Animal Conservation

Animal Conservation. Print ISSN 1367-9430

Rapid assessment of wildlife abundance: estimating animal density with track counts using body mass–day range scaling rules

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Keywords
scaling rules; body mass; track count; spoor survey; density estimation; Formozov–Malyshev–Pereleshin formula; day range; Kalahari.

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Editor: Res Altwegg
Associate Editor: Nick Isaac

Received 12 July 2013; revised 9 February 2014; accepted 10 February 2014

doi:10.1111/acv.12113

Abstract

Limited resources in conservation dictate the need for efficient means of assessing wildlife abundance. Body mass–day range scaling rules and empirical track counts were applied to an established formula to estimate a wide range of wildlife densities. Using the southern Kalahari ecosystem of Botswana as an example, I provide the first comprehensive density estimates for the mammalian wildlife community (>0.2 kg), including densities for several species previously unattainable by other methods. Among a subset of species, empirical day ranges from this area were consistently greater than those predicted using scaling rules modeled with species from diverse ecosystems. I applied a correction factor based on this discrepancy, which generated values congruent with independent density estimates from the area. Although accurate measures of day range are a practical constraint to estimating densities from track counts, the results suggest that modest efforts to obtain location-specific day range estimates for a subset of species can improve density estimates for others derived from general allometric relationships. Given the strength of track surveys to accumulate unbiased observations quickly, in environments where animal tracks are readily visible, this approach shows potential for the rapid assessment of wildlife abundance.

Introduction

Estimating abundance is often necessary for animal conservation. Given the urgency of the biodiversity crisis and unprecedented threats facing most ecosystems, methods that can capture the largest number of species in the most efficient way possible are advantageous (Western, 1992; Silveira, Jacomo & Diniz-Filho, 2003). Because the majority of population estimates of threatened species are based on direct visual counts, there are clearly gaps in our ability to accurately and quickly estimate population size (Katzner *et al*., 2011). Limited resources, especially in tropical countries (Sheil, 2001), dictate the need for practical and efficient means of assessing animal populations.

Indirect observations are a powerful way to detect terrestrial mammals, and are for many species the only practical mode of detecting them (Wilson & Delahay, 2001). Both track counts and more recently camera trap rates have been utilized as indices of abundance and extended to predict density by calibration through double sampling (e.g. Stander, 1998; Carbone *et al*., 2001; Houser, Somers & Boast, 2009; Rovero & Marshall, 2009; Funston *et al*., 2010). The use of population indices has frequently been criticized for assuming unchanging detection probabilities (e.g. Anderson, 2001), so much attention in wildlife population assessment has moved in the direction of estimating detectability (e.g. Pollock *et al*., 2002; MacKenzie *et al*., 2005). But despite advancements, direct observation techniques such as distance sampling have intrinsic limitations for species with low detectability (Lopes & Ferrari, 2000), which includes many, perhaps most, mammal species. They also involve several analytical assumptions often difficult to meet in mammals (Duckworth, 1998).

In contrast to rigorous approaches based on direct observations, the conversion of indirect observations to true density has seen surprisingly little theoretical attention. An exception is the Formozov–Malyshev–Pereleshin (FMP) formula, developed and employed by Russian biologists for decades to convert track counts to true density (Stephens *et al*., 2006). The FMP formula links animal density to the number of track intersections per linear sample distance via the average daily distances that animals travel (day range). Uncommonly reported in the literature, and effort consuming to acquire, empirical day range estimates are the main practical constraint to application of the formula. However, there is a consistent allometric relationship between body mass and day range (Garland, 1983), less well known than that scaling body mass and home-range size (McNab, 1963). Carbone *et al*. (2005) used 200 species of mammals to estimate body mass–day range scaling rules specific to taxonomic groupings. In this paper, I extend these relationships to the FMP formula to evaluate its potential as a tool for

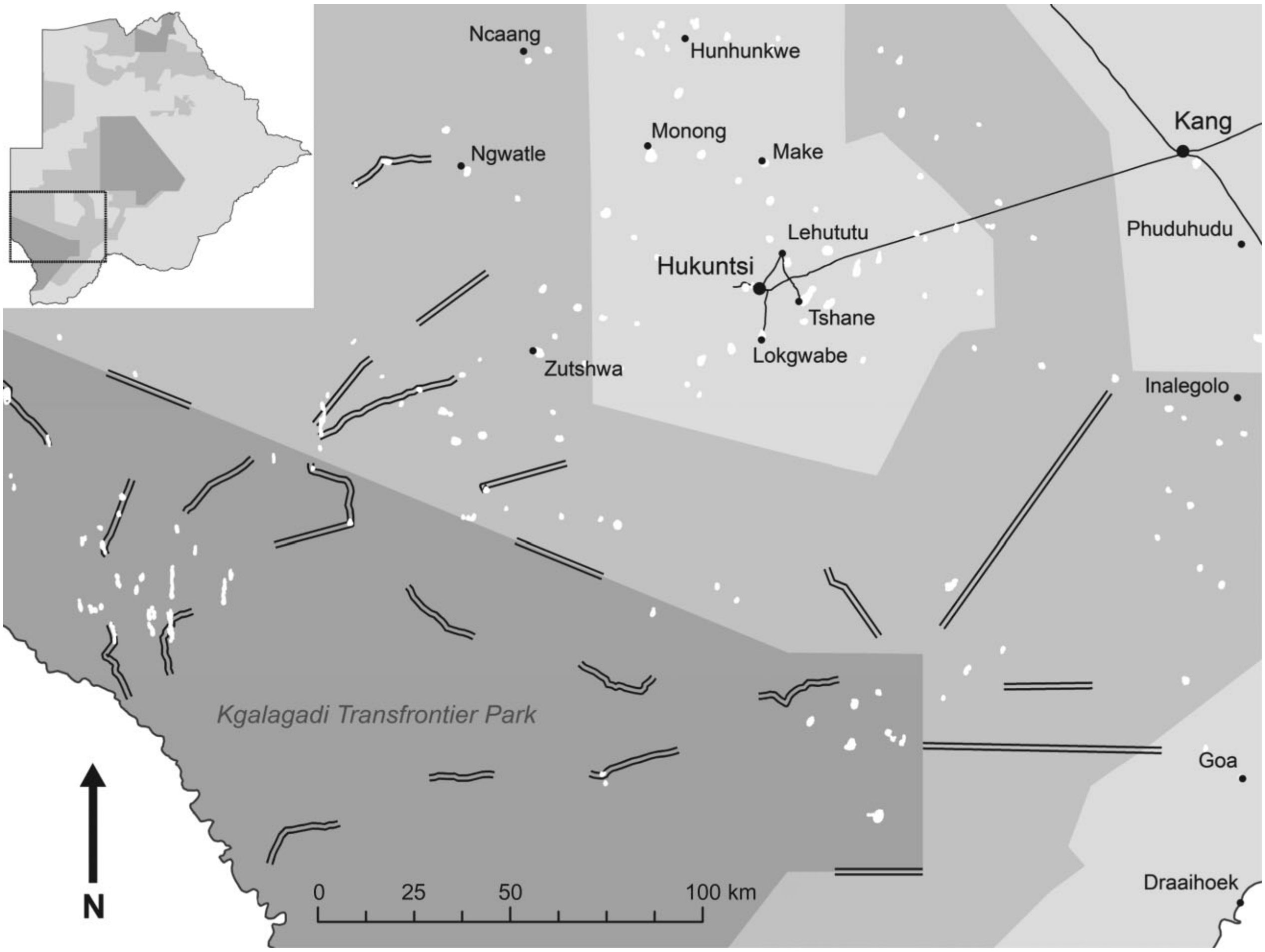

Figure 1 Map of the study area depicting the 24 track transects, ═; in relation to the Kgalagadi Transfrontier Park ▨; wildlife management areas ▨; and communal grazing areas ▨. Pans >500 m in diameter, (white); small towns, ●; villages, •; and improved roads, —; are also shown. The location of the study area in Botswana is shown in the inset at top left.

rapidly estimating animal density across the range of terrestrial species identifiable by their tracks.

This investigation has equal relevance to parallel developments in density estimation using two-dimensional ideal gas models with camera trapping (Rowcliffe *et al*., 2008). I consider tracking because it is pertinent and practical in the environment within which the present study was conducted. The two methods share desirable attributes such as equivalent effectiveness over day and night and the ability to detect secretive species. Although camera trapping has more widespread applicability in all habitats, where soil substrate is suitable for tracking, cameras become mostly redundant. Not only can their expense be limiting, especially for remote areas with low-density populations, but track transects accumulate observations more efficiently (Silveira *et al*., 2003), because they extend the field of detection over greater dimensions than camera point locations.

Materials and methods

Study area and track transects

I examined an area of south-western Botswana that encompasses most of the Kgalagadi Transfrontier Park (Botswana side) and surrounding wildlife management areas, together comprising a contiguous ecological unit under minimal human influence (Fig. 1). It is generally an open semiarid savanna and remarkably uniform, with scarcely any relief and only ephemeral surface water after good rains. Vegetation structure is homogeneous overall, with plant composition varying along subtle gradients of sand texture described by Skarpe (1986); dominant species include trees *Acacia erioloba*, *Ac. luederitzii*, *Boscia albitrunca* and *Terminalia sericea*; shrubs *Grewia flava* and *Ac. mellifera*; and grasses *Schmidtia kalahariensis* and *Stipagrostis uniplumis*. The most distinctive landscape features are clay-bottomed depressions known as pans, which have elevated mineral levels that attract antelope and other wildlife (Parris & Child, 1973). The northern part of the study area overlaps a region known as the Kalahari Schwelle (Parris, 1976), recognized for its concentration of major pans (>500 m in diameter) that are important to large semi-migratory antelope (Williamson, Williamson & Ngwamotsoko, 1988; Verlinden, 1998).

This area is bisected by a low-density network of 4 × 4 trails and firebreaks. Firebreaks are 15-m swaths of cleared vegetation forming straight linear features. With respect to subtle habitat gradients, they are randomly oriented and thus expected to sample habitat in proportion to its occurrence. In contrast, 4 × 4 trails are slightly meandering paths with greater coverage of the study area but more likely to sample major pans than at random. Together, the different features provide favorable coverage of the study area. To address several research questions, I established track transects along these convenient features both randomly within land use types and systematically covering the continuous distance between human settlements and the park boundary. Transects were subsampled from this available pool for the present analysis. I standardized transect length at 20 km mainly to maximize daily coverage and minimize the number of transects with zero counts for low-density species. Total survey effort has an overwhelming influence on estimate accuracy (Stephens *et al*., 2006), so transect length is a somewhat arbitrary practical consideration. Because surveys were comprehensive for species >0.2 kg, the level of attention required to scrutinize track beds constrained the upper limit of daily coverage to about 20 km.

Transects were sampled during the typically wetter season between 15 October and 15 April, with no temporal replication. Where transects abutted one another, the 20-km lengths were combined for analysis into a single transect to reduce spatial autocorrelation in the data structure. This resulted in 24 spatially separated transects with total sample coverage of 634 km. I previously found that human settlements impacted wildlife distribution and abundance up to about 20 km, so transects within this distance of point disturbances were excluded. I therefore suggest the sample coverage represents an area of 'undisturbed' native wildlife community that persists in the southern Kalahari ecosystem. Within the area examined, there are no fences or other barriers to impede wildlife movement.

I precleared transects of old tracks by dragging a heavy steel beam behind a vehicle, so that fresh tracks accumulated over the following 24-h period before sampling. This precisely controlled the capture of tracks over one diel period of animal movement necessary for density estimation. Dragging did not fundamentally alter the transect but caused light disturbance that erased tracks in the space between the vehicle tires, or at least made it simple to distinguish tracks that were fresh from those disrupted by the drag. Surveys began early morning and were conducted by two observers on specialized seats mounted to the front of the vehicle – one an expert local tracker and myself, also a competent tracker. Progressing at a rate between 6 and 8 kph, all track intersections with the transect were recorded as species and numbers with global positioning system (GPS) locations. No assumptions were made about track intersections belonging to same individual animals. Only rarely did the lead tracker fail to count recrossings, mostly in instances where individual tracks became highly tortuous yet remained visually connected over short distances. Although this is expected to bias estimates, because of the low rate of occurrence, the extent of that bias should be very small.

Although transects overlapped two different types of linear features, the width of the track bed was the same – roughly equal the width of a 4 × 4 vehicle. However, these linear features potentially influence animal movements differently. Firebreaks are more substantial disturbances that create a microhabitat of open ground and improved line of sight. Some species could potentially be attracted to these artificial habitats, which would predictably inflate their counts through higher rates of recrossings by individual animals. Any discernible increase in encounter rates on firebreaks is likely to result from this factor, and unlikely to result from either avoidance or low utilization of pans along 4 × 4 trails because such habitats are infrequent point locations in the landscape and small in scale compared with transect length. Conversely, neither features are expected to repel species or prevent their crossing, because naturally occurring areas of open sand are frequent in the Kalahari. For each species, I examined the raw data graphically and used a single-factor analysis of variance to objectively distinguish any bias in track counts between those transects overlapping trails and those overlapping firebreaks.

Daily travel distances (day range)

I predicted day range for all species using allometric relationships described in Carbone *et al*. (2005). These relationships were modeled using a wide range of species from different biomes (data are available in appendix to online edition of Carbone *et al*., 2005). Previously, taxonomic grouping (and its correlate feeding type) was found to influence body mass–day range scaling. I therefore fitted a separate least-squares linear regression to the $\log_e$ transformed data for each of three orders (Artiodactyla, Carnivora, Rodentia) applicable to the present study species (see Table 1 for parameter estimates). These order-specific scaling rules were then most appropriately applied to the Kalahari species (Table 2). To predict daily travel distances, body masses were taken from Kingdon (1997), and where ranges were reported I used the mean value between sexes of

Table 1 Taxonomic groups with respective exponents and intercepts scaling body mass to day range

Taxonomic group	Scaling exponent	SE	Intercept	SE	*n*
Artiodactyla	0.26	0.11	–0.11	0.52	22
Carnivora	0.421	0.09	0.147	0.24	39
Rodentia	0.405	0.14	–0.556	0.40	16

SE, standard error.

Table 2 Species grouped by size-feeding type and arranged by alphabetical common name along with data used for density calculations

Latin binomial	Common name	Track count (mean intersections m^{-1} 24 h^{-1})	CV (%)	Mass (kg)[a]	Mass–day range scaling rule	Empirical day range (km 24 h^{-1}) ± SE (n)	Source day range estimate
Taurotragus oryx	Eland	1.243	40	561	Artiodactyla		
Oryx gazella	Gemsbok	5.055	25	206	Artiodactyla	5.9 ± 0.58 (17)	D. Keeping (unpubl. data)
Alcephalus buselaphus	Hartebeest	3.220	30	161	Artiodactyla		
Tragelaphus strepsiceros	Kudu	0.143	24	210	Artiodactyla		
Antidorcas marsupialis	Springbok	1.821	66	38	Artiodactyla		
Connochaetes taurinus	Wildebeest	0.565	58	214	Artiodactyla	4.3 ± 0.41 (7)	M. Selebatso (unpubl. data)
Sylvicapra grimmia	Duiker	0.526	21	17.5	Artiodactyla		
Xerus inauris	Ground squirrel	0.137	27	0.8	Rodentia		
Lepus capensis and L. saxatilis	Cape and scrub hare	5.170	13	2.63	Rodentia		
Hystrix africaeaustralis	Porcupine	0.416	24	17	Rodentia		
Pedetes capensis	Springhare	1.574	22	3.5	Rodentia		
Raphicerus campestris	Steenbok	6.490	13	11.5	Artiodactyla	4.5 ± 0.45 (6)	D. Keeping (unpubl. data)
Hyaena brunnea	Brown hyena	0.450	10	47.5	Carnivora	31.1 ± 2.1 (42)	Mills (1990)
Acinonyx jubatus	Cheetah	0.049	41	50	Carnivora	9.0 ± 0.79 (24)	M. G. L. Mills (unpubl. data)
Panthera pardus	Leopard	0.060	42	55	Carnivora	9.7 ± 0.9 (31)	Stander (1998)
Panthera leo	Lion	0.060	40	178.5	Carnivora	19.4 ± 1.4 (16)	Stander (1998)
Crocuta crocuta	Spotted hyena	0.018	39	65	Carnivora	26.5 ± 1.7 (140)	Mills (1990)
Felis silvestris	African wild cat	0.413	17	4.75	Carnivora		
Felis nigripes	Black footed cat	0.012	33	1.5	Carnivora		
Vulpes chama	Cape fox	0.502	15	3	Carnivora		
Caracal caracal	Caracal	0.174	24	13	Carnivora		
Mellivora capensis	Honey badger	0.178	24	11.5	Carnivora	10.8 ± 0.8 (144)	Begg et al. (2005)
Canis mesomelas	Black-backed jackal	3.154	10	10	Carnivora		
Herpestes sanguineus	Slender mongoose	0.016	50	0.575	Carnivora		
Genetta genetta	Small spotted genet	0.170	24	1.78	Carnivora		
Ictonyx striatus	Striped polecat	0.569	17	1.05	Carnivora		
Suricata suricatta	Suricate	0.119	47	0.795	Carnivora		
Cynictis penicillata	Yellow mongoose	0.381	22	0.62	Carnivora	3.2 ± 0.43 (7)	Cavallini (1993)
Orycteropus afer	Aardvark	0.246	13	61	Carnivora	8.6 ± 1.54 (4)	D. Keeping (unpubl. data)
Proteles cristatus	Aardwolf	0.161	20	10	Carnivora		
Otocyon megalotis	Bat-eared fox	2.144	14	4.15	Carnivora		
Manis temminckii	Ground pangolin	0.017	53	12.5	Carnivora	3.8 ± 1.53	Skinner & Chimimba (2005)
Ardeotis kori	Kori bustard	0.605	19	9.45	Carnivora		
Struthio camelus	Ostrich	0.814	24	111	Artiodactyla		
Sagittarius serpentarius	Secretary bird	0.027	48	3.4	Carnivora		
Geochelone pardalis and Psammobates oculifer	Leopard and Kalahari tent tortoise	0.079	30	0.325	Rodentia	0.435 ± 0.01 (6)	Hailey & Coulson (1996)

CV, standard error as the percentage of the mean; SE, standard error. [a]mammals – Kingdon, 1997; birds – Hockey, Dean, & Ryan, 2005; reptiles – Keswick, 2012.

the median value for each sex. This is justified because the data used to create the scaling rules were produced in the same way. I assume no substantial day range differences between sexes or age categories in sampled populations as most species cannot be reliably sexed and aged by their tracks, but any deviation is presumably negligible in comparison with error associated with the scaling relationships. Group size influences day range (Carbone *et al.*, 2005; Stephens *et al.*, 2006), but is often difficult to determine from track counts, so was ignored.

Empirical estimates of day range were available for a subset of 12 mammal species, either from the immediate study area or comparable region and habitat. These came from several published and unpublished sources (Table 2), and were typically obtained by radio tracking and following habituated animals. Wildebeest day range was estimated from GPS-collared animals as sums of Euclidean distances between six fixes per 24-h period. These are obviously minimum estimates; true wildebeest day range may be underestimated by a potentially large distance. I acquired more accurate empirical day range estimates for three species (gemsbok, steenbok, aardvark) through following the animals' tracks over a 24-h period with handheld GPS data-loggers programmed to take fixes at 1-s intervals.

Density estimation with the FMP formula

Theoretical derivation of the FMP formula is described in Stephens *et al.* (2006). The derived formula has the form

$$D = \frac{\pi}{2}\frac{x}{S\hat{M}}$$

where x is the total number of track intersections, S is the total sample length of all transects and $\hat{M}$ is the mean travel distance for all individuals of that species in the study area.

Both variance in track counts between spatially separated transects and variance in estimates of day range contribute to uncertainty in density estimates. I used nonparametric bootstrapping (Efron & Tibshirani, 1993) and took the following steps to estimate uncertainty in density estimates for each species:

1 For the appropriate taxonomic group, resampled the raw data with replacement. Then fitted a least-squares regression line to the $\log_e$ transformed bootstrap data to obtain new parameter estimates for slope and intercept, and applied the best estimate of body mass to the equation to produce a single estimate of day range ($\hat{M}$).

2 Resampled 16 or 24 transects with replacement (depending on whether firebreaks were excluded or included, respectively) to generate a bootstrap replicate of x/S.

3 Combined estimates of $\hat{M}$ and x/S in the FMP formula to produce one estimate of density.

4 Repeated steps 1–3 5000 times to obtain the distribution of D, then calculated its mean and bias corrected and accelerated (BCA) 95% confidence intervals.

For select species with empirical day range estimates available, only step 1 differed. Where mean day range and its standard error were reported in the literature, I generated a normal distribution of simulated values based on reported sample sizes, then resampled these with replacement to produce a bootstrap estimate of $\hat{M}$. For those species with raw data available, day range replicates were simply resampled with replacement to produce the bootstrap estimate of $\hat{M}$. Steps 2–4 then followed identically.

Comparison with independent density estimates

Independent estimates from the area are limited in their reliability but, nonetheless, provide the best opportunity to assess the performance of the track-based method. Botswana's wildlife department conducted an aerial strip transect survey (Department of Wildlife and National Parks Botswana, unpublished report) several months after the last track counts were conducted, which provides a comparison for large herbivores. Wallgren *et al.* (2009) offers the only estimates for smaller species using line transect distance sampling from vehicle conducted both during the day and at night with spotlights. Sampling occurred on many of the same trails used for track counts, but several years prior. For large carnivores, Funston *et al.* (2001) produced a simple linear regression of track counts on true density for lions and extrapolated this to other large predators. All estimation methods likely have systematic biases and are not strict benchmarks but rather provide a broad basis of comparison across species to evaluate the track-based approach.

Results

During sampling, and based on casual observations at night, it was obvious certain species were attracted to firebreaks and especially so firebreaks recently cleared of vegetation. Four species (hare, porcupine, springhare and steenbok) had substantially greater encounter rates on firebreaks compared with trails ($P < 0.1$). On several firebreaks counts were hyper-inflated; this upper variability depicted in box-and-whisker diagrams (Fig. 2). The results suggest that these small animals were disproportionately active on firebreaks compared with surrounding habitat, so I dispensed with their firebreak counts from further analyses (i.e. only transects on trails were considered) to avoid upwardly biased density estimates. All four species have presumably small home ranges (Kingdon, 1997) and appear widely and evenly distributed throughout the study region. Their increased activity on firebreaks was therefore unlikely to deduct activity from transects elsewhere, so the removal of firebreaks from their calculations was justified. Kori bustard and ostrich showed slightly greater activity on firebreaks, while there was no discernible differences in track counts among all other species depending on the type of linear feature upon which transects were located. Firebreaks appeared to be just as adequate as 4 × 4 trails for sampling the majority of species.

All 12 mammal species for which empirical day range estimates were available (see Table 2) showed movements

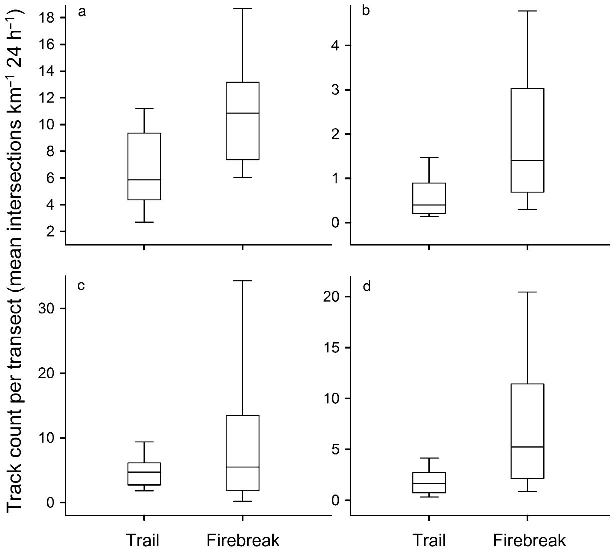

Figure 2 Track counts per transect separated into those overlapping trails (n = 16) and those overlapping firebreaks (n = 8) for (a) steenbok, (b) porcupine, (c) hare and (d) springhare.

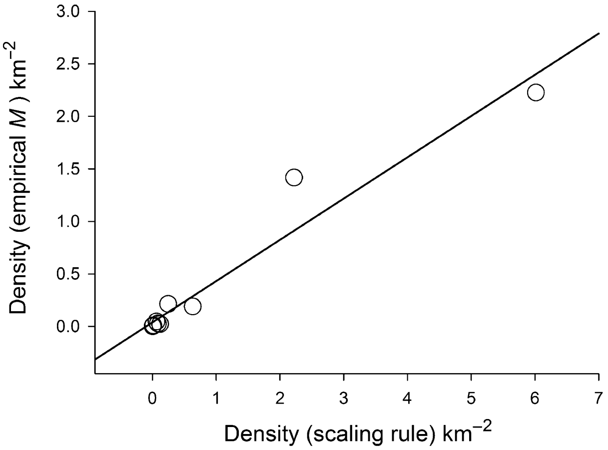

Figure 3 Least-squares regression line showing the relationship between densities estimated using empirical day range and densities estimated using predicted day range from scaling rules for 12 species of Kalahari mammals.

on average 140% (coefficient of variation 93%) longer than those predicted by their respective body mass–day range scaling rule. This pattern occurred across taxonomic groups (although no comparisons were available for Rodentia). The semiarid Kalahari has nutrient-deficient sandy soils and lower productivity compared with other environments from which data were compiled to develop the body mass–day range scaling rules. As animal day range is driven by energetic requirements and food distribution, it is perhaps unsurprising that the subset of Kalahari herbivores, carnivores and insectivores consistently showed greater day ranges than predicted. Begg *et al.* (2005) noted larger home ranges and daily movements of Kalahari honey badgers compared with conspecifics in other environments, and their home ranges were greater than that predicted using scaling rules for other mustelids.

As a result of under-predicted allometric day ranges, their application in the FMP formula generally overestimated species densities in the Kalahari. Point estimates of densities showed a positive difference with independent estimates (Wilcoxon matched pairs test, $n = 22$ species, $z = 2.29$, $P = 0.022$). Empirical data were inadequate to adjust each taxonomic scaling model. However, given the consistently greater empirical day ranges among all species, I used the slope of the least-squares regression equation defining the linear relationship between density estimated using empirical day range, and density estimated using allometric day range (slope = 0.393, y-intercept = 0.039, $r^2 = 0.94$, $F_{1,10} = 168$, $P < 0.001$) (Fig. 3) as a correction factor to achieve best estimates of density (Table 3). Removing the two largest values due to leverage had minor effect on the equation (slope = 0.34, y-intercept = 0.012, $r^2 = 0.70$, $F_{1,8} = 19$, $P = 0.003$). After correction, positive differences between paired estimates disappeared and instead were balanced around zero ($n = 22$, $z = 0.261$, $P = 0.794$) (Fig. 4). Carnivores showed the most improvement whereby estimates of 9 out of 11 species moved closer to their independent estimates after correction; only lion and spotted hyena did not improve, possibly because of low sample sizes. Overall, there was good correspondence between corrected and independent density estimates (Fig. 5).

Discussion

Using day ranges predicted from scaling rules is a coarse approach to the FMP formula. These are model averages of animals from different ecosystems; the actual movement of animals in the study area will determine the accuracy of density estimates. At the very least, however, the approach provides estimates of species abundances relative to one another, which track counts do not. While the inappropriateness of comparing track indices between species has often been suggested (e.g. Beauvais & Buskirk, 1999; Engeman, 2005), here it is demonstrated that differential movement rates confound interspecies comparisons using raw track indices. Relative species rankings based on indices changed after conversion to density (Fig. 6). Clearly, animals with relatively short daily movements can have higher densities than their track counts suggest (e.g. tortoises) and vice versa (e.g. brown hyena). Substituting allometric day range in the FMP formula does make density estimation, however rough, possible for animals that are otherwise impossible to estimate using other multispecies survey methods such as aerial survey and line transect distance sampling. In the Kalahari this included 11 mammalian carnivores, 3 insectivores and 2 herbivores.

Among a subset of Kalahari species, empirical day ranges were consistently greater than those predicted allometrically. Rowcliffe *et al.* (2012) warn how using infrequent telemetry fixes to estimate day range potentially returns severe underestimates. We obtained very accurate

Table 3 Correction-adjusted Formozov–Malyshev–Pereleshin density estimates with 95% confidence limits for Kalahari wildlife species (>0.2 kg) over a contiguous protected and partially protected conservation area in south-western Botswana

Species	Density (100 km^{-2})	LCL	UCL
Eland	16.6	4.3	34.8
Gemsbok	141.7	65.1	206.0
Hartebeest	59.7	22.4	99.1
Kudu	2.5	0.8	3.7
Springbok	49.2	2.3	115.9
Wildebeest	21.4	2.0	47.3
Duiker	17.3	6.5	26.9
Ground squirrel	16.1	5.1	30.7
Hare spp.	376.1	133.1	695.6
Porcupine	14.2	3.7	37.0
Springhare	101.6	31.8	203.0
Steenbok	222.6	151.4	282.9
Brown hyena	2.3	1.6	2.8
Cheetah	0.9	0.1	1.5
Leopard	1.0	0.1	1.7
Lion	0.6	0.2	3.4
Spotted hyena	0.1	0.0	0.2
African wild cat	11.4	5.7	16.6
Black footed cat	0.5	0.1	1.0
Cape fox	16.9	11.9	24.6
Caracal	3.2	1.3	5.0
Honey badger	3.4	1.5	5.8
Jackal	63.9	37.3	86.2
Slender mongoose	1.1	0.1	2.6
Small spotted genet	7.1	2.7	11.7
Striped polecat	29.7	13.3	48.5
Suricate	6.9	0.7	14.9
Yellow mongoose	18.9	7.8	27.8
Aardvark	4.6	2.6	6.4
Aardwolf	3.3	1.6	5.0
Bat-eared fox	62.8	33.9	90.8
Ground pangolin	0.6	0.0	2.6
Kori bustard	13.8	6.6	20.5
Ostrich	18.6	7.3	28.2
Secretary bird	0.8	0.1	1.7
Tortoise spp.	30.0	10.1	54.2

Corrected estimates are substituted with estimates derived directly using empirical day ranges for those species applicable.
LCL, lower confidence limit; UCL, upper confidence limit.

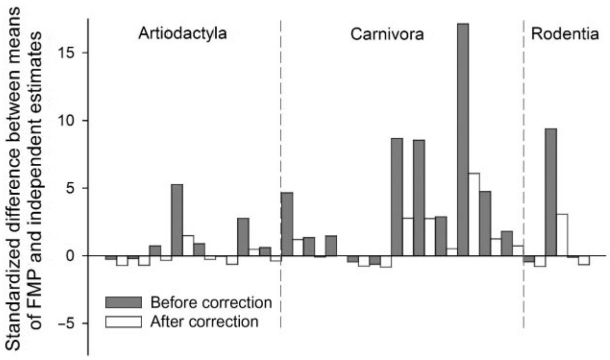

Figure 4 Change in differences between Formozov–Malyshev–Pereleshin (FMP) estimates and independent estimates before and after correction for all 22 species available. FMP estimates were divided by their respective independent estimates to obtain standardized values, and the differences displayed with independent estimates set to zero. Species are segregated into taxonomic groups based on scaling rule applied. Note the overall improvement to density estimates across taxonomic groups after correction (i.e. more balanced around zero).

day range estimates for three species by retracing their movements using frequent fix rates (1 s). However, it seems unlikely there was any systematic bias in the accuracy of empirical day range estimates for Kalahari species compared with those data from which the scaling relationships were derived. For example, the local day range estimate for wildebeest was based on infrequent fixes (once every 4 h), but this estimate was still 20% greater than that predicted allometrically. The consistency suggests that rather than any systematic bias, rates of animal movement in the semiarid Kalahari environment are generally high. This justified the use of a correction factor that improved estimates for most species lacking empirical data. Agreement with independent density estimates reflects some measure of accuracy, accepting that both estimates are of unknown quality. The agreement between density estimates across a large number of species suggests this approach is worth further investigation in other environments. This example warns how application of general scaling rules to the FMP formula can overestimate density of species in ecosystems with low productivity, or conversely, underestimate density in high-productivity environments. Therefore, if accuracy of density estimates is important, it seems prudent to understand location-specific day range among a subset of species to either support or correct the scaling rule-based predictions.

Location-specific data on day range are the primary constraint to estimating density with track counts, as these are typically expensive and time consuming to obtain. Encouragingly, modest sample sizes in the present study returned useful day range estimates for several species. Further, data from both published and unpublished sources were available for several more species even in this under-researched area of the Kalahari. Published day range estimates are relatively scarce compared with reporting on home-range size; however, those same studies may be a hidden repository of data that can be inferred from sequential GPS telemetry locations. Technological advances combined with databases such as Movebank (http://www.movebank.org), where wildlife tracking data are archived and shared, facilitate growing possibilities for FMP application, as it applies equally to recent parallel developments using camera traps (Rowcliffe & Carbone, 2008; Rowcliffe *et al.*, 2008). Utilizing such existing data requires sensitivity to potentially large differences in movement rates between habitat types and geographic regions within a species' range, and to the potential severity by which day range estimates can be underestimated using infrequent telemetry fixes (see Rowcliffe *et al.*, 2012). Estimation of day range at a fine spatial scale

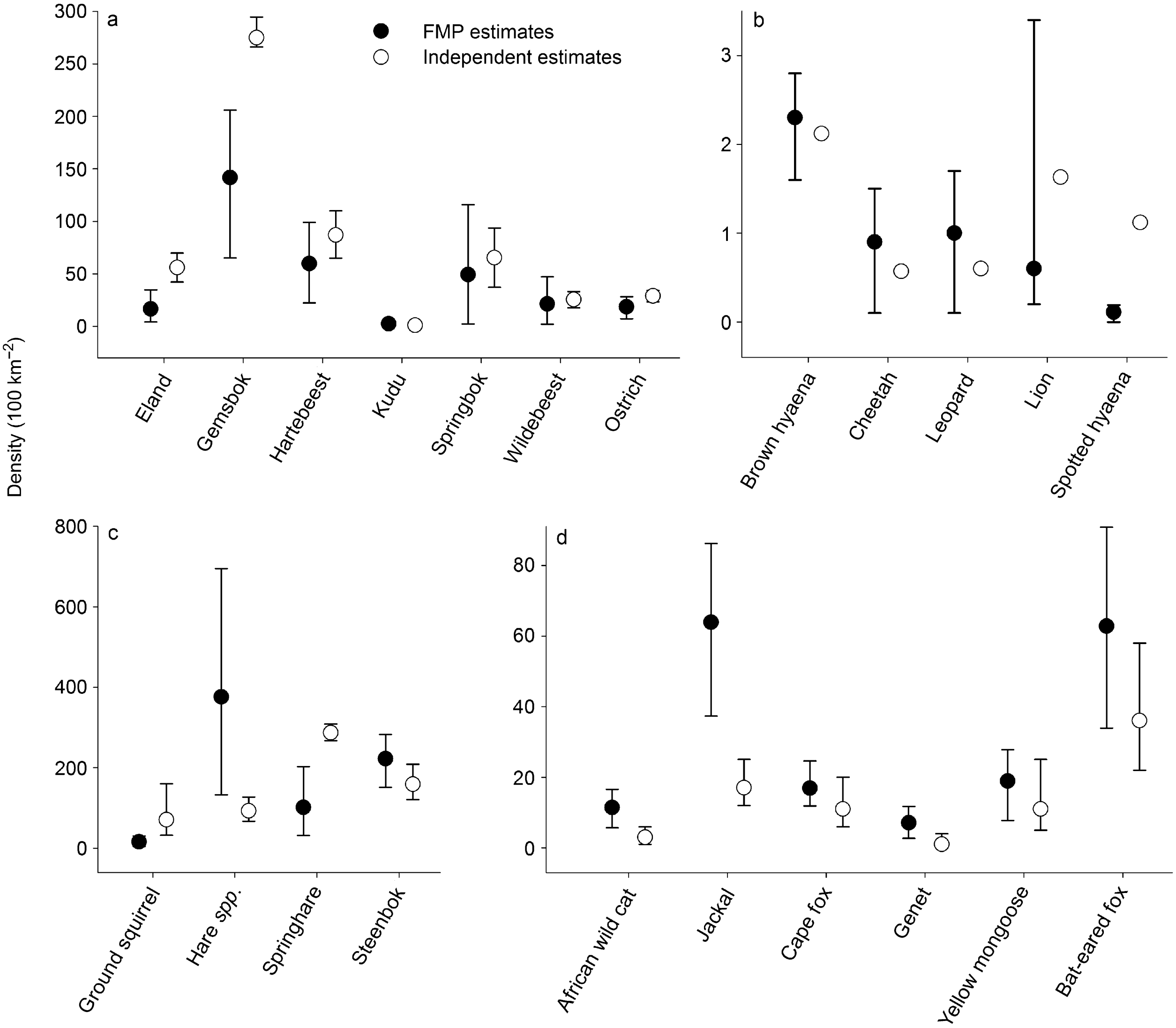

Figure 5 Comparison of correction-adjusted Formozov–Malyshev–Pereleshin (FMP) density estimates to independent estimates with 95% confidence intervals for (a) large herbivores, (b) large carnivores, (c) small herbivores and (d) small carnivores. Independent estimates are from aerial strip transect survey (a), spoor index – true density calibrations (b) and line transect distance sampling by ground vehicle (c) and (d).

(Rowcliffe *et al*., 2012) is presumably important to the accuracy of FMP estimates when each and every track intersection is enumerated (i.e. those belonging to same individuals over short distances), so research into a widely applicable method to obtain unbiased day range estimates from intermittent fixes would increase possibilities for accurate density estimation.

Day ranges are vulnerable to change with time, which is a further limitation to the method. Movement rates often vary intra-annually in environments where primary productivity is seasonal. Major discrete fluctuations in movement such as migration, mating and juvenile dispersal may or may not be temporally predictable, so a cautious approach is to measure day range within a specific time of year, and limit track surveys to that same period. Even then, interannual changes in food availability can affect day range markedly, for example, in the case of predator–prey cycles (Ward & Krebs, 1985). Quantity of precipitation varies widely both temporally and spatially in semiarid environments such as the Kalahari, in turn affecting large herbivore movements in response to forage conditions (Verlinden, 1998), while the timing of precipitation events can trigger surges in animal activity (e.g. Bider, 1968). Ambient temperature was shown to cause substantial fluctuations in the daily movements of marten *Martes martes* (Zalewski, Jedrzejewski & Jedrzejewska, 2004), and even moonlight (Penteriani *et al*., 2013) can have considerable influence on day range. Density estimates can improve from increased understanding of the spatial and temporal factors influencing daily movements (see Stephens *et al*., 2006), and environmental variables

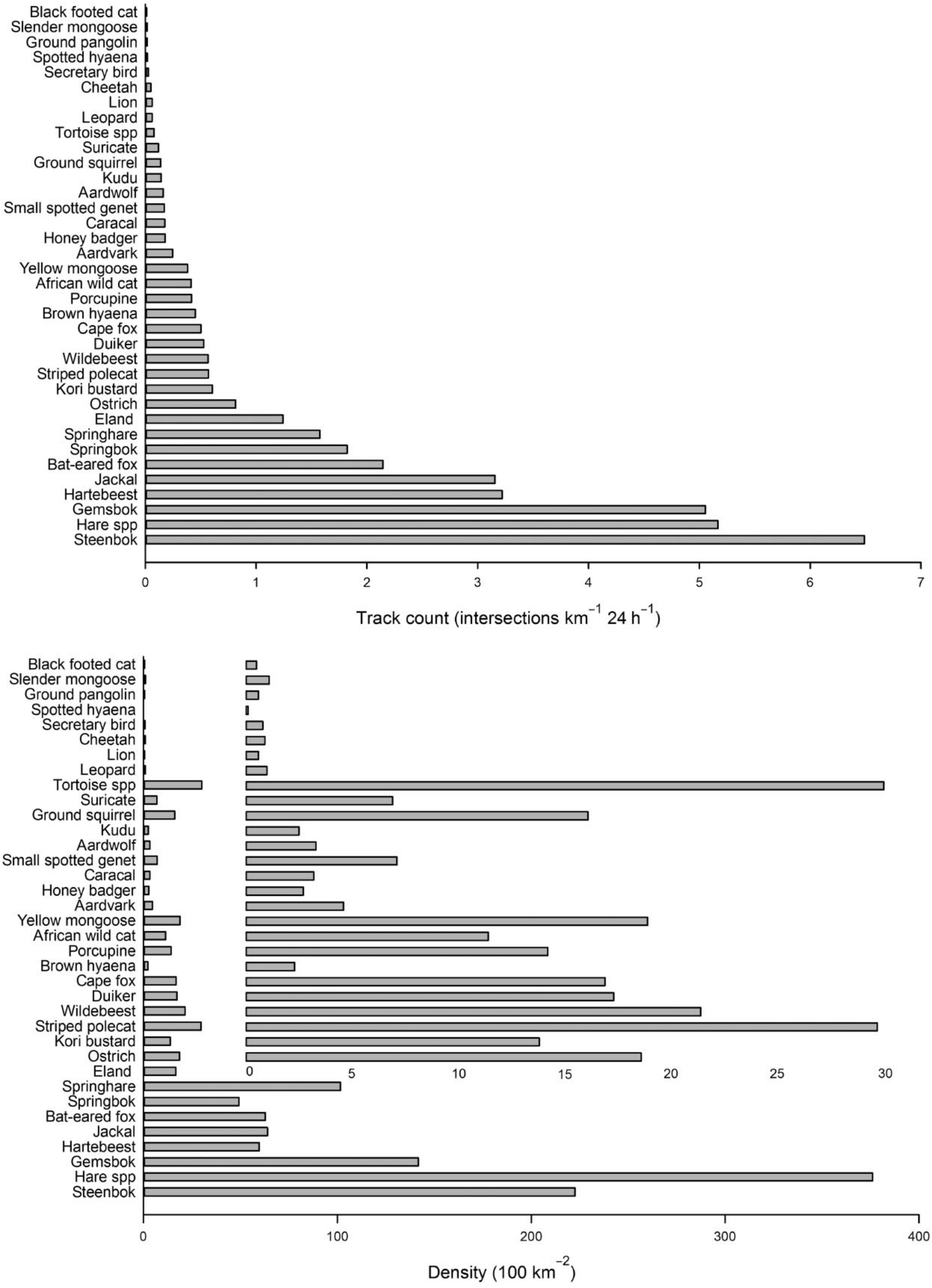

Figure 6 Species ranking based on track counts, with the same rank order after conversion to density. To better illustrate differences among low-density species, the inset in the density panel shows an expanded axis with the eight most numerous species and eland omitted.

measured in the field at the time of tracking could be incorporated into predictive models of day range. Density-dependent movements add further uncertainty, and implicate the frequency with which day range should be reassessed (Stephens *et al.*, 2006). If density is monitored through time, day range either needs to be reassessed or assumed not to have changed. These considerations notwithstanding the allometric approach to extrapolating day ranges, however coarse, appears to have potential for comprehensive snapshot assessments of wildlife communities in remote areas where other methods are unfeasible.

Day range considerations are essential, but animal movement with respect to transects and how tracks are counted also influences estimate accuracy. Density estimates based on direct observation such as aerial survey and ground line transects are vulnerable to distortion by species-specific visibility biases due to appearances and behaviors, while track counts are much less so. Missed tracks may have slightly greater incidence for smaller, lighter foot-loading species, but this is probably negligible as tracks of all species in the present study were readily visible and could be interpreted by more than one observer. Springhare may be an exceptional example that bound over transects without leaving tracks, possibly explaining the disparity between their estimates (Fig. 5). However, an equally plausible explanation for this species along with hare is large changes in populations between the years intervening samples. Rodents have short generation times in addition to known cyclic dynamics of some populations and noncyclic outbreaks of others. It is speculative discussion to tease out the factors influencing differences observed between the track-based and independent estimates. Considering all that could be driving the comparative estimates apart, when interpreted as a whole over taxonomic groups and species in Fig. 5, there was remarkable congruency.

The general accordance between track-based and independent estimates is encouraging evidence that animals are exhibiting unbiased movements with respect to transects, a lingering concern over application of the FMP formula. Density estimates will be most accurate if transects do not influence animal movements, and secondly, if all track intersections are counted regardless of the number of times individual animals may re-intersect a transect. The latter is simple enough to achieve; however, it is interdependent with the former which is often unmet in practice. FMP surveys that utilize linear features for sampling should be interpreted cautiously because unbiased estimates can be assumed only with transect placement that is random and independent of naturally nonrandom animal movements. In the Kalahari environment, I found firebreaks unsuitable for sampling certain small herbivores that are attracted disproportionately to these artificially open microhabitats. Carnivores are a more ubiquitous concern because many habitually travel along linear features to minimize energetic costs, even so subtle as tire spoor from a single-vehicle passing. Such behavior could introduce either negative or positive bias to estimates. For example, some carnivores tend to walk long distances along the transect, but they are counted once regardless of the distance they travel, unless they exit and re-enter the transect. This altered behavior may negatively bias estimates because if these animals simply take advantage of linear features when they happen to be encountered, then one would expect uninfluenced movements that are naturally more tortuous to result in more intersections on average in the absence of the linear feature. Alternatively, animals that tend to travel along the features but consistently make exploratory meanders from side to side would predictably generate positive bias to estimates, and jackal may be an example (Fig. 5). The extent and direction in which FMP estimates are biased by carnivore movement behavior is not as clear as it is for camera trapping whereby snapshots of movement at point locations along linear features clearly tend to positively bias density estimates for those carnivores that utilize them (Wearn *et al.*, 2013). Perhaps an answer can similarly be reached by comparing estimates from transects overlapping linear features to those randomly situated, or through quantifying fine-scale predator movements in relation to linear features (*sensu* Whittington, St. Clair & Mercer, 2004).

Another difficulty is posed by animals that enter the transect and exit the same direction. Strict interpretation of the FMP formula would include animals that cross a one-dimensional transect center line only, and exclude those that enter the two-dimensional track bed but fail to cross the center. This is especially germane on 4 × 4 trails because some predators do occasionally intersect the first tire spoor and travel along it before exiting in the same direction. Notably, transects are exceedingly narrow (4 × 4 vehicle width) relative to the two-dimensional space over which animals range daily, so this only concerns animals influenced by the tire spoor to parallel, but not cross, the one-dimensional center line just centimeters away. Excluding these animals would obviously negatively bias estimates as their daily movements brought them at least to touching the line, if not crossing it. Therefore, I suggest strict adherence to the formula can be relaxed to accommodate these exceptions. Options exist for incorporating the two dimensionality of transects with modified ideal gas models (*sensu* Rowcliffe *et al.*, 2008), but this would not resolve the problem of the transect influencing movement behavior. Such models would be equally affected by violation of the transect-movement independence assumption and in both situations animals are recorded exactly the same – once regardless of the distance they travel along the transect. I suggest that the one-dimensional FMP formula is advantageous in practical simplicity. There seems to be no easy solution to the convenience sampling dilemma, and the interpretation of estimates for animals that habitually travel along transect features is best treated with caution.

The Kalahari semiarid savanna is open country, but despite good visibility, low animal densities and insufficient observations make direct counting a limited multispecies approach. Aerial surveys efficiently cover ground but are conducted irregularly due to expense and restricted to large-bodied, mostly gregarious, grazing antelopes (Jachmann, 2002). Road counts using distance sampling increase those observations to include some of the more common smaller and nocturnal species. Camera trapping could potentially capture everything, but there is a constrained range of animal body size for which camera position and trigger sensitivity can be optimally set. The vastness and remoteness of the area, high initial and maintenance costs, risk of theft or vandalism, and harsh conditions contributing to camera failure rates seem prohibitive.

Tracking supersedes the limitations of other methods, and southern Africa in particular is poised to benefit from increased understanding of the FMP formula. With ideal substrate conditions year round, and latent force of skilled local trackers, there is hardly a better opportunity anywhere to implement track-based wildlife counts and begin compiling a library of species' day ranges through putting trackers on animal trails to trace their movements.

Acknowledgments

The Government of Botswana and Department of Wildlife and National Parks deserve commendation for encouraging research, and I thank them for permission to conduct this study. The project was supported by Comanis Foundation, Kanabo Conservation Link, Natural Sciences and Engineering Research Council of Canada, Safari Club International Foundation and Conservation Force. I am indebted to my tracking companions Panana Sebati and Nicolas Molese of Ngwatle and Zutshwa, without whom field work would have been onerous to impossible. I also thank P.A. Stephens, S. Pawar, A.L. Foote, E.M. Bayne and S. Boutin for comments that greatly improved the paper.

References

Anderson, D.R. (2001). The need to get the basics right in wildlife field studies. *Wildl. Soc. Bull.* **29**, 1294–1297.

Beauvais, G.P. & Buskirk, S.W. (1999). An improved estimate of trail detectability for snow-trail surveys. *Wildl. Soc. Bull.* **27**, 32–38.

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

Bider, J.R. (1968). Animal activity in uncontrolled terrestrial communities as determined by a sand transect technique. *Ecol. Monogr.* **38**, 269–308.

Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J.R., Griffiths, M., Holden, J., Kawanishi, K., Kinnaird, M., Laidlaw, R., Lynam, A., MacDonald, D.W., Martyr, D., McDougal, C., Nath, L., O'Brien, T., Seidensticker, J., Smith, D., Sunquist, M., Tilson, R. & Wan Shahruddin, W.N. (2001). The use of photographic rates to estimate densities of cryptic mammals. *Anim. Conserv.* **4**, 75–79.

Carbone, C., Cowlishaw, G., Isaac, N.J.B. & Rowcliffe, J.M. (2005). How far do animals go? Determinants of day range in mammals. *Am. Nat.* **165**, 290–297.

Cavallini, P. (1993). Activity of the yellow mongoose *Cynictis penicillata* in a coastal area. *Z. Saugetierk.* **58**, 281–285.

Duckworth, J.W. (1998). The difficulty of estimating population densities of nocturnal forest mammals from transect counts of animals. *J. Zool. (Lond.)* **246**, 466–468.

Efron, B. & Tibshirani, R. (1993). *An introduction to the bootstrap*. New York: Chapman & Hall.

Engeman, R.M. (2005). Indexing principles and a widely applicable paradigm for indexing animal populations. *Wildl. Res.* **32**, 203–210.

Funston, P.J., Herrmann, E., Babupi, P., Kruiper, A., Kruiper, H., Jaggers, H., Masule, K. & Kruiper, K. (2001). *Kalahari Transfrontier Lion Project: Final Report. Chapter 3: spoor frequency estimates as a method of determining lion and other large mammal densities in the Kgalagadi Transfrontier Park.* Submitted to South African National Parks and Botswana Department of Wildlife and National Parks.

Funston, P.J., Frank, L., Stephans, T., Davidson, Z., Loveridge, A., Macdonald, D.M., Durant, S., Packer, C., Mosser, A. & Ferriera, S.M. (2010). Substrate and species constraints on the use of track indices to estimate African large carnivore abundance. *J. Zool. (Lond.)* **281**, 56–65.

Garland, T. Jr. (1983). Scaling the ecological cost of transport to body mass in terrestrial mammals. *Am. Nat.* **121**, 571–587.

Hailey, A. & Coulson, I.M. (1996). Differential scaling of home-range area to daily movement distance in two African tortoises. *Can. J. Zool.* **74**, 97–102.

Hockey, P.A.R., Dean, W.R.J. & Ryan, P.G. (2005). *Roberts birds of Southern Africa*. 7th edn. Cape Town: John Voelcker Bird Book Fund.

Houser, A.M., Somers, M.J. & Boast, L.K. (2009). Spoor density as a measure of true density of a known population of free-ranging wild cheetah in Botswana. *J. Zool. (Lond.)* **278**, 108–115.

Jachmann, H. (2002). Comparison of aerial counts with ground counts for large African herbivores. *J. Appl. Ecol.* **39**, 841–852.

Katzner, T.E., Ivy, J.A.R., Bragin, E.A., Milner-Gulland, E.J. & DeWoody, J.A. (2011). Conservation implications of inaccurate estimation of cryptic population size. *Anim. Conserv.* **14**, 328–332.

Keswick, T. (2012). *Ecology and morphology of the Kalahari tent tortoise*, Psammobates oculifer*, in a semi-arid environment*. PhD thesis, University of Western Cape, Bellville.

Kingdon, J. (1997). *The Kingdon field guide to African mammals*. London: Academic Press.

Lopes, M.A. & Ferrari, S.F. (2000). Effects of human colonization on the abundance and diversity of mammals in eastern Brazilian Amazonia. *Conserv. Biol.* **14**, 1658–1665.

MacKenzie, D.I., Nichols, J.D., Sutton, N., Kawanishi, K. & Bailey, L.L. (2005). Improving inferences in population studies of rare species that are detected imperfectly. *Ecology.* **86**, 1101–1113.

McNab, B.K. (1963). Bioenergetics and the determination of home range size. *Am. Nat.* **97**, 133–140.

Mills, M.G.L. (1990). *Kalahari hyaenas: comparative behavioural ecology of two species*. London: Unwin Hyman.

Parris, R. (1976). *A study of the major components of the Kalahari pan ecosystem*. MSc thesis, University of Pretoria, Pretoria.

Parris, R. & Child, G. (1973). The importance of pans to wildlife in the Kalahari and the effect of human settlement on these areas. *J. S. Afr. Wildl. Mgmt. Ass.* **3**, 1–8.

Penteriani, V., Kuparinen, A., del Mar Delgado, M., Palomares, F., López-Bao, J.V., Fedriani, J.M., Calzada, J., Moreno, S., Villafuerte, R., Campioni, L. & Lourenço, R. (2013). Responses of a top and a meso predator and their prey to moon phases. *Oecologia* **173**, 753–766.

Pollock, K.H., Nichols, T.R., Simons, G.L., Farnsworth, G.L., Bailey, L.L. & Sauer, J.R. (2002). Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics* **13**, 105–119.

Rovero, F. & Marshall, A.R. (2009). Camera trapping photographic rate as an index of density in forest ungulates. *J. Appl. Ecol.* **46**, 1011–1017.

Rowcliffe, J.M. & Carbone, C. (2008). Surveys using camera traps: are we looking to a brighter future? *Anim. Conserv.* **11**, 185–186.

Rowcliffe, J.M., Field, J., Turvey, S.T. & Carbone, C. (2008). Estimating animal density using camera traps without the need for individual recognition. *J. Appl. Ecol.* **45**, 1228–1236.

Rowcliffe, J.M., Carbone, C., Kays, R., Kranstauber, B. & Jansen, P.A. (2012). Bias in estimating animal travel distance: the effect of sampling frequency. *Methods Ecol. Evol.* **3**, 653–662.

Sheil, D. (2001). Conservation and biodiversity monitoring in the tropics: realities, priorities, and distractions. *Conserv. Biol.* **15**, 1179–1182.

Silveira, L., Jacomo, A.T.A. & Diniz-Filho, F. (2003). Camera trap, line transect census and track surveys: a comparative evaluation. *Biol. Conserv.* **114**, 351–355.

Skarpe, C. (1986). Plant community structure in relation to grazing and environmental changes along a north-south transect in the Western Kalahari. *Vegetatio.* **68**, 3–18.

Skinner, J.D. & Chimimba, C.T. (2005). *The mammals of the Southern African subregion*. 3rd edn. Cape Town: Cambridge University Press.

Stander, P.E. (1998). Spoor counts as indices of large carnivore populations: the relationship between spoor frequency, sampling effort and true density. *J. Appl. Ecol.* **35**, 378–385.

Stephens, P.A., Zaumyslova, O.Y., Miquelle, D.G., Myslenkov, A.I. & Hayward, G.D. (2006). Estimating population density from indirect sign: track counts and the Formozov–Malyshev–Pereleshin formula. *Anim. Conserv.* **9**, 339–348.

Verlinden, A. (1998). Seasonal movement patterns of some ungulates in the Kalahari ecosystem of Botswana between 1990 and 1995. *Afr. J. Ecol.* **36**, 117–128.

Wallgren, M., Skarpe, C., Bergstrom, R., Danell, K., Bergstrom, A., Jakobsson, T., Karlsson, K. & Strand, T. (2009). Influence of land use on the abundance of wildlife and livestock in the Kalahari, Botswana. *J. Arid Environ.* **73**, 314–321.

Ward, R.M.P. & Krebs, C.J. (1985). Behavioural responses of lynx to declining snowshoe hare abundance. *Can. J. Zool.* **63**, 2817–2824.

Wearn, O.R., Rowcliffe, J.M., Carbone, C., Bernard, H. & Ewers, R.M. (2013). Assessing the status of wild felids in a highly-disturbed commercial forest reserve in Borneo and the implications for camera trap survey design. *PLoS ONE* **8**, e77598.

Western, D. (1992). The biodiversity crisis: a challenge for biology. *Oikos* **63**, 29–38.

Whittington, J., St. Clair, C.C. & Mercer, G. (2004). Path tortuosity and the permeability of roads and trails to wolf movement. *Ecol. Soc.* **9**, 4. http://www.ecologyandsociety.org/vol9/iss1/art4 (Accessed 18 July 2013).

Williamson, D.T., Williamson, J. & Ngwamotsoko, K.T. (1988). Wildebeest migration in the Kalahari. *Afr. J. Ecol.* **26**, 269–280.

Wilson, G. & Delahay, R.J. (2001). A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. *Wildl. Res.* **28**, 151–164.

Zalewski, A., Jedrzejewski, W. & Jedrzejewska, B. (2004). Mobility and home range use by pine martens (*Martes martes*) in a Polish primeval forest. *Ecoscience* **11**, 113–122.