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Research

Efficacy of spotlights and thermal cameras to detect lions *Panthera leo* and spotted hyenas *Crocuta crocuta* depends on species and management regime

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Accurate abundance estimates can contribute to effective management of large carnivore populations. Lion *Panthera leo* and spotted hyena *Crocuta crocuta* populations are frequently estimated at night by eliciting their approach using broadcasted vocalizations. Spotlights are typically used to observe these species on approach but can disturb animals and adversely affect counts. We compared the efficacy of spotlight with red filters and forward looking infrared (FLIR) thermal monocular to enumerate lions and spotted hyenas in Serengeti National Park (SNP; non-hunted area) and Maswa Game Reserve (MGR; hunted area), Tanzania, during 2015–2017. We established 119 call-in sites in SNP and 20 in MGR and conducted repeated call-ins at 1–2 week intervals. During call-ins we conducted systematic paired counts using both devices. We assessed the influence of device order, species, hunting regime and land cover on species counts. We found that FLIR was more efficacious for counting hyenas in MGR and spotlight for counting lions in SNP. We found evidence for temporary artificial light disturbance in MGR, as counts were higher when FLIR was used as the second device. Habitat type within 200 m of call-in sites did not influence device performances. Greater spotlight efficacy in SNP is a likely consequence of lower perceived risk and less anthropogenic disturbance compared to MGR. To improve accuracy of counts and subsequent population estimates for lions and spotted hyenas, we recommend consideration of variation in device efficacy, based on species surveyed and management regime.

Keywords: animal counts, call-in, forward looking infrared (FLIR), large carnivore, lion *Panthera leo*, Maswa Game Reserve, population estimation, Serengeti National Park, spotlight, spotted hyena *Crocuta crocuta*, thermal camera

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Introduction

Populations of many of the world's large carnivores are in decline (Di Marco et al. 2014, Ripple et al. 2014). Though, several species have stable (e.g. red wolves *Canis rufus* and Eurasian lynx *Lynx lynx*) or increasing (American bear *Ursus americanus* and gray wolves *Canis lupus* populations) (Ripple et al. 2014). But more than 60% of large carnivores are threatened with extinction (Ripple et al. 2014). For example, the abundance of African lions *Panthera leo* has declined from about 200 000 individuals historically (Myers 1975) to as few as 20 000–35 000 individuals (Riggio et al. 2013), including a reported 43% decline since 1993 (Bauer et al. 2015). Dominant factors for these declines include land use change (Bauer et al. 2010), poorly regulated legal harvests (Loveridge et al. 2007) and illegal killing of lions and their prey (Bauer and De Iongh 2005, Hayward et al. 2007, Bauer et al. 2008, 2015). Even large carnivores with abundant populations are currently experiencing population declines (e.g. spotted hyena *Crocuta crocuta*) for many of the same reasons (Bohm and Höner 2015).

Credible population estimates are important for management of large carnivores and other wildlife species (Hunter and Gibbs 2006). Such estimates can broadly influence respective conservation policies and actions (Bauer et al. 2015, Elliot and Gopalaswamy 2017), including setting appropriate harvest quotas or assessing the effectiveness of protection measures (Linnell et al. 1998). Most importantly, acquired knowledge especially populations trends, may contribute toward informed decisions for other management approaches including adaptive management (Kaji et al. 2010). Estimating large carnivore abundance is challenging, with numerous techniques used including direct counts (Tumenta et al. 2010), remote cameras (Karanth et al. 2003, Linkie et al. 2006, Cusack et al. 2015), distance sampling (Durant et al. 2011) and mark–recapture techniques (Ogutu et al. 2006, Elliot and Gopalaswamy 2017). For lions and spotted hyenas, the two most frequently used methods are track counts (Smallwood and Fitzhugh 1995, Balme et al. 2009, Funston et al. 2010, Midlane et al. 2015, Belant et al. 2019) and call-in surveys (Ogutu and Dublin 1998, Mills et al. 2001, Ferreira and Funston 2010, 2016, Midlane et al. 2015, Belant et al. 2016, 2017).

Call-in surveys for large carnivores use broadcasted vocalizations to attract individuals and are typically conducted at night (Cozzi et al. 2012) using spotlights (Mills et al. 2001, Cozzi et al. 2013). Spotlights are inexpensive and are effective for detecting animals; however, the bright light emitted can disturb, cause avoidance and reduce animal detection (Belant and Seamans 2000, Mills et al. 2001, Cozzi et al. 2013). Infrared devices such as thermal cameras or forward-looking infrared are expensive but potentially less disturbing as they emit no artificial light (Belant and Seamans 2000, Cozzi et al. 2013). Surveys using spotlights are more common than those using FLIR, however, the differences in detection efficacy between these devices has not been evaluated for large carnivores. We compared the effectiveness of spotlight and FLIR for detecting lions and spotted hyenas in areas with and without hunting in the Greater Serengeti Ecosystem, northern Tanzania. We predicted fewer individuals of both species would be detected using spotlights, particularly in hunted areas due to avoidance behavior (Stillfried et al. 2015). Because response to artificial lights can differ among species (Vinson et al. 2020) and lions are dominant to spotted hyenas (Sinclair and Arcese 1995), we predicted proportionately more lions to be detected with spotlights.

Material and methods

Study area

We conducted this study in Serengeti National Park (SNP; 14 753 km^2) and Maswa Game Reserve (MGR; 2200 km^2), which forms part of the 25 000 km^2 Greater Serengeti Ecosystem in northern Tanzania (Fig. 1). Annual rainfall and vegetation vary from southeast to northwest, with rainfall increasing from 500 to 1100 mm and vegetation transitioning from short grassland to savanna woodland, respectively (McNaughton 1983, Mduma et al. 1999, Holdo et al. 2009). Rainfall typically occurs from November to May, with a dry period from January to March (Sinclair and Arcese 1995). The Serengeti ecosystem supports the world's largest group of migrating ungulates (wildebeest *Connochaetes taurinus,* about 1.3 million individuals, plains zebra *Equus quagga,* 200 000 individuals and Thomson's gazelle *Eudorcas thomsonii,* 440 000 individuals) and the highest known density of large carnivores (Sinclair et al. 2008). MGR is designated for consumptive wildlife use, regulated hunting occurs from July to December, while in SNP hunting is not allowed and photographic tourism is the dominant recreational activity.

Methods

We broadcasted vocalizations at call-in sites following Belant et al. (2016, 2017) during three surveys, two in SNP during 2015–2016 (Belant et al. 2016, 2017, Mwampeta et al. 2021) and one in MGR during 2017 (Mwampeta et al. 2021). Overall, we established 119 call-in sites in SNP and 20 in MGR spaced at least 6–8 km apart (Fig. 1). We conducted call-ins from late May to early November, with each site visited 5–7 times at 1–2 week intervals. Though through tourism and law enforcement activities, lion and hyena populations were habituated to vehicular disturbances, we maintained the lowest level of disturbance possible throughout our survey. We used one vehicle at each site and as suggested by Ferreira et al. (2013), we used the minimum number of people (i.e. 2 or 3) necessary to conduct surveys and took precautions to minimize human and vehicular noise and movements during call-in sessions.

We broadcasted calls from 19:00 to about 02:00 hrs when lions and hyenas are most active (Cozzi et al. 2012). Calls were broadcasted at up to 116 dB using a commercial game calling system (Foxpro Inc., Lewistown, PA, USA). We used

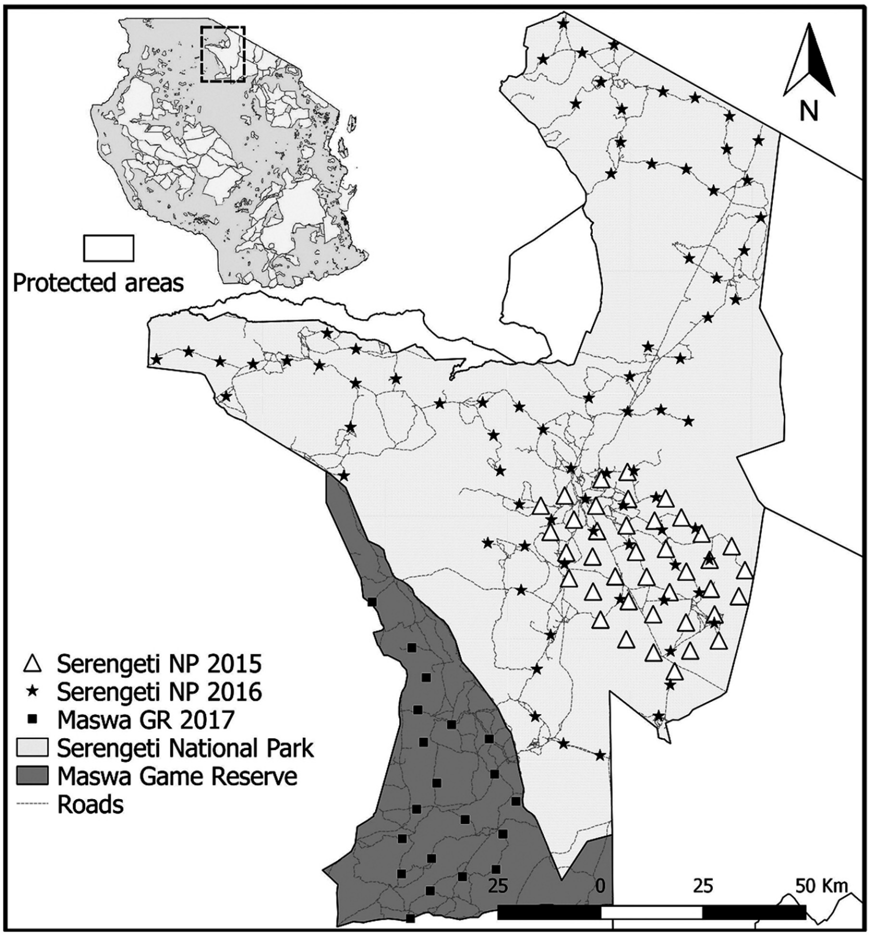

Figure 1. Sites used to elicit lion and spotted hyena approach using broadcasted vocalizations, Serengeti National Park (2015–2016) and Maswa Game Reserve (2017), northern Tanzania.

four speakers mounted at 90-degree intervals on the roof of the vehicle (about 2.4 m above ground). We used a digital recording which consisted of a single female lion roar, distressed prey (wildebeest, warthog, *Phacochoerus africanus*, zebra, and occasionally buffalo *Syncerus caffer*) and a spotted hyena whoop call. We broadcasted at each site for 70 min, playing calls for 10 min followed by a 5 min pause and repeated this pattern 5 times. Each 10 min broadcast consisted of 37 s of a lion, 125 s of respective prey and 38 s of hyena calls, repeated three times.

We used a spotlight with red filter (Enforcer Series Halogen, Light Force, Hindmarsh, Australia) and FLIR (Scout II, FLIR Systems Inc., Arlington, VA, USA) to detect lions and spotted hyenas. Each call-in started with an observer conducting a complete scan of the surrounding area with one of the randomly selected device, immediately followed by scanning the area with the remaining device. This sequence was repeated at the end of each 10-min segment of the broadcast, each time reversing the previous order of the observing device. Our observations for comparison consisted of the paired counts from the spotlight and FLIR. At each site we collected six paired observations; at the beginning and end of each 10 min broadcast. We discarded pairs of observations separated by 3 min or longer to minimize potential bias from animals entering or departing sites between paired observations.

Because vegetation can influence the performance of each device (Belant and Seamans 2000, Vinson et al. 2020), we classified land cover using a 200-m radius buffer around each calling site (Grunblatt et al. 1989, Reed et al. 2009). We then used Landsat imagery (LPDAAC, USGS/EROS, Sioux Falls, SD) to group 24 vegetation assemblages (Reed et al. 2009) into five land covers: bare (non-vegetated area), woodland (single-stem woody vegetation with canopy cover 51–100%), wooded grassland (3–50% canopy cover), grassland (0–2% canopy cover) and shrub (areas dominated by multi-stemmed woody vegetation < 2 m; Cusack et al. 2015).

We modeled factors potentially influencing difference in counts between devices by fitting a linear mixed-effects model. We used difference in counts within each pair as the response and included device type, species and hunting regime with interactions as fixed effects. We considered MGR populations of lions and hyenas as disturbed and in SNP habituated. Further, we regarded lions as dominant to hyenas and tested the influence of habituation through species avoidance on the efficacy of FLIR and spotlight (Supporting information) between MGR and SNP. To account for repeated observations across sites, we fitted land cover and sites as random intercepts. In our initial analysis we found that many paired counts had equal numbers of individuals observed, which created an excess zero in our response. We therefore used zero-inflation in our model to account for this and fitted the model using the 'glmmTMB' package (Brooks et al. 2017) in R ver. 3.6.3 (<www.r-project.org>). We tested for avoidance by comparing the difference in FLIR count between before (FLIR used as the first device in the observation pair) and after (FLIR used as the second device of the observing pair) the spotlight count. A higher FLIR count before than after spotlight count indicates avoidance. Finally, we calculated a coefficient of variation (CV) between devices and protected areas.

Results

Overall, we obtained 3982 (3444 from SNP and 538 from MGR) paired counts for analyses with 1512, 1932 and 538 collected in 2015, 2016 and 2017, respectively. We observed a greater number of hyenas in MGR when using FLIR, where the predicted difference from spotlight to FLIR was 0.73 [95% CI: 0.17, 1.29] individuals and a difference of −0.98 [95% CI: −1.54, −0.43] when using FLIR before spotlight. We found no differences between devices for lion counts in MGR (Table 1). In contrast, we counted greater numbers of lions in SNP using spotlights, with the predicted change from spotlight to FLIR −0.62 [95% CI: −1.02, −0.22] individuals and a predicted increase of 0.55 [95% CI: 0.18, 0.93] individuals detected from FLIR to spotlight. Overall, spotlight performed significantly better in SNP. Additionally, CVs supported our primary results that mean counts of hyenas using FLIR were greater and less variable in MGR than were mean spotlight counts using spotlights (Supporting information). Similarly, mean spotlight counts of lions in SNP were greater and less variable than were counts of lions using FLIR.

Table 1. Parameter estimates and 95% confidence interval (CI) from a zero-inflated linear mixed-effects model assessing the difference in counts between first and second used device, in Serengeti National Park (2015–2016) and Maswa Game Reserve (2017), northern Tanzania. Random effects are reported as variation (σ^2) and 95% CIs. Significant effects ($p < 0.05$) are presented in bold font, and trends ($p < 0.10$) in bold italics. Device = spotlight versus forward looking infrared (FLIR), protected area = Serengeti National Park versus Maswa Game Reserve and species = lion versus spotted hyenas; reference levels are FLIR, spotted hyena and Maswa Game Reserve.

Covariate	Estimate	CI: lower	CI: upper
Fixed effects			
Intercept	0.730	0.172	1.287
Device	**−1.714**	**−2.502**	**−0.926**
PA	**−1.053**	**−1.640**	**−0.465**
Species	**−1.209**	**−2.492**	**0.074**
Device × PA	**1.884**	**1.054**	**2.715**
Device × Species	***1.783***	***−0.065***	***3.631***
PA × Species	0.912	−0.444	2.268
Device × PA × Species	−0.781	−2.727	1.164
Random effects			
Habitat type	0.000	0.000	0.000
Site	0.000	0.000	0.000
Zero-inflation model			
Intercept	1.114	1.056	1.172

Discussion

We demonstrated variation between spotlights and FLIR for conducting counts of lions and spotted hyenas, which further varied between hunted and non-hunted areas. Spotlights were effective in enumerating lions in SNP and are commonly used to detect large carnivores and other wildlife species (Midlane et al. 2015, Belant et al. 2016), but were less effective for detecting spotted hyenas in MGR. One reason for the lower number of detections may be hyena's avoidance behavior due to hunting in MGR; wildlife species are often more wary of humans in hunted areas (Little et al. 2014, Stillfried et al. 2015, Hariohay et al. 2018). However, we conducted the survey in MGR before the hunting season and therefore, fewer hyena detections could be a consequence of other human activities, including poaching and livestock incursion. Poaching occurs in the Serengeti ecosystem (Rentsch and Damon 2012) and although snares are most commonly used to take wildlife illegally (Knapp 2012), poaching at night with use of spotlights also occurs (Fischer et al. 2014).

In contrast to hyenas, lions were detected equally using spotlights and FLIR in MGR. Though lions can legally be hunted in MGR, annual quotas are low and in some years no lions are harvested (L. Masinde 2017, unpubl.). Further, lions are the dominant carnivore in the Serengeti ecosystem (Sinclair and Arcese 1995). Consequently, lower perceived risk by lions may have resulted in lack of avoidance behavior resulting in similar number of detections using spotlights or FLIR. That fewer hyenas were detected with spotlights than with FLIR in MGR may be due to their overall greater perceived risk relative to lions.

We found evidence for hyena spotlight avoidance in MGR, however, this avoidance was temporary as a count of hyenas using FLIR immediately following the count using spotlight was greater. This is a likely consequence of avoidance of the visible light emitted by spotlights, previously demonstrated to disturb wildlife (Gaston et al. 2013). Additionally, we observed different behavioral responses to spotlights that did not occur during observations with FLIR; hyenas immediately ran and sought cover upon a direct spotlight shine. We did not observe this avoidance with lions, which typically walked toward call-in station and turned their heads or walked away when a spotlight was directed toward them. Hyena responses toward this potential human disturbance were more intense in MGR than in SNP and could partly explain why hyenas are relatively more adaptable to human-dominated landscapes than lions (Green et al. 2018). Similarly, Cougar *Panthera concolor* avoided visiting and making kills in artificially illuminated areas (Ditmer et al. 2021).

Spotlights were effective for detecting lions in Serengeti National Park. Most mammalian species possess tapetum lucidum (Ollivier et al. 2004), an adaptation for visual acuity in poor light (Focardi et al. 2001) which reflects light and enhances detection with spotlights. Although this adaptation is more pronounced in lions than in hyenas (Ollivier et al. 2004), subsequent detection is facilitated for both species. Vinson et al. (2020) recorded consistently higher counts of Australian greater gliders *Petauroides volans* using FLIR. Their findings and ours suggest that the effectiveness of these devices varies among species.

We found no evidence that onsite vegetation cover influenced detection variation between devices. A possible reason for this is that both devices are equally influenced by vegetation obstruction. Several studies have demonstrated that FLIR and spotlights were negatively influenced by vegetation (Belant and Seamans 2000, Tizzani et al. 2014, Sokos et al. 2015, Gonzalez et al. 2016, Vinson et al. 2020). Gonzalez et al. (2016) found that in dense vegetation, detection of koala *Phascolarctos cinerus* beyond 60 m was unreliable. Vinson et al. (2020) reported a similar limitation using thermal cameras to observe arboreal mammals in Australia.

Spotlights are inexpensive and easy to use, however as found in our study and previously (Belant and Seamans 2000, Collier et al. 2007), the emitted light can disturb approaching individuals and reduce their potential for detection. The cost of FLIR devices are greater than spotlights but may be advantageous in areas where species exhibit moderate or high avoidance of humans. We demonstrated that spotlights were superior for counting lions in a non-hunted population (Table 1). However, we encourage additional comparisons from multiple sites with these and other species to better generalize factors that may influence detection. Credible estimates of large carnivore density or abundance are critical for effective monitoring and wildlife management and rely on our ability to accurately and consistently detect species during surveys. To improve accuracy and precision of estimates for lions and spotted hyenas, as well as other wildlife species, we recommend consideration of variation in the efficacy of devices used for detection across species and management regimes, to ensure that subtle population changes are effectively detected and properly managed.

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Conflict of interest – There is no conflict of interest to declare.

Author contributions

Stanslaus B. Mwampeta: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (supporting); Project administration (equal); Resources (equal); Software (equal); Supervision (supporting); Validation (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Clay M. Wilton**: Data curation (equal); Investigation (equal); Methodology (equal); Software (lead); Writing – review and editing (supporting). **Imani J. Mkasanga**: Data curation (equal); Investigation (equal); Writing – review and editing (supporting). **Florent Bled**: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Writing – review and editing (supporting). **Lusato M. Masinde**: Investigation (supporting); Resources (supporting); Validation (equal); Writing – review and editing (supporting). **Eivin Røskaft**: Conceptualization (equal); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Peter S. Ranke**: Data curation (equal); Formal analysis (lead); Software (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Robert Fyumagwa**: Conceptualization (equal); Investigation (equal); Resources (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Jerrold L. Belant**: Conceptualization (lead); Data curation (equal); Formal analysis (equal); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Resources (lead); Software (equal); Supervision (lead); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (lead).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.bk3j9kddw> (Mwampeta et al. 2022).

Supporting information

The supporting information associated with this article is available from the online version.

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