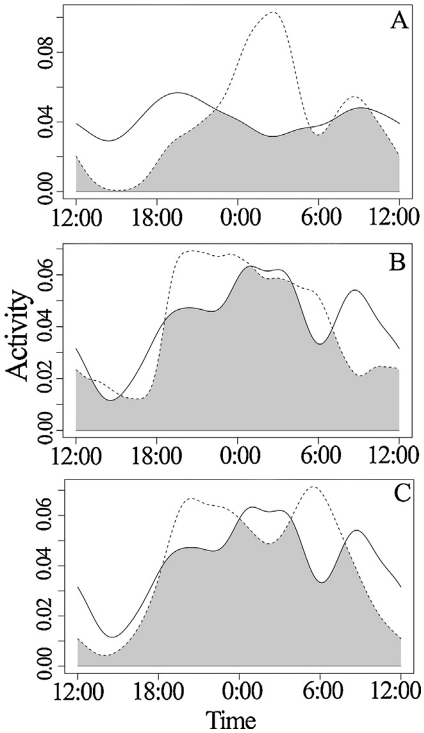

Fig. 1. The temporal activity and overlap (gray-shaded area), estimated with kernel densities, of honey badgers and large carnivores in the Serengeti. (A) represents honey badger activity during different seasons, with wet season represented as a solid line and dry season represented as a dotted line. (B&C) represent overlap of honey badger activity with spotted hyenas (B) and leopards (C), where honey badger activity is represented as solid lines and the large carnivore activity as a dotted line.

ing honey badgers could increase success by choosing microhabitat variables most frequently used by honey badgers, such as heterogeneous aspects of the landscape, or placing camera traps near known tracks, marking sites, food sources or dens. Adjustments like these may be especially important for species like honey badger that are characterized by very low detection rates. Nevertheless, due to the large home ranges of honey badgers and low population densities, detection rates are always likely to be low. The camera traps were placed in the center of 5 km^2 grids, which should be sufficiently large enough for determining population sizes of honey badgers in a spatially explicit capture recapture modeling framework (Chandler and Royle, 2013). Other important topics for future research include increasing detection rates, understanding honey badger selection of microhabitat features, and determining what may affect the distribution of honey badgers. While research of honey badger is difficult and presents many challenges, we encourage future research to understand their ecology and to develop effective conservation and management efforts, where needed.

Acknowledgements

We thank the Snapshot Serengeti team (www.snapshotserengeti.org) for generously providing the data for this study, and Ali Swanson, Emmanuel Do Linh San, and an anonymous reviewer for comments on earlier drafts that greatly improved the manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.mambio.2018.01.001.

References

Allen, M.L., Wallace, C.F., Wilmers, C.C., 2015. Patterns in bobcat (*Lynx rufus*) scent marking and communication behaviors. J. Ethol. 33, 9–14.

Allen, M.L., Wittmer, H.U., Setiawan, E., Jaffe, S., Marshall, A.J., 2016. Scent marking in Sunda clouded leopards (*Neofelis diardi*): novel observations close a key gap in understanding felid communication behaviours. Sci. Rep. 6, 35433.

Bahaa-el-din, L., Henschel, P., Aba'a, R., Abernethy, K., Bohm, T., Bout, N., Coad, L.M., Head, J., Inoue, E., Lahm, S.A., Lee, M., 2013. Notes on the distribution and status of small carnivores in Gabon. Small Carniv. Conserv. 48, 19–29.

Balme, G.A., Pitman, R.T., Robinson, H.S., Miller, J.R., Funston, P.J., Hunter, L.T., 2017. Leopard distribution and abundance is unaffected by interference competition with lions. Behav. Ecol. 28, 1348–1358.

Begg, C.M., 2001. Feeding Ecology and Social Organisation of Honey Badgers (*Mellivora capensis*) in the Southern Kalahari. University of Pretoria, Pretoria, Doctorate thesis.

Begg, C.M., Begg, K.S., du Toit, J.T., Mills, M.G.L., 2003. Sexual and seasonal variation in the diet and foraging behaviour of a sexually dimorphic carnivore, the honey badger (*Mellivora capensis*). J. Zool. 260, 301–316.

Begg, C.M., Begg, K.S., du Toit, J.T., Mills, M.G.L., 2005. Spatial organization of the honey badger *Mellivora capensis* in the southern Kalahari: home-range size and movement patterns. J. Zool. 265, 23–35.

Begg, C.M., Begg, K.S., Do Linh San, E., du Toit, J.T., Mills, M.G.L., 2016. Sexual and seasonal variation in the activity patterns and time budget of honey badgers in an arid environment. In: Proulx, G., Do Linh San, E. (Eds.), Badgers: Systematics, Biology, Conservation and Research Techniques. Alpha Wildlife Publications, Sherwood Park, Alberta, Canada, pp. 161–192.

Bird, T.L., Mateke, C.W., 2013. A preliminary survey of the presence and distribution of small carnivores in the Lower Zambezi Protected Area Complex, Zambia. Small Carniv. Conserv. 48, 47–59.

Brown, J.H., 1984. On the relationship between abundance and distribution of species. Am. Nat. 124, 255–279.

Chandler, R.B., Royle, J.A., 2013. Spatially explicit models for inference about density in unmarked or partially marked populations. Ann. Appl. Stat. 7, 936–954.

Do Linh San, E., Begg, C., Begg, K., Abramov, A.V., 2016. *Mellivora capensis*. The IUCN Red List of Threatened Species 2016, e.T41629A45210107.

Durant, S.M., Craft, M.E., Foley, C., Hampson, K., Lobora, A.L., Msuha, M., Eblate, E., Bukombe, J., Mchetto, J., Pettorelli, N., 2010. Does size matter? An investigation of habitat use across a carnivore assemblage in the Serengeti, Tanzania. J. Anim. Ecol. 79, 1012–1022.

Durant, S.M., 1998. Competition refuges and coexistence: an example from Serengeti carnivores. J. Anim. Ecol. 67, 370–386.

Estes, R.D., 1992. The Behavior Guide to African Mammals. University of California Press Berkeley, Los Angeles.

Grant, J., Hopcraft, C., Sinclair, A.R.E., Packer, C., 2005. Planning for success: serengeti lions seek prey accessibility rather than abundance. J. Anim. Ecol. 74, 559–566.

Greengrass, E.J., 2013. A survey of small carnivores at Putu Mountains, southeast Liberia. Small Carniv. Conserv. 48, 30–36.

Hayward, M.W., Slotow, R., 2009. Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. S. Afr. J. Wildl. Res. 39, 109–125.

Heurich, M., Hilger, A., Küchenhoff, H., Andrén, H., Bufka, L., Krofel, M., Mattisson, J., Odden, J., Persson, J., Rauset, G.R., Schmidt, K., Linnell, J.D.C., 2014. Activity patterns of Eurasian Lynx are modulated by light regime and individual traits over a wide latitudinal range. PLoS One 9, e114143.

Johnson, D.S.P., Macdonald, D.W., Dickman, A.J., 2000. An analysis and review of models of the sociobiology of the Mustelidae. Mammal Rev. 30, 171–196.

Lynam, A.J., Jenks, K.E., Tantipisanuh, N., Chutipong, W., Ngoprasert, D., Gale, G.A., Steinmetz, R., Sukmasuang, R., Bhumpakphan, N., Grassman Jr., L.I., Cutter, P., 2013. Terrestrial activity patterns of wild cats from camera-trapping. Raffles Bull. Zool. 61 (2013), 407–415.

Meek, P.D., Ballard, G., Claridge, A., Kays, R., Moseby, K., O'brien, T., O'Connell, A., Sanderson, J., Swann, D.E., Tobler, M., Townsend, S., 2014. Recommended guiding principles for reporting on camera trapping research. Biodivers. Conserv. 23, 2321–2343.

Newsome, T.M., Greenville, A.C., Ćirović, D., Dickman, C.R., Johnson, C.N., Krofel, M., Letnic, M., Ripple, W.J., Ritchie, E.G., Stoyanov, S., Wirsing, A.J., 2017. Top predators constrain mesopredator distributions. Nat. Commun. 8, 15469.

Norton-Griffiths, M., Herlocker, D., Pennycuick, L., 1975. The patterns of rainfall in the Serengeti ecosystem, Tanzania. East Afr. Wildl. J. 13, 347–374.

Parsons, A.W., Forrester, T., McShea, W.J., Baker-Whatton, M.C., Millspaugh, J.J., Kays, R., 2017. Do occupancy or detection rates from camera traps reflect deer density. J. Mamm. 98, 1547–1557.

Proulx, G., Abramov, A.V., Adams, I., Jennings, A.P., Khorozyan, I., Rosalino, L.M., SantosReis, M., Veron, G., Do Linh San, E., 2016. World distribution and status of badgers — a review. In: Proulx, G., Do Linh San, E. (Eds.), Badgers: Systematics, Biology, Conservation and Research Techniques. Alpha Wildlife Publications, Sherwood Park, Alberta, Canada, pp. 31–116.

R Core Team, 2016. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Rabinowitz, D., Cairns, S., Dillon, T., 1986. Seven forms of rarity and their frequency in the flora of the British Isles. In: Soule, M.E. (Ed.), Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, pp. 182–204.

Ramesh, T., Kalle, R., Downs, C.T., 2017. Staying safe from top predators: patterns of co-occurrence and inter-predator interactions. Behav. Ecol. Sociobiol. 71, 41.

Rich, L.N., Miller, D.A.W., Robinson, H.S., McNutt, J.W., Kelly, M.J., 2017. Carnivore distributions in Botswana are shaped by resource availability and intraguild species. J. Zool. 303, 90–98.
Ridout, M.S., Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. J. Agric. Biol. Environ. Stat. 14, 322–337.
Rovero, F., Marshall, A.R., 2009. Camera trapping photographic rate as an index of density in forest ungulates. J. Appl. Ecol. 46, 1011–1017.
Sagarin, R.D., Gaines, S.D., Gaylord, B., 2006. Moving beyond assumptions to understand abundance distributions across the ranges of species. Trends Ecol. Evol. 21, 524–530.
Sinclair, A.R.E., 1979. The serengeti environment. In: Sinclair, A.R.E., Norton-Griffiths, M. (Eds.), Serengeti: Dynamics of an Ecosystem. University of Chicago Press, PA, pp. 31–45.
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, 150026.
Swanson, A., Kosmala, M., Lintott, C., Packer, C., 2016. A generalized approach for producing, quantifying, and validating citizen science data from wildlife images. Conserv. Biol. 30, 520–531.
Vogt, K., Zimmermann, F., Kolliker, M., Breitenmoser, U., 2014. Scent-marking behaviour and social dynamics in a wild population of Eurasian lynx *Lynx lynx*. Behav. Process 106, 98–106.
Wang, Y., Allen, M.L., Wilmers, C.C., 2015. Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. Biol. Conserv. 190, 23–33.
Wegge, P., Pokheral, C.P., Jnawali, S.R., 2004. Effects of trapping effort and trap shyness on estimates of tiger abundance from camera trap studies. Anim. Conserv. Forum 7, 251–256.