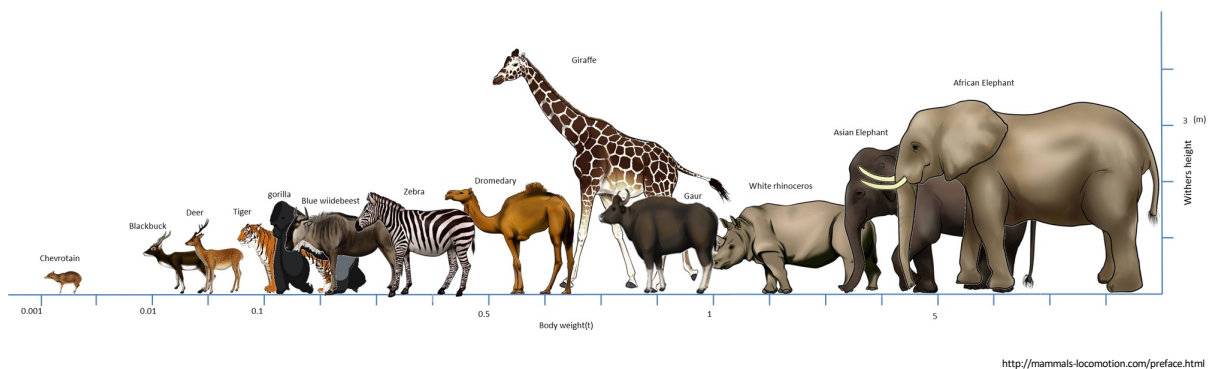


Correction of camera-trap capture rates for detection bias, based on body mass and diet



Thesis code: REG80436

Superevisors: Patrick Jansen, Chris Carbone

Wildlife Ecology and Conservation Group

The Msc report may not be copied in whole or in parts without the written permission of the author and the chair group



WAGENINGEN UR
For quality of life



university of
 groningen

Abstract

Background: Camera traps have become an important tool for estimating species abundance and density in medium- to large-sized mammals. However, though the camera trap rate should contain information about the density of a species, the probability of detection may differ between species hence may not reflect the relative abundance within communities. Given the physical and behavioral mechanisms causing this bias, it should be possible to rescale size and trophic-level traits in surveys to more reliably reflect the relative abundance of species within communities.

Aim: To create a simple method for assessing an unbiased estimate of relative abundance of species within mammal communities from camera-trap data.

Organisms: Mammals.

Methodology: The gas model was used to provide a theoretical basis to correct for size and trophic-level related biases in camera trap rates. Regression equations between three components of detectability – effective detection distance (EDD), speed and activity level, and body mass were used to estimate scaling relationships which were then combined to correct the camera trap rate. The camera trap rates before and after the correction was compared with independently estimated density for a number of mammal communities to see if the corrected capture rate improved the fit to the density data.

Principle findings: All three regression equations were significantly related to body mass providing scaling equations to estimate variation in detectability. Speed additionally varied with diet. These relationships were then used to correct for bias in camera trap rates to provide an unbiased relative abundance index, described here as a macro-corrected relative abundance index (mRAI). After the correction, the mRAI produced and more proportional fits to independent estimated density in herbivores, but not in faunivores. When verifying within different communities, the mRAI of species was better reflected in three out of five communities after the correction.

Conclusion: The correction model in this study made a better estimation of the relative abundance of the species within communities. However, the correction performed better in herbivores than in faunivores. Several improvements can be included in future work. It may be better to divide faunivores into separate carnivore and

omnivour diet groups. More factors that might affect the scaling relationships between body mass and related components can be considered.

1.Introduction

Biodiversity plays an essential role in modulating ecosystem function and stability, and provides multiple services for all life forms on the earth (Singh, 2002). Mammals in particular play an important role in regulating biodiversity. They have ecological functions such as regulating pest populations, providing seed dispersal and pollination, nutrient cycling, grazing and ecosystem engineering, and can therefore be used as indicators of ecosystem health (Lyons et al., 2019). They are the class most heavily influenced by anthropogenic pressures including hunting, poaching, blockage of migration routes by human constructions (Waltert et al., 2009; Berger, 2004). Therefore, conservation methods focused on mammals are instrumental to disentangling the challenges facing a whole ecosystem. Mammals are one of the best-studied classes (Lyons et al., 2019), resulting in their high availability of datasets on life history, abundance, geographic distribution, body size, and community composition. Yet, many questions remain to be answered about patterns of distribution and abundance especially for small-medium species living in the tropics (Berger, 2004; Brooke et al., 2014; Waltert et al., 2009).

Animal abundance estimates are essential to answer important questions in ecology and conservation biology (Gopalaswamy et al., 2012; Buckland et al., 2005). Therefore, abundance estimation is of fundamental value to biodiversity and is a pervasive metric used in ecology (Rowcliffe et al., 2011).

Camera trapping provides a feasible, non-invasive method for surveying mammal communities, and has been extensively used in wildlife and biodiversity research and conservation worldwide over the last two decades (Burton et al., 2015). It can be used not only in species that can be individually recognized (e.g. spotted or striped cats), but also the species without such characters (Rowcliffe et al., 2008). This technique can be used for the estimation of relative abundance, based on the relationship that the number of instances at which a species is photographed is positively correlated with that species' abundance in the mammal community (Meyer et al., 2015). A large amount of mammal trait data in the past ten years has been compiled (Faurby et al., 2018; Zhang, 2017), which provide a strong data foundation for the combination of their study and conservation with camera traps. However, though the number of photographs taken per unit time (trapping rate) should contain information about the density of a species (Rowcliffe et al., 2008), the application of trapping rates to estimate the relative abundance

of species within in the same community (Carbone et al., 2001; Silveira et al., 2003) is complicated by interspecific differences in detection probability (MacKenzie et al., 2002; Pollock et al., 2002).

Detection bias arises from a combination of technical and ecological factors. Nearly all camera traps use passive infrared sensors that detect heat in motion (Kolowski & Forrester, 2017). Animals passing in front of camera traps are thus more likely to be detected as they emit more heat. Larger animals emit more heat and are therefore detected at a greater distance than smaller animals. Moreover, larger animals have longer daily travel distances (Carbone et al., 2005), and are thus more likely to pass in front of camera traps. As an example, the Chevrotain and elephant are two species who have a major difference in their body size, also their day range and detection area, (Fig. 1). If the camera traps record 1 chevrotain and 1 elephant passing by during a certain period, and we assume that elephants walk 20 times as much and are detected 5 times as far as chevrotain, then the indices can translate the capture ratio of 1:1 into 100:1. In other words, chevrotains are supposed to be 100 times as common as elephants compared with the photograph ratio of 1:1. As a result, camera-trapping data are heavily biased among species and do not accurately reflect the relative abundance of species within communities.

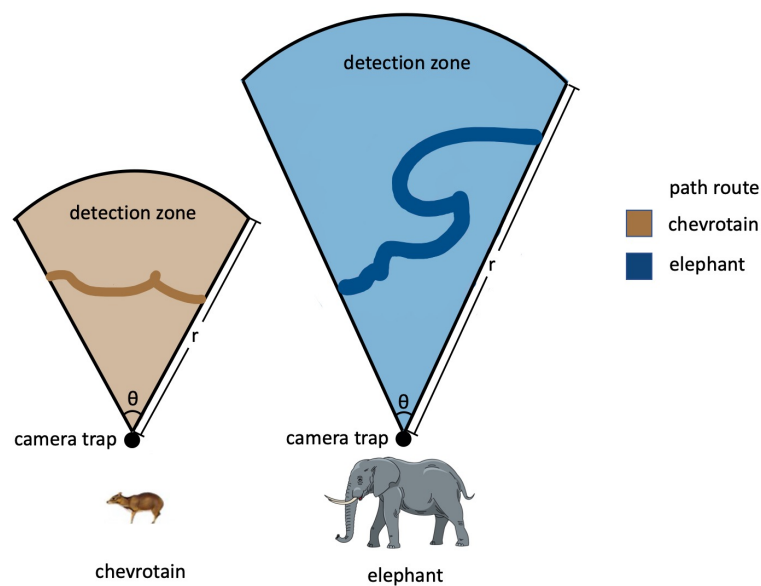


Fig. 1 Different detection zones and passing routes within the detection zone of animals with different body mass. θ refers to detection angle and r refers to detection radius.

Many traits including metabolic rate, heart rate (Peters, 1983), abundance (Damuth, 1981), vary with body mass by power equations (Damuth, 1981). In addition, some of the traits also affect indices of abundance in camera trapping records, which include day range, speed, and detection distance (Carbone et al., 2005; Hofmeester et al., 2017; Rowcliffe et al., 2016). Such patterns may be different among diets because the heat they emit can vary from different food types they take. Moreover, 2.66 times larger travel distance for a given body mass and group size compared with herbivores was found among faunivores (Carbone et al., 2005); Different exponent in scaling relationships in speed and day range (the product of speed and activity level) were found among faunivore and herbivore (Rowcliffe et al., 2016, Fig.2). Based on these findings, the scaling relationships between body mass and detectability by camera traps can differ among diets. Though a bunch of techniques including occupancy models (MacKenzie et al., 2002), population size models (Royle & Nichols, 2003; Stanley & Royle, 2005), and the Random Encounter Model (Rowcliffe et al., 2008) have been used to estimate animal abundance, but these bias corrections were not based on the body mass-related components that can be responsible to the detection probability.

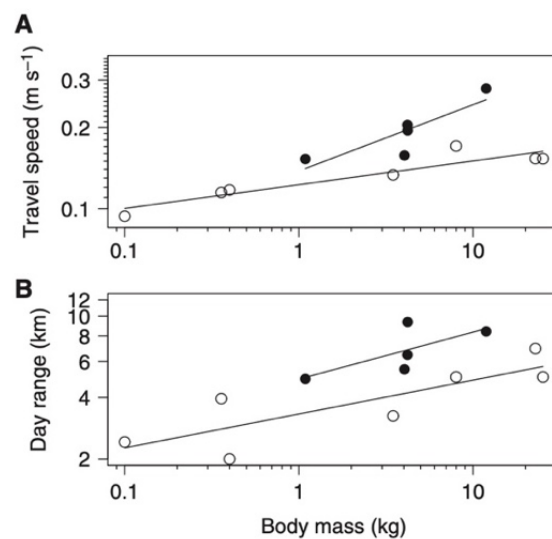


Figure 2. Average travel speeds (A) and day ranges (B) of some mammal species estimated from camera-trap image sequences, as a function of body mass and diet. Axes are log-transformed, and trend lines are fitted with the power functions of the form $y = cx^b$, for faunivores (solid points) and herbivores (open points) (Rowcliffe et al., 2016).

In theory, it should be possible to rescale camera trap capture rate to reflect the relative abundance within communities, through correction based on the scaling of detection distance and travel distance with body mass and diet. To my knowledge, no such correction has been developed.

The aim of this study was to create a simple method for estimating the relative abundance of species within mammal communities from camera-trap rates. A bias correction method for the capture rates in terrestrial camera trapping data was developed and tested. The gas model was used as the fundamental theoretical model, to assess how the camera trapping rate scales with body mass and diets to correct for the bias of the camera trapping rate to have a more robust estimate of relative abundance. I tested the following predictions: (1) Detection distance scales linearly with body mass within studies; (2) Movement speed scales linearly with body mass within studies; (3) Activity level scales linearly within studies. (4) The scaling relationships vary with diet. (5) Corrected camera trap rates of species reflect relative abundance within a community.

To test these predictions, I first estimate the scaling relationship between three body mass-related components of detectability and the body mass, which are EDD, activity level, and speed. The animals were separated into different groups according to their diets. Based on the existing data, I compared the ratio of the camera trap rate (CTR) before and after correction separately to the independent estimated density with 1:1 to test if the camera trap capture rate is getting proportional to the animal abundance and improve the reliability of the capture rate after the correction. Through this correction, the relative abundance of species of different communities can be compared to assess the structural health of the ecosystem of different communities, if the human activities is threatening the population size and give inspirations to the conservation methods and policies.

2. Methods

2.1 Approach

2.1.1 Data collection

I compiled two types of data from former related studies including published papers and theses. The first type included detection distance (m), speed (m/s), activity level (proportion), and body mass of some mammal species. The second type includes camera trap rates and density estimates for a number of mammal communities. All the body mass of the species are either from the studies themselves or from trait databases (Smith et al., 2003; Faurby et al., 2018). The majority of the dataset was supplied by Chris Carbone and Patrick Jansen with the supplement of related paper and theses. The other part was collected through searching the website of google scholar and web of science with the keywords including speed, activity level, EDD, body mass, animal abundance, animal density, and camera trap rate. Some of the data are from same species but different studies, or same studies but different

study years, or different study sites. If specific sites were not stated from the referred studies, then their study site in those studies are assumed to be consistent through all the collected data.

2.12 Fundamental theoretical model: gas model

Gas model was used as the fundamental theoretical model in this study. Biologists have more recently adapted the long-used gas model to describe the rate of contact, including between animal groups, between animals and observers, between sperm and eggs, etc (Rowcliffe et al., 2008). In gas model, the covered area of a particle, which refers to the product of its width and the total distance it moved in a given time can be used to imagine the basis of this two-dimensional ideal model. The ratio of the covered area is assumed to be the expected number of contact (Hutchinson & Waser, 2007). The number of contacts, y , of the moving animals is then easily defined as the product of animal speed (v), time (t), twice the radius of the detection zone (r) and the number of particles (N , i.e., animals) present, divided by area (A) (Hutchinson & Waser, 2007; Rowcliffe et al., 2008):

$$y = 2rtvD \quad \text{eqn 1}$$

N/A is then replaced by density (D). Based on this model, if using activity level and detection distance of the animals instead of time and detection zone, equation 1 can be adapted to:

$$\lambda = d*(sa)*n*C \quad \text{eqn2}$$

where the camera trapping rate (λ) is the product of detection distance (d), speed (s), activity level (a), animal abundance (n) and a constant (C).

2.13 Data Analysis

All the data was stored in Microsoft Office Excel (version 16.50). Exponential regressions were performed by log-transforming the continuous explanatory and response variables and then conducting linear models and linear mixed models using $lm()$ function or $lme()$ function from nlme package (Pinheiro et al., 2013; R Core Team, 2019). If the data were collected from multiple study sites, then site was added as a random effect in the model (Table 1). T test were conducted in R through $summary()$ function. In the t test, if the estimates of the exponents are applicable were decided by the difference of between two diets, instead of if the estimates were significantly

different from 0, which means that when using diet as a variable in the model, if the estimates between faunivore and herbivore were not close (>0.1), then separate exponents for faunivore and herbivore were applied; if the estimates were close (<0.1), the estimate without diet as a variable was applied. When verifying the exponents, instead of comparing the estimate with 0, the t test output showed the comparison of the estimate with 1 to have a close look at if the CTR is approaching density after the correction (Lenth, 1989). *plot* in R was used for data visualization.

Table 1. Models applied in this study. Continuous variables are log-transformed.

variables	models
speed & body mass	$\text{lme}(\text{speed} \sim \text{body mass} * \text{diet} + 1 \text{site})$
activity level & body mass	$\text{lme}(\text{activity level} \sim \text{body mass} + 1 \text{site})$
effective detection distance & body mass	$\text{lme}(\text{effective detection distance} \sim \text{body mass} + 1 \text{site})$
verification with the whole dataset	$\text{lme}(\text{density} \sim \text{CTR} + 1 \text{site})$
	$\text{lme}(\text{density} \sim \text{CTR} * \text{diet} + 1 \text{site})$
	$\text{lme}(\text{density} \sim \text{cCTR} + 1 \text{site})$
	$\text{lme}(\text{density} \sim \text{cCTR} * \text{diet} + 1 \text{site})$
calibration within communities	$\text{lm}(\text{relative density} \sim \text{relative CTR})$
	$\text{lm}(\text{relative density} \sim \text{relative cCTR})$

2.14 Study approach

Overall, to get the bias correction for the trapping rate, three steps were applied in this study. First, the scaling relationships between body mass and three related indices, which are detection distance, activity level, and speed were built to provide exponents to the gas model (Hutchinson & Waser, 2007) based on data collected from existing studies. To verify if the exponents from the scaling of the three components are reliable, they were tested with existing data to see if the fit between corrected trap rate and independent estimated density is approaching 1:1 both in all species, among different diets, and within different communities (Fig. 3). When illustrating the difference of the slope estimates, a dotted line with the slope of 1 was put on the plot. It came across the point whose x axis equals to the mean of the estimated density and y axis equals to the mean of the CTR before and after correction when their estimated density equals to the mean estimated density (Fig. 5 & Fig. 6).

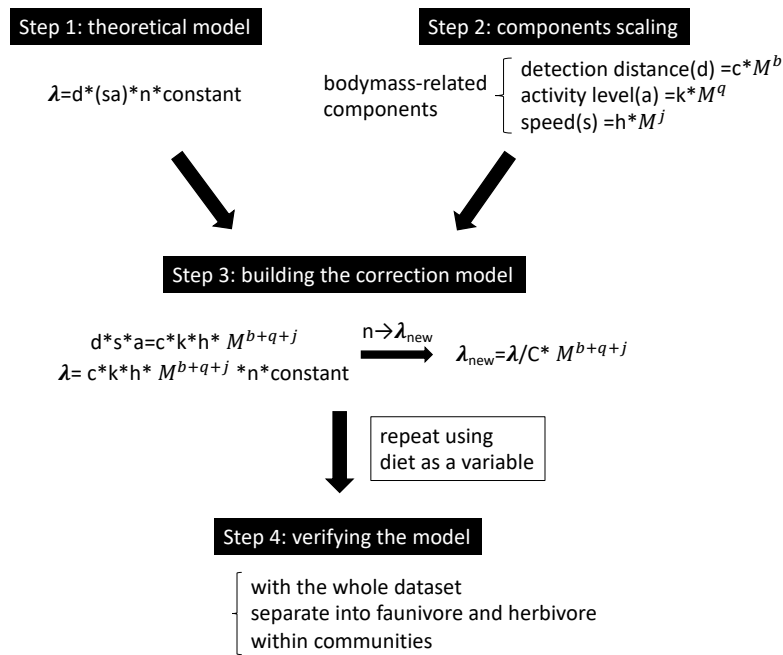


Figure 3. Flow graph of the study. In the equations, detection distance, activity level, and speed were abbreviated to d , a , and s . Lowercase c , k , and h are the constants of their separate relationships with body mass. λ refers to camera trapping rate.

2.2 Build a correction from scaling relationships

2.2.1 Scaling of detectability with body mass

Three components of animal detectability were considered in this study, which are the effective detection distance d (in m), speed s (in m/s), and activity level a (a proportion). EDD, the detection distance at which the number of animals detected further away equals the number of animals missed nearer by, reflects the sensitivity of the sensors to a certain species under certain environmental conditions (Hofmeester et al., 2017). Activity level is the proportion of time spent active. It provides a key metric to understand energetics, foraging effort and exposure to risk (Rowcliffe et al., 2014). Through the exponential models between speed, activity level, EDD and body mass, the exponents of which were acquired to get the scaling relationship between body mass, body mass related components, the camera trap rate and estimated density (eqn 3-5). Equation 2 was then adapted to equation 6 with the acquired exponents.

$$\begin{array}{l}
 s = k * M^q \longrightarrow q \quad \text{eqn3} \\
 a = h * M^j \longrightarrow j \quad \text{eqn4} \\
 d = c * M^b \longrightarrow b \quad \text{eqn5}
 \end{array}
 \left. \vphantom{\begin{array}{l} s \\ a \\ d \end{array}} \right\} \longrightarrow \lambda/n = C * M^{b+q+j} \quad \text{eqn6}$$

2.22 Building the correction

Camera trap rate, animal density, and body mass from former studies were applied when verifying the model. λ_{new} in equation 7 was adapted from n in equation 6. In equation 7, λ_{new} represents the corrected camera trap rate (the trap rate after correction from λ , cCTR hereafter).

$$\lambda_{\text{new}} = \lambda / C * M^{b+q+j} \quad \text{eqn7}$$

2.3 Verification of the correction model

I compared the fit between corrected trap rate (λ_{new}) and independent estimated density with 1:1 to see if it improved, which means, if the corrected CTR was getting more proportional to the estimated density than the original CTR. The model was verified in all species, among faunivores, and among herbivores.

The constant C in equation 7 was assumed to be affected by different environment (e.g. vegetation density) (Hofmeester et al., 2017). Based on the assumption that the constants vary among different sites (communities) and consistent within the same site (community), to erase the difference of the constants among communities, relative independent density estimation, relative corrected trap rate and relative density estimation within each community were calculated and compared. Data from communities with adequate number of species and observations were picked to compare the CTR between before and after calibration.

3. Results

3.1 The scaling of detectability

Movement speed, activity level and EDD all scaled linearly with body mass (LME; Table 2). The estimates of speed differed between herbivores and faunivores (Table 2), while activity level and EDD did not (Table 2). Thus,

the exponent q in equation 3 was estimated as 0.47 for faunivores and 0.32 for herbivores; b in equation 4 in was estimated as 0.06; j in equation 5 was estimated as 0.18 (Table 2; Fig. 4). Equation 7 can then be parametrized as:

$$\text{faunivore: } \lambda_{new} = \lambda/C * M^{0.56}$$

$$\text{herbivore: } \lambda_{new} = \lambda/C * M^{0.70}$$

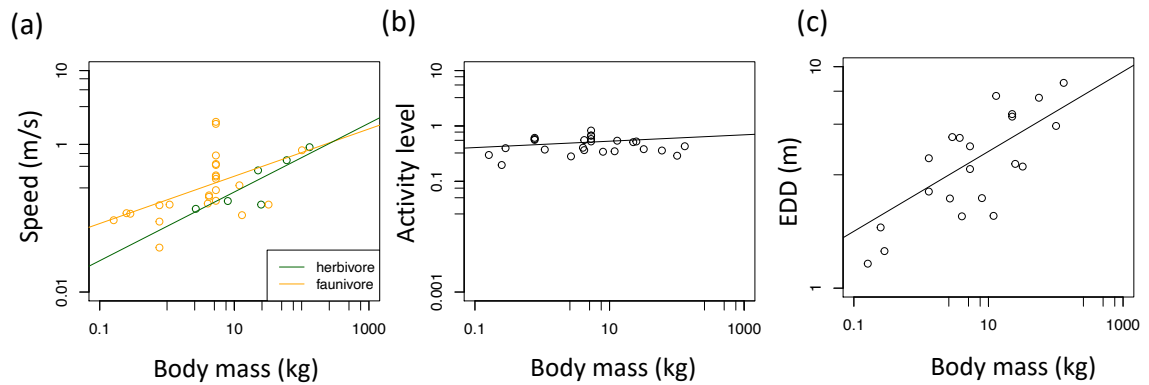


Figure 4. (a) Average travel speeds (m/s) as a function of body mass and diet of some mammal species. (b) Activity level (proportion) as a function of body mass and diet of some mammal species. (c) Effective detection distance (m) as a function of body mass and diet of some mammal species. Axes are log-transformed and trend lines are fitted with power functions of the form $y = cx^b$.

Table 2. Summary result of linear models and linear mixed models between body mass and three components with axes log-transformed and site as a random factor.

		Estimate	Std.Error	DF	t value	Pr(> t)
speed~body mass	body mass	0.2761	0.0921	21	2.9980	0.0069 **
speed~body mass*diet	faunivore	0.3204	0.1087	19	2.9471	0.0083 **
	faunivore : herbivore	0.1451	0.2738	19	0.5301	0.6022
activity level~body mass	body mass	0.0577	0.0335	17	1.7230	0.1030
activity level~body mass*diet	faunivore	0.0529	0.0361	15	1.4652	0.1635
	faunivore : herbivore	0.0936	0.0884	15	1.0584	0.3066
EDD~body mass	body mass	0.1803	0.0220	17	8.1847	<.0001***
EDD~body mass*diet	body mass	0.1496	0.0231	15	6.4731	<.0001***
	body mass : diet	0.0740	0.0507	15	1.4587	0.1653

3.2 Verification

When not separated into different diets, CTR scaled with density by a factor 0.71 to 0.70 before and after correction, respectively. The Pearson correlation coefficient between CTR and density increased from 0.46 to 0.66. When separating the dataset into herbivores and faunivores, correction increased the slope from 0.65 to 0.80 among faunivores and from 0.87 to 1.01 among herbivores. Less difference compared with the slope of 1 can be shown from the p value of the LME model after correction among herbivores, while significant difference from the slope of 1 can still be seen after the correction among faunivores (Table 3, Fig. 5). Correction increase the Pearson correlation coefficient from 0.34 to 0.75 among faunivores, and from 0.69 to 0.77 among herbivores.

When applied to individual communities, different degrees of a better fit of 1:1 were shown in 3 out of 5 communities. Exception were Kinnaird and O'Brien (2012) and Swanson (unpublished) (Fig. 6 & Table 4). Overall, CTR is approaching independent estimated density after the correction among herbivores, and within most of the communities.

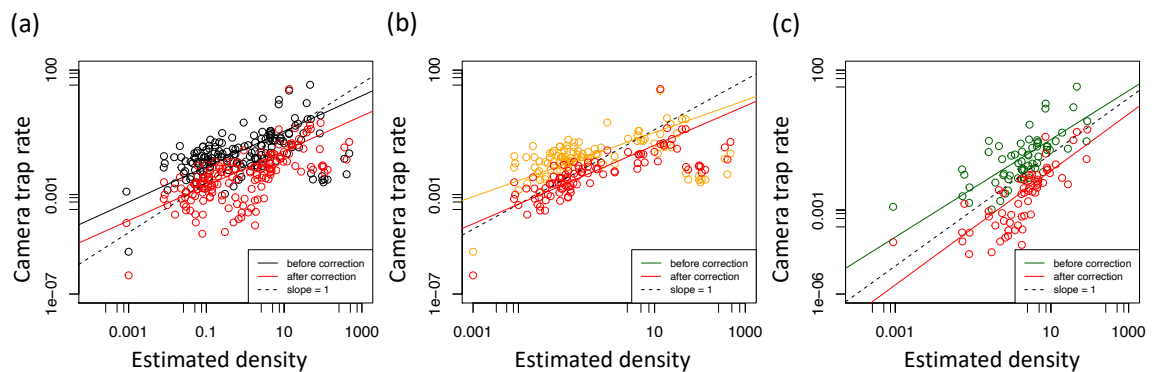


Figure 5. Scaling of camera trap rates of species with density estimates, before and after correction for detection bias based on body mass or body mass and diets (a) for all species; (b) for faunivores only; (c) for herbivores only. Black, orange, and green lines are regressions of from the data before correction. Red lines are regressions from the data after correction; Dotted lines are lines with slope = 1, plotted through the mean value of density and midpoint of the regression before and after correction when their x axis equal to the mean value of density.

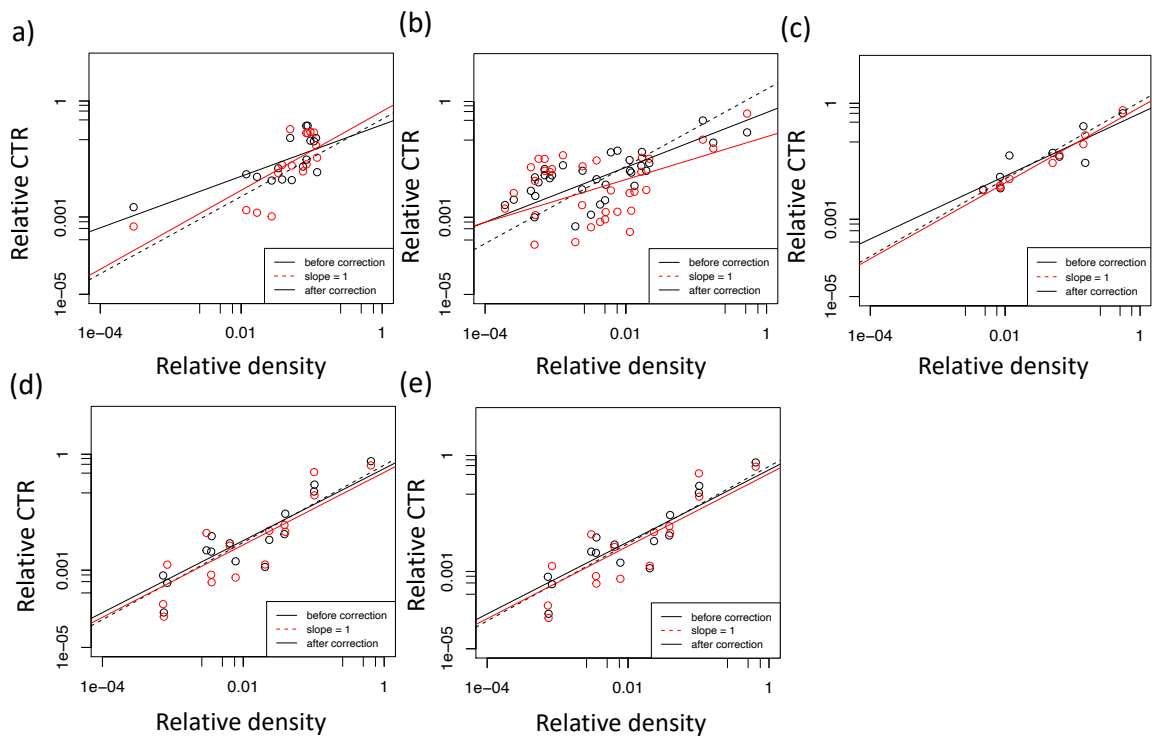


Figure 6. CTR before and after bias correction as a function of body mass or body mass and diets within 5 communities. Black lines are regressions of before correction. Red lines are regressions after correction; Dotted lines are lines with slope = 1, plotted through the mean value of density and midpoint of the regression before and after correction when their x axis equal to the mean value of density. (a) Data from O'Brien (2003); (b) Data from Kinnaird & O'Brien (2012); (c) Data from BCI team (unpublished); (d) Data from Swanson (unpublished); (e) Data from Wearn (2015).

Table 3. Summary result of linear model $CTR \sim \text{density} * \text{diet}$, $cCTR \sim \text{density} * \text{diet}$ with axes log-transformed and site as a random effect. The dataset include all species, herbivores, and faunivores before and after bias correction.

		Estimate	Std.Error	DF	t value	Pr(> t)
(compared with 1)						
all species	before correction	0.7122	0.0515	138	-5.5898	1.1730e-07 ***
	after correction	0.7010	0.0581	138	-5.2034	9.0640e-07 ***
herbivore	before correction	0.8717	0.0650	54	-1.9727	0.0537 .
	after correction	1.018	0.0800	54	-0.2267	0.8215
faunivore	before correction	0.6457	0.0795	77	-4.4560	2.7940e-05 ***
	after correction	0.7950	0.0703	77	-2.9172	0.0046 **

Table 4. Summary result of linear models CTR~density, cCTR~density with axes log-transformed. The dataset is from 5 separate communities.

		Estimate	Std.error	DF	t value	Pr(> t)	Adjusted-R ²
					(compared with 1)		
O'Brien et al., 2003	before	0.6665	0.1782	14	-1.8715	0.0823 .	0.4641
	after	1.0212	0.2339	14	0.0906	0.9291	0.5463
Kinnaird & O'brien, 2012	before	0.7103	0.1031	32	-2.8099	0.0084 **	0.5848
	after	0.5549	0.1532	32	-2.9054	0.0066 **	0.2686
BCI team, unpublished	before	0.8135	0.1761	7	-1.0591	0.3247	0.7176
	after	0.9808	0.0616	7	-0.3121	0.7641	0.9693
Swanson, unpublished	before	0.9321	0.1098	7	-0.6184	0.5462	0.8256
	after	0.9381	0.1413	7	-0.4381	0.6680	0.7418
Wearn, 2015	before	0.8004	0.2751	8	-0.7256	0.4888	0.4534
	after	0.9496	0.2374	8	-0.2123	0.8372	0.6251

4. Discussion

To create a more accurate method for mammal community composition estimation, I developed and tested a method for correcting the species-specific detection bias capture rates in terrestrial camera trap data. The gas model was used as the fundamental theoretical model to access how the camera trap rate scales with body mass and diet. I first estimated the scaling relationship between three body mass-related indices and the body mass to get the exponents in the gas model. After the correction, to verify if the correction made CTR proportional to the animal density, I compared the CTR before and after correction with the independent estimated density to the fit of 1:1 both with all species, in different diets, and within communities from different studies. I found that the CTR indeed got more proportional to independent estimated density in herbivores, but not in faunivores. Three out of five communities showed a better fit to 1:1 after the correction.

Several innovations can be found in this study. Not only gas model has been adapted and used to estimate the relative abundance of species that are not individually identifiable, but also this study built a bridge between different components of detectability and body mass to provide a simplified method for estimation of the relative

abundance of species within communities, which, to my knowledge, has not been addressed in the former studies. Both random encounter model and this study use gas model as the theoretical biological model, which enables the abundance estimation to include species that are not individually identifiable. However, in random encounter model, density of species was estimated, while in the correction in this study, relative abundance within communities was estimated.

To parametrize the correction, I used data from relevant published studies, several master theses, and a PhD thesis. Some of these studies see diet as a variable in the relationships between the index and body mass, while the others do not. In my study, diet was used as a predictor variable in scaling models of three components of detectability. When verifying the correction, the dataset was separated into groups according to their diets. The three components of detectability, speed, activity level, and EDD increased with the body mass when not using diet as a variable, however, different result can be shown in this study when adding diet as a variable, which leads to different correction model for different diets. Consistent with former studies, a positive correlation can be seen in the relationships between speed, activity level, EDD, and body mass in former studies (Rowcliffe et al., 2016; Rowcliffe et al., 2011; Hofmeester et al., 2017; Rowcliffe et al., 2014; Cid et al., 2020).

Different from Rowcliffe et al. (2016), who estimated an exponent between speed and body mass of 0.25 for faunivores and 0.09 for herbivores, the exponents for faunivores and herbivores in this study were 0.45 and 0.24, respectively. The difference may be due to a different number of observations (i.e. 30 in this study and 12 in Rowcliffe's study), but it might also lie in the environment. The speed of the same species can vary among different habitats with different vegetation density, which might require them to move with different speed to avoid predator and searching for food (Katzner et al., 2011; Marcus Rowcliffe et al., 2012). The reference of EDD is mainly from two studies, which are Rowcliffe's study in 2011, and Hofmeester's study in 2017 (Hofmeester et al., 2017; Marcus Rowcliffe et al., 2011). When using scaling model, the exponent from Rowcliffe's data is 0.16 and 0.21 from Hofmeester's data for all species, which are similar to the result in this study.

It has been shown in many former studies that larger animals have a longer activity time (Jarman, 1974; McNab, 1963; Ramesh et al., 2015; Rowcliffe et al., 2014), so is the result in this study. The exponent of the herbivore is 0.06 in this study, which is similar to the exponent with the scaling model from Rowcliffe et al. (2014). This result is also consistent with the assumptions that large herbivores spend more time searching for food due to their low-quality food and generalist nature and that large carnivores spend more time travelling over large home range

(Jarman, 1974; McNab, 1963; Weckerly, 2013). However, De Cuyper et al (2018) and Rizzuto et al. (2018) shared different opinions (De Cuyper et al., 2019; Rizzuto et al., 2018). In their studies, relationship between body mass and activity level or killing frequency can be negative when it comes to predators with bigger prey size, while the relationship between body mass and activity level for predators with smaller prey size remains to be positive. If the prey size for faunivores is a key point when testing the relationships between activity level and body mass, then the negative result in this study might be from majority of the prey size among faunivores in this study have a preference on preys with bigger size.

Compared with faunivores, the CTR of herbivores got more proportional to the density after the correction. Three explanations might be responsible for the poor fit in faunivores. First of all, different predators have different hunting strategies, i.e, ambush predators, that take prey by surprise from hide-outs, and pursuit predators that actively chase prey (Combes et al., 2013). Different strategies demand different energy, which might lead to different speed and active time of the species. Secondly, the result from Annelies's study in 2018 and Matteo's study in 2018 as has also been mentioned above indicate that the activity time of faunivores might not only lies in how big they are, but also how big they eat (De Cuyper et al., 2019; Rizzuto et al., 2018). Lastly, the diet in my study is grouped into faunivores and herbivores, while it is possible that some of the omnivores who feed mainly on vegetations are grouped into faunivores, which might cause the inaccurate exponents of the scaling models when using diet as a variable.

A closer fit of 1:1 can be shown among 3 out of 5 communities after the correction and 1 remains similar proportion which is close to 1:1 before and after the correction, which might indicate that the constants do vary in different environment and it can be necessary to make the CTR and density relative within communities to erase the effect of the constants. A better fit was not shown in from the data of Kinnaird and O'brien (2012). One possible explanation might be that there are 32 observations in this study, which might represent more than one community. It is also possible that a better correction can be shown if the dataset is separated into different diets.

In future studies, several aspects can be included to make the correction more accurate. First, to have a more accurate result, more data can be included, especially the data of omnivores to have a more concrete diet category; Second, take more factors that might affect the scaling relationships between the body mass and related components into account, especially among activity level and body mass (e.g. the body mass of the prey). Third, the environment, especially the vegetation density can be used as a variable to see how different environment are

affecting the scaling models and correction models. Finally, this correction model can be compared with density estimates for a larger number of communities.

5. References

- Berger, J. (2004). The last mile: How to sustain long-distance migration in mammals. *Conservation Biology*, 18(2), 320–331.
- Brooke, Z. M., Bielby, J., Nambiar, K., & Carbone, C. (2014). Correlates of Research Effort in Carnivores: Body Size, Range Size and Diet Matter. *PLoS ONE*, 9(4), e93195.
<https://doi.org/10.1371/journal.pone.0093195>
- Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., Bayne, E., & Boutin, S. (2015). REVIEW: Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, 52(3), 675–685. <https://doi.org/10.1111/1365-2664.12432>
- 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. J. L., ... Shahrudin, W. N. (2001). The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation*, 4(1), 75–79.
<https://doi.org/10.1017/S1367943001001081>
- Carbone, C., Cowlshaw, G., Isaac, N. J. B., & Rowcliffe, J. M. (2005). How Far Do Animals Go? Determinants of Day Range in Mammals. *The American Naturalist*, 165(2), 290–297. <https://doi.org/10.1086/426790>
- Cid, B., Carbone, C., Fernandez, F. A. S., Jansen, P. A., Rowcliffe, J. M., O'Brien, T., Akampurira, E., Bitariho, R., Espinosa, S., Gajapersad, K., Santos, T. M. R., Gonçalves, A. L. S., Kinnaird, M. F., Lima, M. G. M., Martin, E., Mugerwa, B., Rovero, F., Salvador, J., Santos, F., ... Oliveira-Santos, L. G. R. (2020). On the scaling of activity in tropical forest mammals. *Oikos*, 129(5), 668–676.
<https://doi.org/10.1111/oik.07022>
- Combes, S. A., Salcedo, M. K., Pandit, M. M., & Iwasaki, J. M. (2013). Capture Success and Efficiency of Dragonflies Pursuing Different Types of Prey. *Integrative and Comparative Biology*, 53(5), 787–798.
<https://doi.org/10.1093/icb/ict072>

- Damuth, J. (1981). Population density and body size in mammals. *Nature*, 290(5808), 699–700.
<https://doi.org/10.1038/290699a0>
- De Cuyper, A., Clauss, M., Carbone, C., Codron, D., Cools, A., Hesta, M., & Janssens, G. P. J. (2019). Predator size and prey size-gut capacity ratios determine kill frequency and carcass production in terrestrial carnivorous mammals. *Oikos*, 128(1), 13–22. <https://doi.org/10.1111/oik.05488>
- Faurby, S., Davis, M., Pedersen, R. Ø., Schowanek, S. D., Antonelli1, A., & Svenning, J. (2018). PHYLACINE 1.2: The Phylogenetic Atlas of Mammal Macroecology. *Ecology*, 99(11), 2626–2626.
<https://doi.org/10.1002/ecy.2443>
- Gopalaswamy, A. M., Royle, J. A., Delampady, M., Nichols, J. D., Karanth, K. U., & Macdonald, D. W. (2012). Density estimation in tiger populations: Combining information for strong inference. *Ecology*, 93(7), 1741–1751. <https://doi.org/10.1890/11-2110.1>
- Hofmeester, T. R., Rowcliffe, J. M., & Jansen, P. A. (2017). A simple method for estimating the effective detection distance of camera traps. *Remote Sensing in Ecology and Conservation*, 3(2), 81–89.
<https://doi.org/10.1002/rse2.25>
- Hutchinson, J. M. C., & Waser, P. M. (2007). Use, misuse and extensions of “ideal gas” models of animal encounter. *Biological Reviews*, 82(3), 335–359. <https://doi.org/10.1111/j.1469-185X.2007.00014.x>
- Jarman, P. J. (n.d.). *IN RELATION TO THEIR ECOLOGY*. 53.
- 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: Inaccurate estimation of cryptic population size. *Animal Conservation*, 14(4), 328–332. <https://doi.org/10.1111/j.1469-1795.2011.00444.x>
- Kinnaird, M. F. (2021). *Effects of Private-Land Use, Livestock Management, and Human Tolerance on Diversity, Distribution, and Abundance of Large African Mammals*. 15.
- Kolowski, J. M., & Forrester, T. D. (2017). Camera trap placement and the potential for bias due to trails and other features. *PLOS ONE*, 12(10), e0186679. <https://doi.org/10.1371/journal.pone.0186679>
- Lenth, R. V. (1989). Algorithm AS 243: Cumulative Distribution Function of the Non-Central t Distribution. *Applied Statistics*, 38(1), 185. <https://doi.org/10.2307/2347693>

- Lyons, S. K., Smith, F. A., & Ernest, S. K. M. (2019). Macroecological patterns of mammals across taxonomic, spatial, and temporal scales. *Journal of Mammalogy*, *100*(3), 1087–1104.
<https://doi.org/10.1093/jmammal/gyy171>
- MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Andrew Royle, J., & Langtimm, C. A. (2002). ESTIMATING SITE OCCUPANCY RATES WHEN DETECTION PROBABILITIES ARE LESS THAN ONE. *Ecology*, *83*(8), 2248–2255. [https://doi.org/10.1890/0012-9658\(2002\)083\[2248:ESORWD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2)
- Marcus Rowcliffe, J., Carbone, C., Jansen, P. A., Kays, R., & Kranstauber, B. (2011). Quantifying the sensitivity of camera traps: An adapted distance sampling approach: *Quantifying camera trap sensitivity. Methods in Ecology and Evolution*, *2*(5), 464–476. <https://doi.org/10.1111/j.2041-210X.2011.00094.x>
- Marcus Rowcliffe, J., Carbone, C., Kays, R., Kranstauber, B., & Jansen, P. A. (2012). Bias in estimating animal travel distance: The effect of sampling frequency: *Estimating animal travel distance. Methods in Ecology and Evolution*, *3*(4), 653–662. <https://doi.org/10.1111/j.2041-210X.2012.00197.x>
- McNab, B. K. (1963). Bioenergetics and the Determination of Home Range Size. *The American Naturalist*, *97*(894), 133–140. <https://doi.org/10.1086/282264>
- Meyer, N. F. V., Esser, H. J., Moreno, R., van Langevelde, F., Liefjing, Y., Ros Oller, D., Vogels, C. B. F., Carver, A. D., Nielsen, C. K., & Jansen, P. A. (2015). An assessment of the terrestrial mammal communities in forests of Central Panama, using camera-trap surveys. *Journal for Nature Conservation*, *26*, 28–35.
<https://doi.org/10.1016/j.jnc.2015.04.003>
- O'Brien, T. E., Ray, J. G., & Chan, W.-S. (2003). Maternal Body Mass Index and the Risk of Preeclampsia: A Systematic Overview: *Epidemiology*, *14*(3), 368–374.
<https://doi.org/10.1097/01.EDE.0000059921.71494.D1>
- Peters, R. H. (1983). *The ecological implications of body size*. Cambridge University Press.
- Pollock, K. H., Nichols, J. D., Simons, T. R., Farnsworth, G. L., Bailey, L. L., & Sauer, J. R. (2002). Large scale wildlife monitoring studies: Statistical methods for design and analysis. *Environmetrics*, *13*(2), 105–119. <https://doi.org/10.1002/env.514>
- Ramesh, T., Kalle, R., Sankar, K., & Qureshi, Q. (2015). Role of body size in activity budgets of mammals in the Western Ghats of India. *Journal of Tropical Ecology*, *31*(4), 315–323.
<https://doi.org/10.1017/S0266467415000188>

- Rizzuto, M., Carbone, C., & Pawar, S. (2018). Foraging constraints reverse the scaling of activity time in carnivores. *Nature Ecology & Evolution*, 2(2), 247–253. <https://doi.org/10.1038/s41559-017-0386-1>
- Rowcliffe, J. M., Field, J., Turvey, S. T., & Carbone, C. (2008). Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology*, 45(4), 1228–1236. <https://doi.org/10.1111/j.1365-2664.2008.01473.x>
- Rowcliffe, J. M., Jansen, P. A., Kays, R., Kranstauber, B., & Carbone, C. (2016). Wildlife speed cameras: Measuring animal travel speed and day range using camera traps. *Remote Sensing in Ecology and Conservation*, 2(2), 84–94. <https://doi.org/10.1002/rse2.17>
- Rowcliffe, J. M., Kays, R., Kranstauber, B., Carbone, C., & Jansen, P. A. (2014). Quantifying levels of animal activity using camera trap data. *Methods in Ecology and Evolution*, 5(11), 1170–1179. <https://doi.org/10.1111/2041-210X.12278>
- Royle, J. A., & Nichols, J. D. (2003). ESTIMATING ABUNDANCE FROM REPEATED PRESENCE–ABSENCE DATA OR POINT COUNTS. *Ecology*, 84(3), 777–790. [https://doi.org/10.1890/0012-9658\(2003\)084\[0777:EAFRPA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0777:EAFRPA]2.0.CO;2)
- Silveira, L., Jácomo, A. T. A., & Diniz-Filho, J. A. F. (2003). Camera trap, line transect census and track surveys: A comparative evaluation. *Biological Conservation*, 114(3), 351–355. [https://doi.org/10.1016/S0006-3207\(03\)00063-6](https://doi.org/10.1016/S0006-3207(03)00063-6)
- Singh, J. S. (2002). The biodiversity crisis: A multifaceted review. *Current Science*, 82(6), 638–647.
- Smith, F. A., Lyons, S. K., Ernest, S. K. M., Jones, K. E., Kaufman, D. M., Dayan, T., Marquet, P. A., Brown, J. H., & Haskell, J. P. (2003). BODY MASS OF LATE QUATERNARY MAMMALS: *Ecological Archives E084-094*. *Ecology*, 84(12), 3403–3403. <https://doi.org/10.1890/02-9003>
- Stanley, T. R., & Royle, J. A. (2005). ESTIMATING SITE OCCUPANCY AND ABUNDANCE USING INDIRECT DETECTION INDICES. *Journal of Wildlife Management*, 69(3), 874–883. [https://doi.org/10.2193/0022-541X\(2005\)069\[0874:ESOAAU\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2005)069[0874:ESOAAU]2.0.CO;2)
- Waltert, M., Meyer, B., & Kiffner, C. (2009). Habitat availability, hunting or poaching: What affects distribution and density of large mammals in western Tanzanian woodlands? *African Journal of Ecology*, 47(4), 737–746.
- Wearn, O. R. (n.d.). *Mammalian community responses to a gradient of land-use intensity on the island of Borneo*. 260.

- Weckerly, F. W. (2013). Conspecific body weight, food intake, and rumination time affect food processing and forage behavior. *Journal of Mammalogy*, 94(1), 120–126. <https://doi.org/10.1644/12-MAMM-A-066.1>
- Zhang, J. (2017). Biodiversity science and macroecology in the era of big data. *Biodiversity Science*, 25(4), 355. <https://doi.org/10.17520/biods.2017037>

