

Evaluating relative abundance indices for terrestrial herbivores from large-scale camera trap surveys

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Funding information

University of Minnesota, Twin Cities, Grant/Award Number: Alexander & Lydia Anderson Grant, Ecology, Evolution, and Behavior Research Award, Ecology, Evolution, and Behavior Travel Award, James W. Wilkie Fund for Natural History Fellowship and Thesis Research Grant; National Science Foundation, Grant/Award Number: DEB-1020479 and GRFP-00039202; National Geographic Society, Grant/Award Number: Explorer Grant

Abstract

The ability to directly monitor animal populations across time and space is a key element of wildlife conservation and management, but logistically difficult to achieve. Photographic capture rates from camera trap surveys can provide relative abundance indices (RAIs) for a wide variety of medium- to large-bodied wildlife species. RAIs are less complex than other estimation methods and are commonly used when true abundance is difficult or costly to measure. However, this method is controversial as it does not account for potential bias arising from imperfect detection. Here, we evaluate the reliability and precision of RAI estimates drawn from a large-scale camera trap survey for ten African herbivore species by comparing them against preexisting aerial survey data. RAIs correlated strongly with independent estimates, particularly when indices were derived from counts of all photographed animals. RAIs were most reliable for species that were nonmigratory, occurred in open habitats and had high rates of daily movement. Increasing survey coverage and duration both had strong but comparable effects on improving RAI precision. Our results suggest that RAIs from camera traps hold substantial promise as a tool for monitoring herbivore relative abundances, and we provide guidelines on the utility of this approach for ecological inference.

Résumé

La capacité de suivre directement des populations animales dans le temps et dans l'espace est un élément clé de la conservation et de la gestion de la faune sauvage mais, logistiquement, elle est difficile à atteindre. Le taux de prises photographiques par les pièges peut donner des indices d'abondance relative (RAI) pour une large variété d'espèces sauvages de taille moyenne à grande. Les RAI sont moins complexes que d'autres méthodes d'estimation et ils sont assez souvent utilisés lorsque l'abondance précise est difficile ou coûteuse à mesurer. Mais cette méthode est controversée et elle ne tient pas compte de biais potentiels dus à une détection imparfaite. Nous évaluons ici la fiabilité et la précision des estimations de RAI tirées d'une étude avec piège photographique de grand format pour dix grands herbivores africains, en les comparant à des données obtenues lors d'une étude aérienne antérieure. Les RAI étaient fortement liés aux estimations indépendantes, spécialement lorsque les indices étaient dérivés de comptages de tous les animaux photographiés. Les RAI

étaient surtout fiables pour des espèces non migratrices, qui vivent dans des habitats ouverts et ont un rythme élevé de déplacements quotidiens. Le fait d'augmenter la couverture et la durée d'une étude avait des effets solides mais comparables sur l'amélioration de la précision des RAI. Nos résultats suggèrent que les RAI dérivés de pièges photographiques sont prometteurs comme outils pour suivre l'abondance relative d'herbivores, et nous donnons des lignes directrices sur l'utilité de cette approche pour des déductions écologiques.

KEYWORDS

abundance estimation, camera traps, count data, RAI, relative abundance index, unmarked individuals

1 | INTRODUCTION

Deriving reliable abundance estimates for terrestrial herbivores is an important first step for many biological investigations and can be used to guide the management of these ecologically and economically valuable species (Ripple et al., 2017, 2015). Abundance estimates are used for assessing conservation efforts (Danell, Bergström, Duncan, & Pastor, 2006; Loibooki, Hofer, Campbell, & East, 2002), setting hunting or harvest quotas (Caughley & Sinclair, 1994; Morellet et al., 2007; van der Waal & Dekker, 2000), gauging prey availability for carnivores (O'Brien, Kinnaird, & Wibisono, 2003) and managing wildlife areas for tourism (Ogutu, 2002; Ottichilo, Leeuw, Skidmore, Prins, & Said, 2000; Ripple et al., 2015) or other land-use objectives (McShea, 2012; McShea, Underwood, & Rappole, 1997; Putman & Moore, 1998). Typically, herbivore abundance is estimated using aerial or ground transects in conjunction with distance or sightability models (Pollock et al., 2002). However, these types of surveys are implemented infrequently (once every year or few years) and at coarse spatial scales due to substantial associated expenses (Jachmann, 2001, 2002; Wilson, Cole, Nichols, Rudran, & Foster, 1996).

In the past two decades, camera trapping has emerged as a versatile tool in ecological research, allowing for cost-effective animal monitoring across considerable spatiotemporal expanses (O'Connell, Nichols, & Karanth, 2011; Rowcliffe, Kays, Kranstauber, Carbone, & Jansen, 2014; Steenweg et al., 2017). A large body of statistics has been developed that uses camera trap data to calculate population estimates for uniquely identifiable animals (Karanth, 1995; Kéry, 2010; MacKenzie et al., 2006; Royle & Nichols, 2003). However, far less is available for animals without conspicuous individual markings, even though "unmarked" animals (including most terrestrial herbivores) represent the majority of species targeted by camera trapping surveys (Sollmann, Mohamed, Samejima, & Wilting, 2013). Implementing the recently developed approaches for unmarked animals (e.g., Royle, 2004; Rowcliffe, Field, Turvey, & Carbone, 2008; Chandler & Royle, 2013) is not always feasible: these methods require complex and computationally intensive statistics, their results can be difficult to interpret, they require additional

and often difficult-to-verify assumptions, and the broad reliability of these emerging methods remains to be tested (Dénes, Silveira, & Beissinger, 2015). Such complications necessitate a comprehensive consideration of alternative measures (O'Brien, 2011; O'Brien et al., 2003).

Analysis of photographic capture rates is a promising alternative for deriving indices of animal abundance (Kelly, 2008; Rovero & Marshall, 2009). Capture frequency can be used as a *relative abundance index* (RAI), which is typically calculated as the number of sightings per camera trap days (i.e., number of cameras times number of days operational; Carbone et al., 2001; O'Brien et al., 2003). As indices, RAIs are assumed to be linearly correlated to overall abundance and can be calibrated against independent counts to provide correlation coefficients between the index and population size (Caughley, 1977; Jenelle, Runge, & MacKenzie, 2002; Srbek-Araujo & Chiarello, 2013). RAIs are easy to calculate, intuitive to understand, and can be applied to a wide variety of sampling regimes (Ancrenaz, Hearn, Ross, Sollmann, & Wilting, 2012; Jenks et al., 2011; O'Brien et al., 2003).

The use of RAIs is hotly contested, however, as these measures do not account for bias arising from variable encounter probabilities (Anderson, 2001; Foster & Harmsen, 2012; Pollock et al., 2002; Sollmann et al., 2013; Tobler, Carrillo-Percestequi, Leite Pitman, Mares, & Powell, 2008). In any given survey, not all individuals are photographed, and detectability of different species can vary across space and time (Cutler & Swann, 1999; Iknayan, Tingley, Furnas, & Beissinger, 2014; Keever et al., 2017). For example, animals that are larger in size, have more extensive home ranges, move farther in a single day or live in open habitats may trigger cameras more frequently than smaller, less active or less visible species (Wearn & Glover-Kapfer, 2017). While indices implicitly assume that encounter probability is constant over the spatial or temporal dimension of inference, changes in the index values may reflect variation in encounter probabilities rather than true changes in underlying abundance (Foster & Harmsen, 2012; O'Brien, 2011; Sollmann et al., 2013).

RAIs can perform poorly for small- or medium-sized cryptic carnivores (e.g., Matthews, Mark Higley, Scott Yaeger, & Fuller, 2011; Sargeant, Johnson, & Berg, 2003; Sollmann et al., 2013). However,

positive, linear relationships between RAIs and independent density estimates have been found across space, time and species for larger herbivores (Carbone et al., 2001; Kinnaid & O'Brien, 2012; O'Brien et al., 2003; Rovero & Marshall, 2009; Rowcliffe et al., 2008), and we suggest that these indices may provide a valid way to monitor populations and communities of these large-bodied, slow-moving and more easily detectable species (Rowcliffe, Carbone, Jansen, Kays, & Kranstauber, 2011; Tobler et al., 2008). Despite this metric's common usage in camera trapping studies to draw ecological and management inference, validations of the RAI approach for large herbivores remain rare (Sollmann et al., 2013).

Here, we assessed the reliability and precision of RAIs drawn from a large-scale camera trap survey compared to preexisting aerial survey estimates for ten large herbivore species that differ in a variety of functional characteristics. Our goals were to (a) assess the overall reliability of RAIs (both the traditional number of photographs per unit time and a "weighted" version which accounts for the number of individuals in each photograph) to produce comparable abundance estimates, (b) ascertain the ecological characteristics for which this method is particularly successful and (c) decompose the contributions of camera trap effort across space and time to produce reliable and precise RAI estimates using finite resources.

We utilised two years of data produced by a systematic and continuously operating grid of 210 cameras covering an area of 1,125 km² in Serengeti National Park, Tanzania and evaluated how RAIs derived from this sampling effort reflected the most recent estimates of animal abundance across the encompassing Greater Serengeti-Mara Ecosystem. First, we calculated how well RAIs derived from the number of (a) photographs and (b) individuals within photographs correlated with independent aerial survey estimates of species abundance. We note that while these estimates were not taken concurrently with the camera trap survey, population sizes of most species within the larger ecosystem have changed little since the early 2000s (Sinclair, Metzger, Mduma, & Fryxell, 2015). To examine potential biases arising from spatial and temporal variation in encounter probability, we compared estimates derived from the entire dataset against three paired subsets of data: wet and dry season, day and night, and across the two primary habitat divisions, woodlands and plains (*sensu* Cusack et al., 2015; Keever et al., 2017). We further assessed whether RAIs

could detect temporal changes in relative abundance by comparing estimates between the wet and dry seasons. Four of our focal species traverse the study system yearly, and we therefore expected to observe substantial seasonal fluctuations in the relative abundance of these migratory species but see little change in that of resident herbivores.

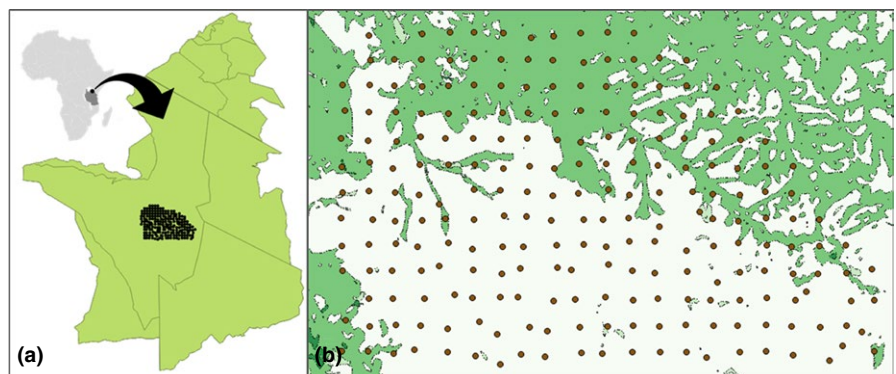
Finally, we determined the amount of camera trapping effort, in terms of both survey length and number of cameras, required to arrive at precise (e.g., low coefficient of variation) estimates for each species. We anticipated that RAIs would be most accurate and precise for species with high and consistent detectability, which should result from (a) larger body size (Rowcliffe et al., 2011; Tobler et al., 2008), (b) larger group size (Treves, Mwima, Plumptre, & Isoke, 2010), (c) higher rates of daily movement (Sollman et al., 2013), (d) consistent occupancy within the sampling area (Keiter et al., 2017) and (e) preference for habitats with higher camera trap detection zones (e.g., open areas, Cusack et al., 2015; Keiter et al., 2017).

2 | METHODS

2.1 | Study site

The Greater Serengeti-Mara Ecosystem (GSME; Figure 1a) covers approximately 25,000 km² of the East Africa acacia savannah zone (1°15' to 3°30'S, 34° to 36°E), encompassing portions of Kenya (Masai Mara and surrounding concessions; ~1,700 km²) and Tanzania (Serengeti National Park, Ngorongoro Conservation Area, Loliondo Game Control Area, Maswa Game Reserve, Grumeti Game Reserve and Game Control Area, and the Ikorongo Game Control Area; ~23,300 km²). The southern portion of the GSME is covered primarily by shortgrass treeless plains, while taller grasses and mixed woodlands are predominant in the central and northern sections. The system is annually perturbed by the migration of 1.6 million wildebeest, zebra and Thomson's gazelle, which follow seasonal rainfall. The wet season spans November to May and dry season from June to October. A detailed description of the GSME can be found in Sinclair et al. (2008). Within this larger area of inference, our 1,125 km² sampling grid is located within Serengeti National Park, covering a gradient of open plains and woodland savannah habitat (Figure 1a & b).

FIGURE 1 The Greater Serengeti-Mara Ecosystem (GSME) (Panel A), spanning the Kenya-Tanzania border in east Africa. The camera trap study area (camera locations in black; expanded in Panel b) lies in the centre of Serengeti National Park and covers the intersection of woodlands (dark green) and plains (light green) [Colour figure can be viewed at wileyonlinelibrary.com]



2.2 | Study species

We focused on ten species of herbivores that are abundant and widely distributed within the GSME (Table 1). These species differ in body mass, residency patterns, group sizes and habitat preference in ways that were anticipated to influence probability and rate of encountering camera traps.

2.3 | Data collection & processing

2.3.1 | Camera trapping

In 2010, we established a 210-unit camera trapping survey in the centre of Serengeti National Park, Tanzania (34°45'–34°14' E, 2°22'–2°55' S; Figure 1b). Complete details on survey design can be found in Swanson et al. (2015). We used ScoutGuard S565 camera traps, which were equipped with passive infrared sensors that trigger via a combination of heat and motion. Each camera was placed at the predetermined centre of a 5 km² grid cell, on the nearest suitable tree within 250 m of the centre or on poles if no trees were available. Habitat type (plains or woodland) was characterised for each camera trap location from 30 m resolution vegetation layers (Serengeti GIS & Data Center, 2007). For this analysis, we used data collected during the wet and dry seasons of 2012 and 2013 (01 November 2011 to 31 October 2013). Images taken by the cameras were classified through the *Snapshot Serengeti* citizen science website (<https://snapshotserengeti.org>), on which volunteers identified and counted the species present in each photograph. In images that contained more than ten animals, volunteers binned counts as 11–50 and 51 + animals; for our analyses, we assigned these bins the count values of 31 and 75, respectively. Validation of volunteer classifications demonstrated that final volunteer species classifications agree

with experts 97% overall (Swanson et al., 2015). We limited all analyses in this paper to images with at least 60% agreement among raw classifications, guaranteeing 99% accuracy (see Swanson, Kosmala, Lintott, & Packer, 2016 for additional details). Independent capture events are defined by a 10-min time-lag between consecutive capture events of the same species (validated by Palmer, Fieberg, Swanson, Kosmala, & Packer, 2017), such that animals remaining in front of a camera triggering multiple images were only considered a single capture event.

2.3.2 | Aerial surveys

Independent ecosystem-wide abundance estimates for the focal species were derived from intermittent wet season aerial strip transect surveys conducted by the Tanzanian Wildlife Research Institute and the Frankfurt Zoological Society between 1996 and 2012 (Supplemental Table 1). Using a systematic reconnaissance flight survey, fixed-wing aircraft covered the 26,827 km² GSME by searching along 89 established transects spaced 5 km apart (Norton-Griffiths, 1978). Population estimates were then calculated from observed counts using Jolly's method of two unequal-sized units (Jolly, 1969). The most recent counts available were used for each species.

2.4 | Relative abundance estimation & validation

All analyses were run in Program R v. 3.4.0 (R Core Team, 2013) and results considered significant at $\alpha = 0.05$.

2.4.1 | Reliability

For each focal species, we evaluated capture rates derived from the total number of (a) independent photographs ("RAI_{photos}") and (b)

TABLE 1 Focal herbivores and associated characteristics that may affect detection by camera traps. Averaged values derived from Serengeti-specific parameters wherever possible. Body mass given is for adult females. Group size represents the average number of individuals in female/offspring and bachelor herds weighted by the relative abundance of these types of associations where these values were available. Note that all migratory species also have smaller resident populations that remain within the study area year-round

Species	Scientific name	Weight (kg)	Average group size	Daily movement (km)	Residency	Habitat
Buffalo	<i>Syncerus caffer</i>	350–600	350	5.5	Resident	Woodlands
Eland	<i>Taurotragus oryx</i>	390–595	11.8	8.4	Migrant	Woodlands
Elephant	<i>Loxodonta africana</i>	2,700–6,000	6.9	4.4	Resident	Woodlands
Impala	<i>Aepyceros melampus</i>	40–53	10.3	4	Resident	Woodlands
Giraffe	<i>Giraffa camelopardalis</i>	550–1,180	9	6.8	Resident	Woodlands
Thomson's gazelle	<i>Eudorcas thomsonii</i>	13–23.5	86	3.5	Migrant	Plains
Warthog	<i>Phacochoerus aethiopicus</i>	48–78	3.4	3	Resident	Plains
Waterbuck	<i>Kobus defassa</i>	160–200	5	4.4	Resident	Woodlands
Wildebeest	<i>Connochaetes taurinus</i>	118–208	28.4	3.8	Migrant	Plains
Zebra	<i>Equus quagga</i>	175–250	5.1	4	Migrant	Plains

Source: Clough, 1970; FitzGibbon & Fanshawe, 1988; Hopcraft et al., 2014; Jarman & Jarman, 1973; Kingdon, 1982a, 1982b, 1982c; Klingel, 1969; Laws, 1970; McQualter, Chase, Fennessy, McLeod, & Leggett, 2016; Owen-Smith, 1992; Pellew, 1983; Rodgers, 1977; Sachs, 1967; Setsaas, Holmern, Mwakalebe, Stokke, & Røskoft, 2007; Sinclair, 1974, 1977; Spinage, ; Watson, 1969; Wittemyer, Getz, Vollrath, & Douglas-Hamilton, 2007.

animals summed across all independent photographs ("RAI_{individuals}") in a given time period, each divided by the number of camera trap days in that same period (O'Brien et al., 2003). Note that the same individual may be captured across independent capture events; we were not attempting to equate the total animals counted across independent captures with total unique individuals. We calculated 95% confidence intervals using nonparametric bootstrapping (Efron & Tibshirani, 1993), resampling camera locations with replacement 10,000 times (as per Rowcliffe et al., 2008). The relationship between bootstrapped RAIs and density estimates was analysed using log-log regression. Given that the aerial survey numbers are also estimates of true underlying species abundance and are derived from a larger area than covered by the camera trap survey, we were not anticipating a perfect 1:1 relationship between RAI values and aerial survey estimates. Rather, we assumed that relative densities of these species across the GSME were similar to those within our representative study site, as we were only aiming to evaluate how well the RAIs compared to the more intensive aerial surveying method.

To explore whether restricting our analyses to subsets of the data reduced spatial or temporal bias in encounter probabilities (e.g., areas where camera trap visibility was greater or times when animals move more frequently or randomly with respect to camera placement), we bootstrapped indices from capture rates pooled across (a) seasons (wet or dry), (b) habitat types (woodlands or plains) and (c) time of day (day or night, based on civil twilight; see Palmer et al., 2017 for details), and compared these indices to independent density estimates using the technique described above.

Finally, we assessed whether the camera survey could detect intra-annual temporal changes in the relative abundance of migratory species. As RAI_{individuals} ultimately performed better than RAI_{photos}, these and all following analyses were performed with RAI_{individuals} values only. We compared seasonal RAI_{individual} values for resident and migrant species using a two-sample Wilcoxon test to evaluate whether these values changed significantly across times of year. We used the same test to determine if the magnitude of change across seasons differed between residents and migrants.

2.4.2 | Precision

We calculated the rate at which variation in bootstrapped species-specific RAI values decreased with increasing temporal survey effort across one year of trapping. For each of n sequential weeks ($n_{\text{weeks}} = 1-52$), we bootstrapped the data 10,000 times with replacement, calculating the RAI estimate for each bootstrap and the coefficient of variation (standard deviation divided by the mean) across the set of iterations. This process was repeated 10 times for every week, producing 10 estimates of the coefficient of variation for each length of time. For each iteration, we chose a new starting date, ensuring that the period was not truncated by the end of the survey. We used linear regression to quantify the rate of decrease in variation (slope) as a function of $\sqrt{}$ (camera trap effort). To determine whether species-specific traits predicted this decline, we ran additional regressions in which the decrease in

variation was modelled as a function of both $\sqrt{}$ (camera trap effort) and species characteristics including average group size, female body weight, daily distance moved and resident/migrant status. Whenever possible, these variables were derived from published literature in the Serengeti or East Africa (Table 1). Continuous variables were centred and rescaled using their mean and standard deviation prior to regression.

Finally, we quantified the effect of additional camera trap effort on reductions in variance for bootstrapped species-specific RAI estimates. Camera trap effort can be accumulated in two ways: by increasing the number of cameras used in the survey and by increasing the length of time over which the survey takes place. We calculated the cumulative effort and coefficient of variation in bootstrapped RAI estimates for each species derived from different-sized sections of the camera trap grid over increasing temporal periods. As most surveys contain fewer than 100 camera traps (Sollmann et al., 2013), we subsampled grids containing 25, 49, 71 and 99 camera traps (camera numbers were chosen such that the overall shape of the grid subsets was similar in an attempt to minimise edge effects and to maintain the 5 km² spacing between adjacent camera traps). Ten subgrids of each size were randomly drawn from the overall sampling setup and for each set of grid sizes (see Supplemental Figure 1 for an example), we bootstrapped RAI values at increasing levels of temporal survey effort ($n_{\text{weeks}} = 1-52$) 10,000 times. Linear regressions were used to determine the magnitude of improvement that increasing spatial and temporal effort added to the precision of each species' index and to explore which type of effort augmentation had a greater magnitude of effect depending on the functional characteristics of individual species.

3 | RESULTS

3.1 | Camera trap effort

From 01 November 2011 to 31 October 2013, the camera survey accumulated 70,299 camera trap days and collected a total of 15,153 independent images of the focal species (range: 57 to 5,020 captures per species; Supplemental Table 2). Due to camera damage and loss, a subset of sites was inactive at any period of time, giving an average of 136.2 functioning cameras per month (mean: 3,854.8 camera trap days per month).

3.2 | Reliability

Log-log regression revealed that bootstrapped RAI_{photos} and RAI_{individuals} were both significantly correlated to independently observed population densities across the ten large herbivore species (Figure 2), but RAI_{individuals} explained more variation than RAI_{photos} (Table 2). A slope of 1 indicates that a proportional change in one variable corresponds to an equal proportional change in the other. For all subsets of the data, the 95% confidence intervals for the slope included 1 (Table 2). RAI_{individual} capture rates obtained using the entire dataset resulted in $\beta = 1.001$, with those derived exclusively from daytime images ($\beta = 0.986$) or during the wet season ($\beta = 0.958$) also very close to 1.

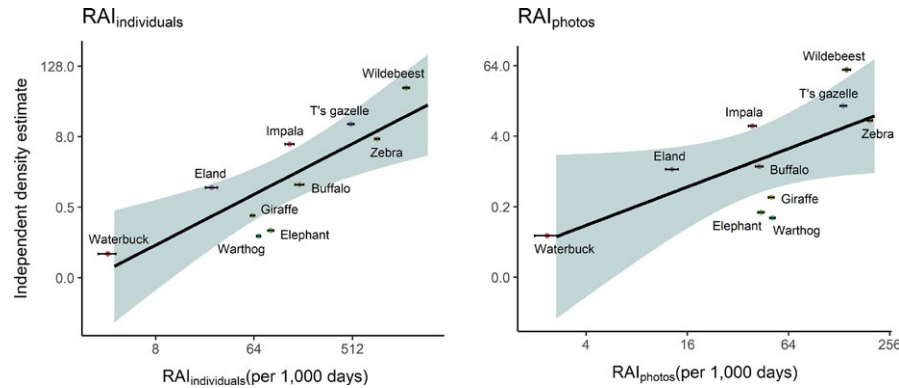


FIGURE 2 Linear regression with standard error between camera trap capture rates (derived from the entire data set) and aerial estimates for $RAI_{individuals}$ and RAI_{photos} . These two measures are significantly related across all focal species. Untransformed values are plotted on log–log scales; RAI values are multiplied by 1,000 to represent capture rate per 1,000 days (as per O'Brien et al., 2003). Error bars depict bootstrapped 95% confidence intervals [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Results of the linear regression of bootstrapped camera trap RAI estimates on aerial survey estimated population sizes for capture rates weighted by animal counts in the photographs ($RAI_{individuals}$) or raw photographic rate (RAI_{photos})

Data subset	$RAI_{individuals}$					RAI_{photos}				
	Beta	Std. error	Adj- R^2	p-Value		Beta	Std. error	Adj- R^2	p-Value	
All	1.001	0.226	0.673	0.002	**	1.154	0.428	0.411	0.027	*
Wet season	0.958	0.243	0.619	0.004	**	1.088	0.474	0.321	0.051	.
Dry season	0.927	0.308	0.472	0.017	*	0.960	0.438	0.297	0.060	.
Day	0.986	0.225	0.670	0.002	**	1.128	0.430	0.395	0.031	*
Night	0.952	0.219	0.667	0.002	**	1.049	0.342	0.483	0.015	*
Woodlands	1.000	0.313	0.506	0.013	*	1.058	0.536	0.244	0.084	.
Plains	0.607	0.204	0.467	0.018	*	0.593	0.306	0.235	0.088	.

Note. Significant relationships ($p < 0.05$) are denoted by asterisks; near-significant relations ($p < 0.10$) by periods.

Seasonal $RAI_{individual}$ values varied significantly for all ten species (all $p < 0.001$), but the magnitude of these differences differed dramatically between resident and migrants. Given potential for substantial noise from bootstrapping small sample sizes, we removed the two rarest species (eland and waterbuck; each <350 total photographs) from our analysis and found highly divergent responses across seasons in migrant species compared to resident populations ($W = 15$, $p = 0.036$). $RAI_{individual}$ estimates for two migratory species, wildebeest and Thomson's gazelle, rose by over 1,000% and 500%, respectively, whereas the other migratory species only varied by 43% (zebra). In contrast, the six resident species showed seasonal variations of 6% to 45% (Figure 3).

3.3 | Precision

RAI estimates became more precise with increasing camera trap effort (all $p < 0.001$; Figure 4). In linear regressions that included species functional traits in addition to $\sqrt{(\text{camera trap effort})}$, all characteristics except for group and body size contributed strongly to precision. Residency had the strongest effect, with RAI precision increasing more quickly for residents than migrants

($\beta_{\text{residency}[\text{resident}]} = -0.459$; $p < 0.001$). Precision also improved more rapidly for species occurring in the plains versus the woodlands ($\beta_{\text{habitat}[\text{plains}]} = -0.214$; $p < 0.001$). Higher rates of daily movement also had a significant, but weaker, effect on RAI precision ($\beta_{\text{movement}} = -0.082$; $p < 0.001$).

Increasing both number of weeks deployed and number of camera traps significantly reduced variation in RAI estimates for all species (all $p < 0.05$), except for survey duration in buffalo, impala and eland (Supplemental Table 3; Supplemental Figure 2). There was no interaction between survey duration and grid size for any species except waterbuck, although the magnitude of this effect was minor compared to those of duration and grid size independently (Supplemental Table 3). Overall, for the same level of survey effort (number of camera trap days), there was little difference in the amount of variation in RAI estimates regardless of how effort was decomposed into grid size versus duration (Supplemental Figure 2). The effect strength of each variable on improving estimate precision was approximately the same within and across species (Figure 5). The only exceptions were impala, where survey size reduced variation to a greater extent than duration, and waterbuck, where survey duration was more important.

FIGURE 3 Seasonal differences in $RAI_{individual}$ estimates derived during the wet seasons (closed circles) and dry seasons (open circles). The most abundant migrant species (wildebeest, zebra and gazelle) display marked temporal variation in $RAI_{individual}$ values, while $RAI_{individual}$ estimates for resident species remain consistent throughout the year. Error bars represent bootstrapped 95% confidence intervals [Colour figure can be viewed at wileyonlinelibrary.com]

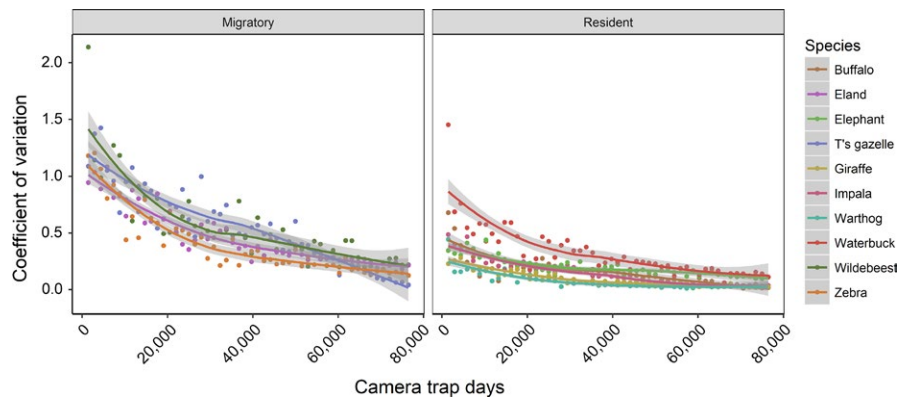
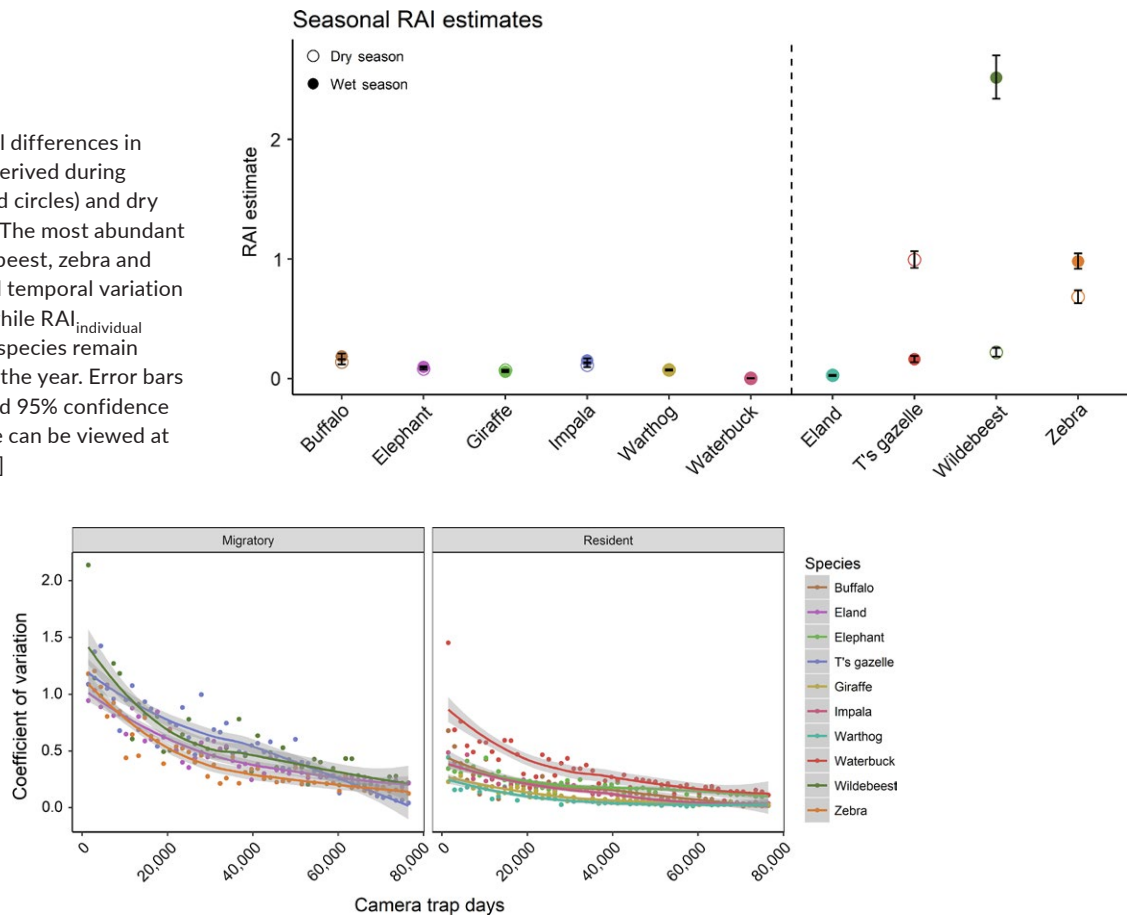


FIGURE 4 Decrease in variation across bootstrapped RAI estimates with increasing camera trap effort (camera trap days = number of camera traps \times number of active days) across the entire trapping grid ($N_{\text{camera traps}} = 210$). Each point represents the coefficient of variation in 10 iterations of bootstrapping RAI values 10,000 times with replacement for individual species every week for a one-year period. Trends in variation estimate decrease for each species fit with a loess smoother (span = 0.9), but for statistical analysis we used $\sqrt{(\text{camera trap days})}$ as an offset since the CV declines linearly with \sqrt{n} . Species are divided by residency status (migrant or resident), the variable with the strongest influence on the rate at which variation in RAI estimates decreased (Table 3) [Colour figure can be viewed at wileyonlinelibrary.com]

Species traits continued to influence the rate of decline in estimate variability, interacting significantly with both survey duration and grid size (Table 3). Larger grids and longer durations increased precision of RAI values for species with smaller body and group sizes. Larger grids also increased precision for species with lower movement rates. Migrant and woodlands species required larger grids and longer durations to stabilise their RAI values than did resident and plains species.

4 | DISCUSSION

Relative abundance indices are commonly used to draw inference about the ecology of unmarked terrestrial herbivores, despite the potential for bias to arise from nonlinear relationships between the index and true abundance across species, space and time (Foster & Harmsen, 2012; Sollmann et al., 2013). Our findings suggest that RAI estimates derived from systematic camera trap surveys can indeed provide reliable and precise

indices of relative abundance for medium to large herbivores, allowing us to gain important insight into community structure and dynamics.

4.1 | Reliability and precision of RAIs

4.1.1 | Reliability

We found a strong isometric relationship (i.e., slope of log-log regression ≈ 1) between camera trap-derived RAI values and independently gathered density estimates across ten herbivore species, indicating that the photographic captures can serve as a reliable index of relative abundance for communities of African herbivores (Garel, Bonenfant, Hamann, Klein, & Gaillard, 2010). Our temporal analyses further support that RAIs could potentially be used to monitor longitudinal changes in herbivore population sizes that result from movement or demographic processes, despite the possibility of detectability changing through time (Pollock et al., 2002; Sollmann et al., 2013).

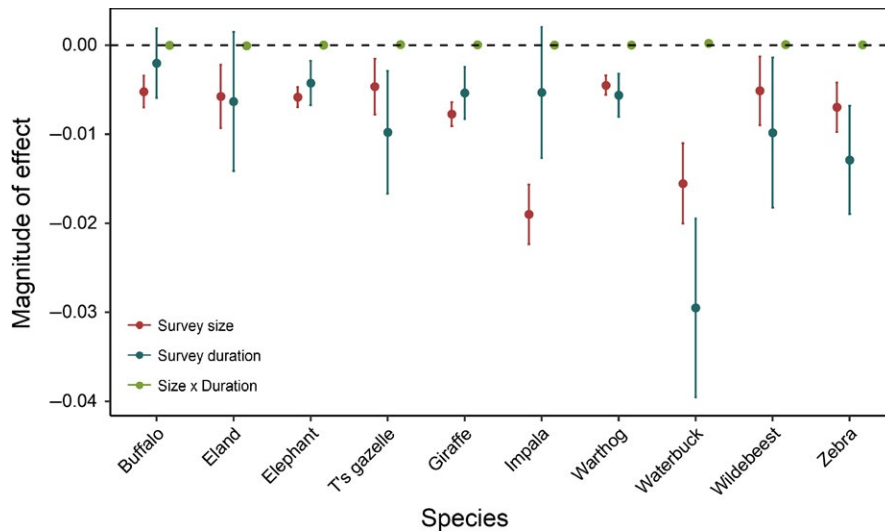


FIGURE 5 Contribution of increasing survey size, duration and interactions between the two factors on magnitude of decrease in bootstrapped variation for RAI estimates. Coefficients are from species-specific linear regression models. While increases in number of cameras and length of survey both decreased RAI variability, in general, each had approximately the same effect strength both within and across species, with the exception of impala and waterbuck. Error bars represent 95% confidence intervals [Colour figure can be viewed at wileyonlinelibrary.com]

	Estimate	Std. error	t Value	p-Value	
Survey duration	-0.0111	0.0823	-6.14	<0.001	***
Survey size	-0.0136	0.0010	-13.64	<0.001	***
Group size	-0.2842	0.0221	-12.88	<0.001	***
Daily movement	-0.7219	0.0383	-18.86	<0.001	***
Body size	-0.5510	0.0241	-22.87	<0.001	***
residency (resident)	-1.3192	0.0740	-17.82	<0.001	***
Habitat (plains)	-2.5287	0.0994	-25.43	<0.001	***
Survey duration × group size	0.0017	0.0005	3.52	<0.001	***
Survey duration × movement	0.0015	0.0008	1.77	0.077	.
Survey duration × body size	0.0017	0.0005	3.21	0.001	**
Survey duration × residency	0.0048	0.0016	2.94	0.003	**
Survey duration × habitat	0.0061	0.0022	2.80	0.005	**
Survey size × group size	0.0017	0.0003	6.32	<0.001	***
Survey size × movement	0.0034	0.0005	7.34	<0.001	***
Survey size × body size	0.0025	0.0003	8.69	<0.001	***
Survey size × residency	0.0028	0.0009	3.10	0.002	**
Survey size × habitat	0.0132	0.0012	10.99	<0.001	***

Note. Significant *p*-values are denoted with asterisks; near-significant values by a period.

RAIs calculated from counts of individuals within photographs out-performed estimates based on number of photographs alone. This was not surprising as many of our focal species travel in herds of tens to hundreds of individuals (a single photograph could contain over a dozen animals), but worth noting given that many studies do not weight RAIs by animal counts (e.g., O'Brien et al., 2003; Tobler et al., 2008; Treves et al., 2010). Other analyses commonly recommended as alternative ways to analyse camera trap data, including

occupancy modelling (Ahumada et al., 2011; MacKenzie et al., 2006; Sollmann et al., 2013), also treat abundance as binary (present or absent rather than a count); our findings suggest that these models would perform poorly for gregarious species.

While estimates derived from the entire dataset performed best (i.e., highest adjusted R^2 -slope closest to a 1:1 log-log relationship), we also obtained strong relationships between independent estimates and RAI values from subsets of images captured during the

TABLE 3 Output of model regressing survey duration, survey size and interactions between these drivers and large herbivore traits anticipated to bias detectability and precision of RAIs on the coefficient of variation in bootstrapped RAI estimates

wet seasons (when herbivore migrations bring animals from across the GSME into the study site; Sinclair & Norton-Griffiths, 1995) or during the daytime. For studies that must concentrate camera trapping effort, reliable RAI estimates could be obtained from data collected during times of year when the sampling area is most representative of the entire study system and further improved by using only information collected during hours when visibility is greatest or animals are most active (Cusack et al., 2015; Keever et al., 2017). The linear relationship was noticeably less strong for subsets of data containing only plains habitat, and our precision analyses suggest that habitat has a large effect size on variability of the resulting estimate. As we discuss in more detail below, our survey was not stratified in terms of coverage by habitat compared to that of the GSME. There is a distinct possibility that our disproportionate coverage of plains habitat may have affected our overall estimates of animal abundance across the entire system, producing precise estimates of abundance for plains species due to high coverage of these areas, but low overall accuracy for the community of species which include inhabitants of woodland areas. We stress that stratification of survey area to overall area of inference is likely key to improving inference from camera trap studies.

Although RAIs perform poorly for rare and cryptic carnivores (Foster & Harmsen, 2012; Jenelle et al., 2002; Sollmann et al., 2013), even the smallest (Thomson's gazelle) and least common (eland, waterbuck) of our focal herbivores were reasonably well-represented by RAIs. However, we suspect that certain life history characteristics may have affected overall RAI accuracy. Warthogs, for example, appeared to be over-represented in our calculations and are the only focal species to produce litters (up to four piglets annually versus the single offspring of most antelope or equids; Boshe, 1981). As such, their population sizes fluctuate strongly across years (Ogutu, Piepho, Dublin, Bhola, & Reid, 2010). This highlights two limitations of our study: first, we did not know true population sizes during the time span of our camera survey, and second, the aerial surveys were not collected concurrently with the camera trap data. Although population levels for the majority of the focal species are presumed to have remained relatively stable over the past 20 years (Sinclair et al., 2015), the cameras may have captured minor population shifts in the years following the aerial estimates.

We obtained strong correlations between RAIs and independent abundance estimates despite our camera trap grid covering a portion of study area representing 5% of the total area surveyed by the aerial transects (1,250 km² within 25,000 km²) and containing fewer habitat types than found within the larger surveyed ecosystem (Sinclair et al., 2008). If our camera trap survey had been designed to derived abundance estimates for the GSME (e.g., cameras covering a larger or more representative area), we strongly suspect that we would have produced even more reliable results (Pollock et al., 2002; Wearn & Glover-Kapfer, 2017). We found that impala, for instance, were under-represented by the RAI estimate compared to the aerial surveys (Figure 2), which we hypothesise is an artefact of insufficient coverage within this species' preferred woodland habitats (the camera trap survey contains 23.7% cameras in the woodlands compared

to 76.3% in the plains). Conversely, elephant numbers increased more rapidly in central Serengeti National Park between 2009 and 2014 than in other parts of the GSME (Morrison et al., 2017), and this higher-than-average elephant density within our camera trap grid appears to be reflected in over-representation of elephants in our RAI values (Figure 2). Determining the specific factors contributing to this observed variation warrants further species-specific investigation.

4.1.2 | Precision

Augmenting camera trap effort by expanding both grid size and survey duration increased RAI precision for almost all species, with each approach having approximately equal effects on improving precision. This suggests that practitioners could rely on increased spatial replication if constrained by time or increased temporal replication if constrained by cameras. The only exceptions were for impala, eland and buffalo—three resident woodlands species—for which increasing survey duration did not provide better RAI precision. As the overall sampling area again contains only 23.7% woodlands, our randomly drawn subgrids might not have covered representative amounts of preferred habitat. No amount of time would permit smaller surveys to capture organisms that live outside the sampling area, emphasising again the need to strategically select representative sampling areas.

As expected, RAIs tended to be more stable for species that remained resident in the study area year-round. Precision also increased quicker for species that occupied open habitats, likely due to increased detectability and better coverage by the camera survey (Cusack et al., 2015; Keiter et al., 2017). Across all data, daily movement was the only physical characteristic that was expected to predispose animals to trigger camera traps (by increasing likelihood of encountering cameras) that did contribute to more precise estimates. For the more commonly sized (<100 camera trap) surveys, expanding both grid size and survey duration was important for species with smaller group sizes and smaller body sizes, as well as for migrant and woodland species. Increasing grid size was more important than duration for species that travelled less distance during the day: this relative immobility reduces their chance of encountering traps unless the cameras are placed specifically within areas of high utilisation, necessitating the additional spatial effort (Dénes et al., 2015; Sollmann et al., 2013).

4.2 | Further management recommendations and considerations

Our work suggests that RAIs from camera trap surveys produce relative abundance estimates comparable to those produced by other methods (Bodie, Garton, Taylor, & McCoy, 1995; Caughley, 1974; Rice, Jenkins, & Chang, 2009). Camera trapping, however, comes with numerous additional advantages: cameras are relatively inexpensive (Rovero, Zimmermann, Berzi, & Meek, 2013; Silveira, Jacomo, & Diniz-Filho, 2003), capture information on multiple

species in areas that may be difficult to regularly monitor (O'Connell et al., 2011; Rowcliffe & Carbone, 2008), operate continuously, documenting immediate population-level responses to perturbations (Jachmann, 2001; Morellet et al., 2007) and can be used to capture additional information on behaviour and ecological relationships (Palmer et al., 2017; Palmer & Packer 2018). The high-resolution data captured by camera traps therefore provide the potential for more fine-tuned adaptive management (O'Brien, Baillie, Krueger, & Cuke, 2010; O'Connell et al., 2011).

In systems such as ours where a proportional linear relationship exists between species' RAI and underlying density, survey data from prior monitoring could be used to calculate correction factors (e.g., ratio or slope of this established relationship) that convert RAI estimates into overall abundance counts (Conroy, 1996; O'Brien et al., 2003; Pollock et al., 2002). To obtain finer-scale inference across space or time, this relationship should be periodically calibrated to update the proportionality constant (Pollock et al., 2002; Williams, Nichols, & Conroy, 2002). While infeasible with our current data, such calibration would be particularly tractable in fenced wildlife areas which are "closed" systems. However, managers interested in using camera trap data to produce population estimates that do account for spatiotemporal variation in detectability and occupancy should investigate application of *N*-mixture models (Royle, 2004), random encounter models (Rowcliffe et al., 2008) and spatially explicit capture–recapture models for unmarked animals (Chandler & Royle, 2013). It should be noted that these methods have so far been tested primarily via simulation, and the reliability of these methods has been inconsistent in the field (e.g., Kéry, Royle, & Schmid, 2005; Rowcliffe et al., 2008; Chandler & Royle, 2013; Cusack et al., 2015). There is a pressing need for additional rigorous real-world validation of these techniques (Dénes et al., 2015).

An important implication of our work is that camera trap efforts can be focused based on traits of the system and species of interest. Limiting deployment of camera trap surveys to specific times of year can minimise expenses while still providing reliable RAI estimates. Even shorter periods of camera trapping may be sufficient in reserves that are not as open or dynamic as our system. Experimental design, including survey size, duration and stratification of effort across habitat types, can be tailored by the functional characteristics of target species: more active, larger and more gregarious the species require less overall effort to obtain reasonable estimates. As we can only comment on contributions to RAI accuracy and precision within the context of our specific method, we recommend that practitioners pilot studies within their own systems to identify the amount of effort needed to reach levels of precision that are appropriate for making specific management decisions (Carbone et al., 2001; O'Brien et al., 2003; Rovero & Marshal, 2009).

In conclusion, we found that, while this technique makes numerous assumptions that may not always reflect natural conditions, even under imperfect circumstances (e.g., open system, small and unstratified coverage of area of inference), RAIs can be used to infer relative abundance with reasonable accuracy and precision. Camera

trap deployment can be further tailored based on focal species characteristics, providing a very tractable method for monitoring herbivore populations and communities. A well-designed camera trap survey should yield key information on the population dynamics of entire communities and capture spatial and temporal responses to natural and anthropogenic perturbations (Ahumada, Hurtado, & Lizcano, 2013; Burton et al., 2015; Rovero, Martin, Rosa, Ahumada, & Spitale, 2014).

ACKNOWLEDGEMENTS

Research clearance was provided by the Tanzania Wildlife Research Institute and Tanzania National Parks. We thank members of the Serengeti Lion Project, particularly D. Rosengren and N. I. Munuo, the Zooniverse staff, and the >70,000 volunteers who contributed to *Snapshot Serengeti* classifications (<https://www.snapshot-serengeti.org/#/authors>). The authors would like to acknowledge the Minnesota Supercomputing Institute (<https://www.msi.umn.edu>) for providing resources that contributed to data storage, processing and analysis. This work was supported by NSF grant DEB-1020479 to C. Packer for maintenance of the Serengeti Lion Project, National Geographic explorer grants, NSF GRFP Grant #00039202, the James W. Wilkie Fund for Natural History Fellowship, the University of Minnesota Thesis Research Grant, the Alexander & Lydia Anderson Grant, and the University of Minnesota Ecology, Evolution, and Behavior Department Research and Travel awards.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Palmer MS, Swanson A, Kosmala M, Arnold T, Packer C. Evaluating relative abundance indices for terrestrial herbivores from large-scale camera trap surveys. *Afr J Ecol*. 2018;56:791–803. <https://doi.org/10.1111/aje.12566>