





RESEARCH ARTICLE

Predicting bushmeat biomass from species composition captured by camera traps: Implications for locally based wildlife monitoring

Shun Hongo¹  | Zeun's C. B. Dzefack² | Latar N. Vernyuy³ | Sosuke Minami^{4,5} |
Kaori Mizuno¹ | Ryoma Otsuka^{1,6,7}  | Yukiko Hiroshima¹ | Champlain Djiéto-Lordon³ |
Yoshihiro Nakashima⁸  | Hirokazu Yasuoka¹ 

¹The Center for African Area Studies, Kyoto University, Kyoto, Japan; ²Projet Coméca, Yaoundé, Cameroon; ³Faculty of Science, University of Yaoundé I, Yaoundé, Cameroon; ⁴Graduate School of Asian and African Area Studies, Kyoto University, Kyoto, Japan; ⁵Japan Society for the Promotion of Science (JSPS), Tokyo, Japan; ⁶Wildlife Research Center, Kyoto University, Kyoto, Japan; ⁷Graduate School of Information Science and Technology, Osaka University, Suita, Japan and ⁸Nihon University College of Bioresource Sciences, Fujisawa, Japan

Correspondence

Shun Hongo

Email: hongo.shun.8s@kyoto-u.ac.jp**Funding information**

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Handling Editor: Maria Paniw**Abstract**

1. Facing the bushmeat crisis, tropical forests require effective monitoring for sustainable wildlife management. To gain credibility with local people and conservation officials, the monitoring needs indicators that comply with local knowledge and predict the available faunal resources.
2. This study explores predictive indicators for bushmeat biomass—the total biomass of five main hunted mammals—in a Cameroonian rainforest. We employed camera trapping and the Random Encounter and Staying Time (REST) model to estimate the spatial variation in each species' population density and bushmeat biomass at three sites. We then calculated six indicators from camera-trap capture rate estimates and assessed their predictive performance for the total wild meat amount.
3. Duikers generally increased with distance from the public road, but two red duiker species were more markedly affected by the distance than blue duikers. Spatial density patterns of brush-tailed porcupines and Emin's pouched rats differed between sites. Consequently, bushmeat biomass displayed exponential growth away from the road with varying degrees among the sites.
4. Of the six indicators, the R/B ratio (red-to-blue duiker ratio) and the D/R ratio (duiker-to-rodent ratio) exhibited positive linear-like correlations to bushmeat biomass at all sites. The correlation lines were moderately similar across sites in the R/B ratio but largely different in the D/R ratio, suggesting that the latter is unsuitable for sharing information between neighbouring communities.
5. *Synthesis and applications.* The two indicators based on captured animal composition may effectively predict the total biomass of the main target species

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for bushmeat hunting, given a reasonably large sample size. The R/B ratio (red duikers/blue duikers) is recommended as a first choice; the D/R ratio (duikers/rodents) can be a good alternative when information sharing is not essential. Because local hunters are aware of depletion-related changes in species composition of caught animals, these indices may be effectively incorporated into community-based wildlife monitoring.

KEYWORDS

biomass indicator, community-based monitoring, duiker, population density, REST model, tropical rainforest, wild meat, wildlife management

1 | INTRODUCTION

Bushmeat hunting is a global concern for biodiversity and food security across tropical forests (Harrison et al., 2016; Nasi et al., 2011). Millions of rural people still need wild meat as an essential source of protein and income (Ingram et al., 2021). However, current hunting rates are unsustainable and pose severe threats to many mammal species, particularly in the Congo Basin (Cawthorn & Hoffman, 2015). This dilemma over bushmeat hunting has often led to conflicts between conservation officials and the local community: Strict legal restrictions on hunting are often seen as unrealistic and unacceptable by local people (Bennett et al., 2007; van Vliet, 2018).

Effective wildlife monitoring is essential for the sustainable management of bushmeat hunting (Stephenson, 2019). In African rainforests, scientist-led monitoring has long been central to wildlife management (White & Edwards, 2000). The recent spread of camera trapping is accelerating this trend (Agha et al., 2018)—this new technology can accurately estimate the absolute density of medium- to large-sized terrestrial mammals, at least theoretically (Burton et al., 2015). However, monitoring relying solely on highly-technical scientific methods is rarely sustainable due to the high costs and great labour in fieldwork and analysis (Glover-Kapfer et al., 2019). Furthermore, management decisions informed exclusively by scientific experts are often poorly understood and considered irrelevant by local people because of the lack of their involvement (Wheeler & Root-Bernstein, 2020). Thus, monitoring of this kind is less applicable to the local management of natural resources in the long run.

Locally based wildlife monitoring is a promising alternative to purely scientific monitoring (Beirne et al., 2019; Rist et al., 2010). Participation of local people can raise awareness of the wild meat issue and increase their capacity and accountability to address it (Milner-Gulland & Bennett, 2003). Management decisions are also more likely to be accepted by the community if their contributions are properly incorporated. Yet, the credibility of abundance indicators derived from harvest counts of locally based monitoring, such as Catch Per Unit Effort (CPUE), is often questioned because accurate measurement of hunting effort is highly challenging (Rist et al., 2008).

Researchers have attempted to address this problem with alternative indicators of hunting pressure based on studies of bushmeat hunting and trade. Some use species compositions of hunted animals

(van Vliet et al., 2018; Yasuoka et al., 2015); others combine the species compositions with other parameters (Fa et al., 2015; Ingram et al., 2015). These indicators are easily calculated solely from hunting results without measuring hunting effort. Moreover, a hunting self-monitoring study in the northern Republic of Congo demonstrated that two indicators (the blue duiker proportion and the mean body mass) correlated with hunting pressure and the CPUE of large mammals (Marrocoli et al., 2019).

A critical problem with the bushmeat indicators is that previous studies have only examined their predictability of hunting pressure—an abstract state variable difficult to measure directly. Ideally, wildlife monitoring should directly monitor the faunal abundance. But the relationship between hunting pressure and abundance is not always clear (Fukasawa et al., 2020). A severely hunted area may, for example, have fewer animals due to intense hunting (Scabin & Peres, 2021); however, this area may, conversely, harbour more animals and thus allow for intense hunting (Ueno et al., 2014). For effective locally based bushmeat monitoring, we need simple indicators that can be easily calculated by local people and that successfully predict the amount of available faunal resources, such as the total biomass of bushmeat targets.

This study examines the predictive performance of various indicators on the total biomass of main bushmeat species in a rainforest of southeast Cameroon. The local people here mainly hunt five terrestrial mammals using snare traps (Bobo et al., 2015; Yasuoka, 2014): Peters's duikers *Cephalophus callipygus*, bay duikers *C. dorsalis*, blue duikers *Philantomba monticola*, brush-tailed porcupines *Atherurus africanus*, and Emin's pouched rats *Cricetomys emini*. We first use camera traps to estimate the population densities of the five species and their spatial variations around three villages. Second, we estimate the spatial variations in the total biomass of the five species—hereafter *bushmeat biomass*—using the camera-trap density estimates and the mean body mass estimates from data on hunted animals. Third, we calculate six bushmeat indicators from estimations of camera-trap capture rates. Lastly, we examine how the indicators vary with bushmeat biomass to assess their predictive performance.

To assess the usefulness of the bushmeat indicators in locally based monitoring, we set three critical performance criteria:

1. *Simplicity*—the number of parameters required to calculate an indicator should be small to ease use by local people;

2. *Monotonic increase*—positive and monotonic correlation with bushmeat biomass is essential as a reliable indicator;
3. *Linearity*—an indicator should correlate with bushmeat biomass linearly (not exponentially or logarithmically). The constantly linear relationship facilitates predicting large changes in bushmeat biomass.

Additionally, satisfying the following two criteria will enhance an indicator's effectiveness:

1. *Generality*—the correlation trends should be similar across different sites to facilitate information sharing and management discussions among neighbouring communities;
2. *Precision*—the low uncertainty in the estimated relationships at a given sample size is preferable for the robust prediction.

2 | MATERIALS AND METHODS

This study complies with the laws of the Republic of Cameroon and received approval from the Ministry of Scientific Research and Innovation (MINRESI, N°0190/MINRESI/ProjetCOMECA/PM/07/2018) and the Ministry of Forestry and Wildlife (MINFOF, N°1527/L/MINFOF/SETAT/SG/DFAP/SDCF/SEP/EP).

2.1 | Study area

We conducted the study in and around the northern parts of Boumba-Bek and Nki National Parks in the East Region, Cameroon

(Figure 1). The study area consists primarily of evergreen and semi-deciduous forests. The only public road runs through the area from northeast to southwest, and about 2,000 people live in settlements distributed sparsely near the road. Most residents fall into two ethnic groups, Baka and Konabémbé, both involved in agriculture and natural resource use, including wildlife hunting.

This area is subject to a complex zoning regime, with permitted human activities varying from zone to zone. Wildlife hunting is prohibited in national parks but permitted in logging zones (designated as Forest Management Units) and agroforestry zones under some regulations. In reality, however, a certain level of hunting activity was also observed in national parks. Logging activity is also prohibited in national parks but practised in logging and agroforestry zones. Agriculture is permitted only in agroforestry zones.

2.2 | REST model

We used the Random Encounter and Staying Time (REST) model (Nakashima et al., 2018) to estimate the animal density. Assuming that animals are certainly filmed in a small predetermined detection area right in front of the camera, the REST model formulates the animal density in the detection area of camera i (A_i , in km^{-2}) as the following equation:

$$A_i = \hat{Y}_i \cdot \hat{T}_i / (s \cdot H_i \cdot I) \tag{1}$$

where \hat{Y}_i is the expected value of the number of animal passes in the detection area i , derived from the camera-trap data and a statistical

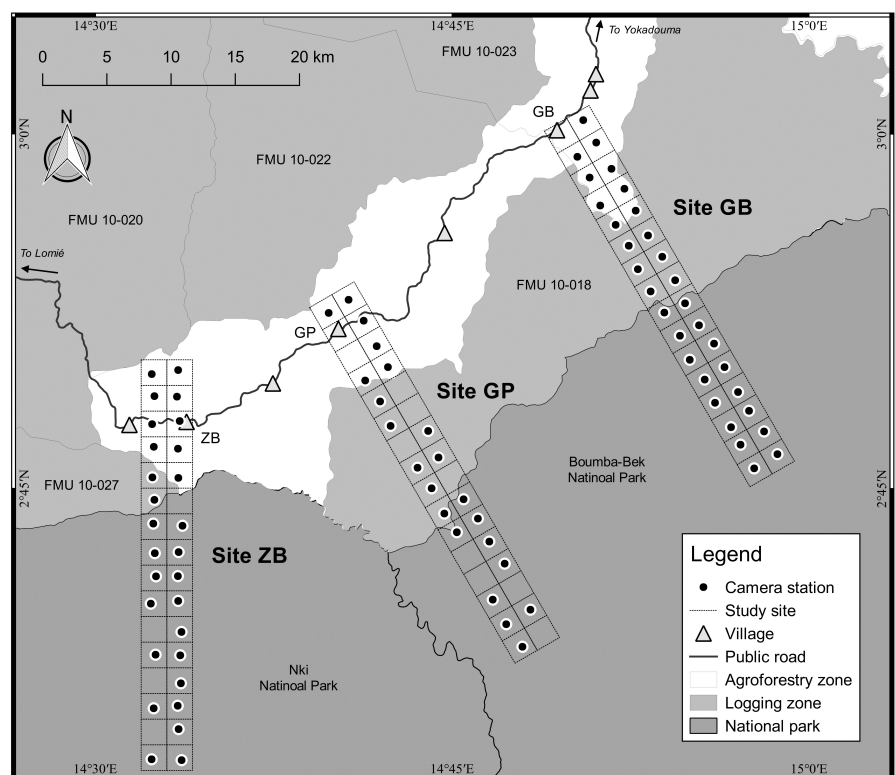


FIGURE 1 Map of the study area in Southeast Cameroon. Camera stations are shown only for those that provided valid data for at least 1 day.

model; \hat{T}_i is the expected value of the mean staying time (time spent in the detection area, in seconds), derived from the camera-trap data and a statistical model; s is the size of the detection area (in km^2); H_i is the operating time of camera i (in seconds) and l is activity level (average proportion of time an animal is actively moving in a day) (Rowcliffe et al., 2014). Palencia et al. (2021) tested the REST model in different habitats in Spain, including woodland, and demonstrated its good performance. Moreover, REST can incorporate habitat covariates and random effects into the linear predictors of staying time and density. Previous studies (Nakashima et al., 2020; Yokoyama et al., 2020) applied this approach to successfully estimate spatial density variations in forest ungulates, including duikers.

2.3 | Camera trap surveys and video analysis

We conducted camera trap surveys from September 2018 to February 2019, using Browning® Strike Force HD Pro (model BTC-5HDP; Prometheus Group). We conducted terrestrial and arboreal camera trapping concurrently (Hongo et al., 2020), but this study used only terrestrial camera data. The terrestrial cameras recorded videos of 20 s with a minimum interval of 1 s.

We set sampling sites around three villages: GB, GP and ZB (Figure 1). These villages differ in population size (around 770, 30 and 160 people, respectively; Toda, 2014) and distance from Yokadouma, the town with a bushmeat market nearest to the area (73, 102, and 118 km, respectively). We employed a stratified-random camera placement (Hongo & Yajima, 2022) with the procedure as below. First, we used QGIS version 2.16 (QGIS Development Team, 2021) to set up a rectangular grid of $4 \times 32 \text{ km}$ (128 km^2) at each site, extending from the village towards the national parks to cover the area used by local people (Figure 1). Second, we divided each site into 32 grid cells of $2 \times 2 \text{ km}$ and set a circle of a 250-m radius at each cell's centre. Lastly, we determined camera stations by generating a random point in each circle. Therefore, cameras kept a minimum distance of 1.5 km, larger than the home range diameters of the focal species (Kingdon et al., 2013), allowing us to avoid spatial pseudoreplication.

At each station, we decided on the exact station point using a handy GPS device and fixed a camera at the height of 40 cm, parallel to the ground. That is, stations were not intentionally placed on animal trails. The detection area was defined as an equilateral triangle with sides of 1.9 m (1.56 m^2), and the distance between the camera and the detection area's nearest vertex was set to 1.9 m (Figure S1). We cleared undergrowth in and around this small triangle. We used no baits. This station design has been tested in an outdoor environment in Japan using a 3.0-kg plastic bottle filled with 37°C hot water to ensure that it is certainly detected in the area. Our estimations made in the study area nonetheless suggested that the detection was not perfect with this station layout (Nakashima et al., 2022); however, we assumed that the degree of the density underestimation had little impact on this study's objectives because the detection probabilities were very high (0.87–0.97) and similar across all the focal species (Nakashima et al., 2022).

We aimed to place cameras at all 96 stations but could not do so at eight stations at Site GP for logistical reasons. This resulted in 88 deployed stations, with cameras in place for a mean of $40.0 \pm SD 7.3$ days. Of these, 81 stations provided valid data for at least 1 day (Figure 1). These valid cameras were operational for a mean of $33.3 \pm SD 8.4$ days (range: 4–54) and 2,700 camera days in total, obtaining 11,301 videos. Table S1 provides detailed descriptive statistics of the camera surveys per site.

We used Timelapse (Greenberg et al., 2019) to analyse the videos. First, we discarded the data recorded on the days of installation, retrieval and failure of cameras to avoid potential bias due to human presence and camera failure. We then identified animal species in the videos referring to Kingdon et al. (2013) and counted the number of passes per camera and species. Lastly, we quantified the time of day and the staying time for each pass.

2.4 | Statistical analysis

We performed statistical analyses using R ver. 4.1.0 (R Core Team, 2021) and RStudio version 1.4.1106 (RStudio Team, 2021). All models were constructed in a Bayesian framework written in Stan language (Stan Development Team, 2021) using CmdStan ver. 2.26.1 via the *cmdstanr* ver. 0.4.0 (Gabry & Češnovar, 2021).

For all models, we obtained 10,000 samples from the posterior distribution using an MCMC sampling method with four chains, 500 warmups, and uniform prior distributions for covariate parameters (see Supplementary Results S1–S4 for detailed MCMC settings and model results). We checked the model estimates applying the Gelman-Rubin convergence diagnostics (Gelman & Rubin, 1992)— \hat{R} hat (<1.01) and the effective sample size ($>20\%$)—as well as visual inspections of posterior distributions. We then compared all candidate models using the widely applicable information criteria (WAIC; Watanabe, 2010) to select a single optimal model. Marginal-level WAIC (Millar, 2018) was used for random effect models.

2.5 | Spatial variation in population density

To examine spatial variations in staying time and density of the five bushmeat species, we considered three habitat covariates: sites, zones and the distance from the public road. Site category variables (GB, GP [control] and ZB) were predetermined for each camera station. Zone category variables (agroforestry zone [control], logging zone, and national park) were obtained from the Forest Atlas of Cameroon (MINFOF & World Resources Institute, 2017). Note that we manually labelled the logging zone FMU 10-027 as a 'national park' because this zone had not yet experienced any logging activity during the surveys. Distance from each station to the nearest road was measured using QGIS.

We followed three steps to estimate the density per species (sample sizes are listed in Table S2). First, we estimated activity levels from the time-of-day data using the *fitact* function of the *activity*

ver. 1.3.1 (Rowcliffe, 2021). Following Nakashima et al. (2018), the estimated activity level was used as a constant in the REST model.

Second, we determined the best combination of probability distribution and covariates in predicting the staying time. The staying time where the animal reacted to cameras was excluded. We used an exponential, gamma, lognormal or Weibull distribution to account for the staying time variation. The linear predictor could include the five variables: the three habitat covariates, the interaction between the site and the distance-from-road covariates, and a station-specific random effect. We constructed models with all possible combinations of probability distributions and linear predictor components. However, we did not simultaneously include the zone and distance covariates in a given model because of their strong correlation ($r^2 > 0.8$). For bay duikers with a small sample size ($N = 21$), we considered only the distance covariate and the random effect: Coefficients for the site and zone covariates—both three-level categorical variables—were difficult to estimate accurately because each level had only a few data points.

Lastly, we estimated the density variation with the REST model using the optimal staying time model structure. For Peters's duikers, we excluded beforehand two large outlier points, where the numbers of passes (27 and 40) were >30 times larger than the mean number in the other 79 stations (0.78 passes, range: 0–7). We used a negative binomial distribution to account for the variation in the number of passes. The linear predictor of the density could include the three habitat covariates and the site–distance interaction.

2.6 | Mean body mass

We estimated the mean adult body mass of the four species except for Emin's pouched rats using the records of hunted animals in the study area (Yasuoka, 2006). We constructed two models with normal or lognormal distribution (without covariates) for each species. For

Emin's pouched rats, a fixed value of 1.0 kg was used (Duplantier & Granjon, 2013).

2.7 | Bushmeat biomass

We formulated bushmeat biomass (kg/km^2) at a point i as:

$$\text{Bushmeat biomass}_i = \sum_{k=1}^5 (M_k \times A_{ik}) \quad (2)$$

where M_k (kg) is the mean body mass of k th species, and A_{ik} (km^{-2}) is the density of the k th species at the point i . We estimated spatial variations in bushmeat biomass using the optimal density and mean body mass models. We first generated 10,000 MCMC samples of predicted density at every kilometre point from the road per site using the optimal REST model and then obtained the posterior distribution of the biomass for each point using the MCMC samples of density and mean body mass.

2.8 | Bushmeat indicators

We calculated six candidate indicators on the basis of camera-trap capture rates (Table 1). All but the mean body mass indicator were reciprocally transformed from the originals, expecting them to positively correlate with bushmeat biomass. Similarly to the density modelling, we assumed that the number of passes (offset by the camera operating days) followed a negative binomial distribution and considered that the linear predictor could include the three habitat covariates and the site–distance interaction.

After determining the optimal capture-rate models, we generated 10,000 MCMC samples of predicted values at every kilometre point from the road per site. Then, the posterior distributions of the indicators for each point were obtained from the MCMC samples.

TABLE 1 Candidate indicators examined for their performance in predicting bushmeat biomass

Indicator	Definition	Formula in this study at the point i^a	References
R/B ratio	The capture ratio of red (Peters's and bay) duikers to blue duikers	$\frac{CR_i \text{ Peters's duiker} + CR_i \text{ bay duiker}}{CR_i \text{ blue duiker}}$	Yasuoka et al. (2015)
Red proportion	The capture proportion of red duikers among all duikers	$\frac{CR_i \text{ Peters's duiker} + CR_i \text{ bay duiker}}{CR_i \text{ blue duiker} + CR_i \text{ Peters's duiker} + CR_i \text{ bay duiker}}$	Yasuoka et al. (2015); Marrocoli et al. (2019)
D/R ratio	The capture ratio of duikers to rodents	$\frac{CR_i \text{ blue duiker} + CR_i \text{ Peters's duiker} + CR_i \text{ bay duiker}}{CR_i \text{ porcupine} + CR_i \text{ pouched rat}}$	Rowcliffe et al. (2003); van Vliet et al. (2018)
Duiker proportion	The capture proportion of duikers among duikers and rodents	$\frac{CR_i \text{ blue duiker} + CR_i \text{ Peters's duiker} + CR_i \text{ bay duiker}}{\sum_{k=1}^5 CR_{ik}}$	Rowcliffe et al. (2003); van Vliet et al. (2018)
Mean body mass	The mean body mass of captured animals	$\frac{\sum_{k=1}^5 (M_k \times CR_{ik})}{\sum_{k=1}^5 CR_{ik}}$	Ingram et al. (2015); Marrocoli et al. (2019)
Reciprocal mean-rmax	The inverse of the mean of the intrinsic rate of natural increase (r_{max}) among captured animals	$\frac{\sum_{k=1}^5 CR_{ik}}{\sum_{k=1}^5 (r_{\text{max}k} \times CR_{ik})}$	Fa et al. (2015); Marrocoli et al. (2019)

^a CR_{ik} , the camera-trap capture rate (the number of animal passes per 30 days) of the k th species at a point i ; M_k , the mean body mass of the k th species; $r_{\text{max}k}$, the r_{max} value of the k th species taken from Fa et al. (2015).

2.9 | Predictive performance of the indicators

To assess the indicators' predictive performance, we quantitatively evaluated the five criteria (Table 2). For the monotonic increase and the linearity, we calculated representative values per site from the posterior medians, and the probability that the value is positive ($Pr > 0$) was estimated from the 10,000 MCMC samples of bushmeat biomass and indicators. For the generality and precision criteria, we obtained representative values from the posterior medians and 95% credible intervals from the MCMC samples. Note that the slope CQV values (the quantitative measure of the precision) tend to be large because the MCMC samples of biomass and indicators were generated independently of each other.

3 | RESULTS

3.1 | Spatial variation in population density of bushmeat species

Activity level estimates were similar across the five species (Peters's duikers, 0.376; bay duikers, 0.354; blue duikers, 0.379; brush-tailed porcupines, 0.371; Emin's pouched rats, 0.422). Peters's and blue duikers were diurnal and showed bimodal patterns; bay duikers, porcupines and pouched rats were strictly nocturnal (Figure S2).

Optimal model structures for the staying time differed between the species (Table S3). The optimal REST models (Table 3) also rendered different spatial density patterns across species (Figure 2). Red (Peters's and bay) duikers increased exponentially with distance from the public road and were less abundant at Site GB than at the other sites (Figure 2a,b). By contrast, the increase in blue duiker

density with the distance was more linear and identical across sites (Figure 2c). For the two rodents, the direction of distance covariate effects differed among sites (Figure 2d,e). Both species slightly increased away from the road at Site GB but decreased at Site ZB. Table S4 presents the predicted densities at 2, 10 and 25 km from the road for each site.

3.2 | Mean body mass

We measured the adult body mass of 122 animals of the four species and estimated their mean body masses: Peters's duikers ($N = 61$), posterior median [95% CI] = 16.3 [15.7–16.9] kg; bay duiker (35), 16.3 [14.8–17.8] kg; blue duikers (20), 4.5 [4.2–4.8]; brush-tailed porcupine (5), 2.8 [1.8–3.8] kg.

3.3 | Bushmeat biomass

Bushmeat biomass displayed an exponential rise with distance from the road and a marked difference across sites, with Site GB being much lower than the other sites (Figure 2f).

3.4 | Predictive performance of bushmeat indicators

Camera-trap capture rates of the five species varied spatially (Figure S3), and thus so did the six candidate indicators (Figure S4). But their relationships with bushmeat biomass differed from each other. Our quantitative assessment (Table 4) demonstrated that all

TABLE 2 Criteria for assessing the predictive performance of bushmeat indicators and their quantitative indices

Criterion	Quantitative measure	Description
Simplicity	Number of parameters used in the indicator	<ul style="list-style-type: none"> For example, the mean body mass uses capture rates and body mass of all five species ($N = 10$) A smaller number indicates that the indicator is simpler
Monotonic increase	Pearson's correlation coefficient (Pearson's r)	<ul style="list-style-type: none"> Bushmeat biomass was taken on the x-axis and indicators on the y-axis A value closer to 1.0 means that the correlation is closer to a straight line
Linearity	Linearity index ^a = $\left(r_{linear} - r_{logarithmic} \right) \times 100$	<ul style="list-style-type: none"> The index is positively and negatively larger if the correlation is more linear and logarithmic, respectively
Generality	Coefficient of variation (CV) of the regression slopes among the three sites	<ul style="list-style-type: none"> Linear regression was performed with the intercept fixed to the theoretical minimum^b A smaller CV value indicates that the relationships are more similar across sites
Precision	Coefficient of quartile variation (CQV) = $(Q_3 - Q_1) / (Q_3 + Q_1) \times 100$	<ul style="list-style-type: none"> CQV of the regression slopes among the 10,000 MCMC samples was calculated per site A smaller CQV value means that the estimated relationship is more precise

^a r_{linear} : Pearson's r of the indicator with the biomass; $r_{logarithmic}$: Pearson's r of the indicator with log-transformed biomass.

^bR/B ratio, Red proportion, Duiker proportion, 0.0; Mean body mass, 1.0 (the body mass of the pouched rat); Reciprocal mean-rmax, 1.4 (inverse of the pouched rat's r_{max} value).

TABLE 3 Structure and parameter estimates of density covariates in the REST models for main bushmeat species in Southeast Cameroon. Models with Δ WAIC less than 2.0 are displayed

Species	WAIC (Δ WAIC)	Posterior median (95% CI)					
		Intercept	Site (GB)	Site (ZB)	Distance from the road	Site (GB) \times Distance	Site (ZB) \times Distance
Peters's duiker	820.9 (0.0)	-1.40 (-3.16 to 0.17)	-1.98 (-3.57 to -0.59)	0.51 (-0.79 to 1.88)	0.17 (0.10 to 0.25)	x	x
Bay duiker	217.7 (0.0)	-1.08 (-2.89 to 0.46)	-2.01 (-3.94 to -0.48)	0.05 (-1.28 to 1.25)	0.11 (0.05 to 0.21)	x	x
Blue duiker	1,814.7 (0.0)	2.21 (1.54 to 2.95)	x	x	0.03 (-0.01 to 0.08)	x	x
	1,815.0 (0.3)	2.72 (2.36 to 3.09)	x	x	x	x	x
	1,816.2 (1.5)	2.41 (1.55 to 3.33)	-0.79 (-1.79 to 0.18)	-0.27 (-1.19 to 0.64)	0.05 (0.00 to 0.09)	x	x
Brush-tailed porcupine	589.2 (0.0)	-0.37 (-2.42 to 1.46)	0.63 (-1.58 to 3.04)	2.25 (0.12 to 4.65)	0.10 (0.00 to 0.22)	-0.03 (-0.17 to 0.09)	-0.22 (-0.39 to -0.07)
	590.3 (1.1)	1.21 (0.62 to 1.88)	x	x	x	x	x
Emin's pouched rat	2,173.8 (0.0)	2.75 (1.86 to 3.80)	-1.08 (-2.50 to 0.35)	1.07 (-0.23 to 2.38)	-0.06 (-0.13 to 0.00)	0.08 (-0.01 to 0.17)	-0.06 (-0.17 to 0.04)

Notes: 'x' marks: the model did not include the variable. 'Site \times Distance': the interaction between the site and the distance-from-road covariate.

indicators met the monotonic increase criterion with certainty at all sites. By contrast, the linearity index showed that the indicators increased more or less logarithmically with increased biomass (Figure 3). Nevertheless, the R/B and D/R ratios had larger linearity index values. Conversely, the other indicators reliably exhibited logarithmic relationships at least for one site, with smaller indicator changes as the biomass increased.

For the generality across sites, the red proportion and the mean body mass indicators marked the smallest CV values of regression slopes (Table 4). Contrarily, the correlation slopes in the D/R ratio were markedly different between Site ZB and the other sites (Figure 3c). Regarding the precision criterion, the indicators with logarithmic relationships tended to have lower uncertainties than those exhibiting linear relationships (Figure 4).

4 | DISCUSSION

Locally based monitoring is a promising approach to sustainable wildlife management in tropical forests, but the monitoring needs effective bushmeat indicators. We used camera traps to estimate the spatial variation in the population density of main bushmeat targets and their total biomass in a Cameroonian rainforest. Subsequently, we calculated six candidate indicators from camera-trap capture rates and assessed their predictive performance for the biomass. The results demonstrated that all indicators rose monotonically with increasing biomass. The R/B ratio and the D/R ratio also possessed linear-like relationships with the biomass, although their precision was relatively low, and the latter had low generality between the sites.

4.1 | Species-specific patterns of spatial density variation

Our camera trapping and REST model revealed marked differences in the spatial density patterns between species and sites (Figure 3). The trends of duiker densities varied considerably between red and blue duikers: Blue duikers exhibited a weaker effect of distance from the public road than red duikers and no site differences (Figure 3a-c). Blue duikers are more reproductive and less selective in habitat use and diets (Hart & Kingdon, 2013), suggesting their higher resilience to hunting and disturbances than red duikers (Akomo-Okoue et al., 2015; Lwanga, 2006).

Densities of the two rodents exhibited different patterns between sites (Figure 3d,e). At the remotest Site ZB, the rodents were more abundant near human settlements, consistent with other studies (Koerner et al., 2017; Lhoest et al., 2020). However, the trends were inverse at the most populated Site GB. Compared to the other villages, local hunters in the GB village capture rodents much more frequently (Bobo et al., 2015), perhaps due to the depletion of red duikers. This may have led to even rodents beginning to deplete near the village.

Altogether, wildlife managers should consider species-specific differences in spatial density patterns when making their plans. Further research needs to clarify the ecological factors underlying these variations.

Our density estimates generally showed large 95% credible intervals (Figure 2). This problem will be overcome by refining the study design and the estimation model. First, the spatial heterogeneity of animal densities in our broad study area (c. 380 km²) was

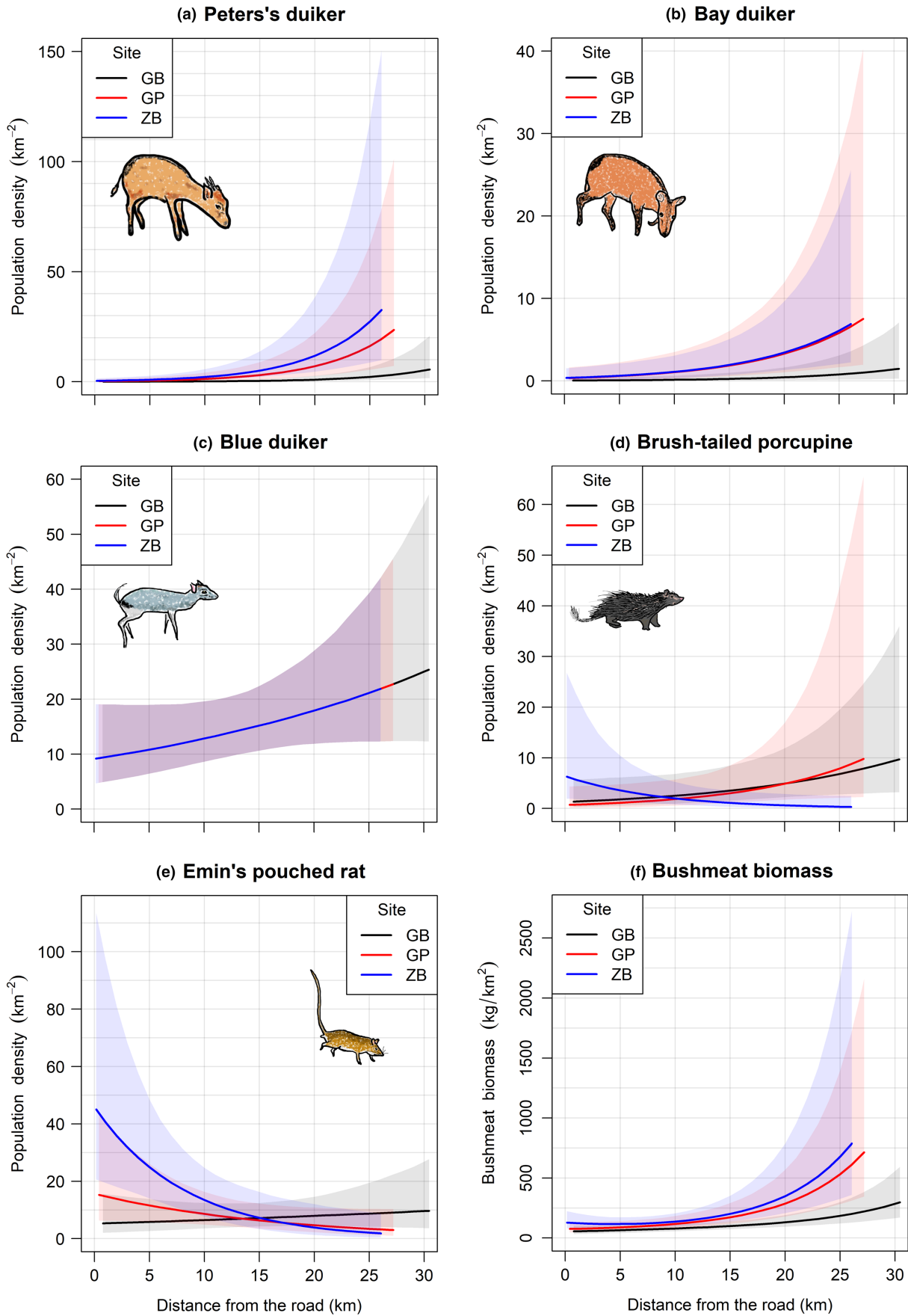


FIGURE 2 Spatial variation in the population density of main bushmeat species (a–e) and the total bushmeat biomass (f) in a rainforest of Southeast Cameroon. Solid curves and shades represent the posterior median estimates and 95% credible intervals, respectively.

TABLE 4 Assessment of the predictive performance of bushmeat indicators on bushmeat biomass. Desirable and undesirable values are bold and italic, respectively (monotonic increase and linearity); the lowest and the second-lowest values are underlined (simplicity, generality and precision)

Indicator	Site	Simplicity	Monotonic increase	Linearity	Generality	Precision
		Num. Of parameters	Pearson's <i>r</i> (Pr [>0])	Linearity index (Pr [>0])	Slope CV among sites (95% CI)	Slope CQV among MCMC samples
R/B ratio	GB	<u>3</u>	1.00 (97.4%)	1.3 (65.6%)	24.4	35.5
	GP		0.99 (98.0%)	-0.6 (46.5%)	(9.8–107.9)	44.3
	ZB		0.98 (98.2%)	-1.9 (32.1%)		43.3
Red proportion	GB	<u>3</u>	0.99 (97.4%)	-0.1 (48.6%)	<u>16.8</u>	30.0
	GP		0.99 (98.0%)	-3.3 (15.8%)	(<u>7.2</u> –89.2)	36.6
	ZB		0.98 (98.2%)	-5.1 (3.2%)		33.9
D/R ratio	GB	5	0.99 (99.4%)	-0.4 (47.5%)	119.1	27.8
	GP		0.98 (99.6%)	-1.5 (39.4%)	(41.9–157.6)	40.1
	ZB		0.99 (100.0%)	6.7 (99.7%)		45.4
Duiker proportion	GB	5	0.95 (99.3%)	-4.3 (4.6%)	18.3	<u>19.5</u>
	GP		0.87 (99.6%)	-10.5 (0.4%)	(5.4–78.6)	<u>27.1</u>
	ZB		0.79 (100.0%)	-11.2 (0.4%)		<u>26.6</u>
Mean body mass	GB	10	0.98 (100.0%)	-2.0 (27.9%)	<u>15.9</u>	<u>18.7</u>
	GP		0.93 (100.0%)	-6.4 (3.4%)	(<u>5.6</u> –72.1)	<u>28.2</u>
	ZB		0.89 (100.0%)	-7.7 (0.5%)		28.3
Reciprocal mean-rmax	GB	10	0.98 (96.9%)	-2.0 (26.2%)	17.7	26.7
	GP		0.91 (98.5%)	-8.1 (2.5%)	(6.3–76.9)	29.3
	ZB		0.85 (100.0%)	-9.4 (0.4%)		<u>26.2</u>

Note: Pr (>0), the probability that the value is positive; 95% CI, 95% credible intervals.

possibly too large to precisely estimate with only 81 camera traps. The estimation precision of the REST model depends strongly on the number of camera stations (Nakashima et al., 2018), and more intensive camera trapping is necessary for finer examinations. Second, the REST model is not recommended for scarce animals as it discards many detections outside small, predetermined focal areas (Palencia et al., 2021). Our Peters's and bay duikers were scarce near the road, and brush-tailed porcupines were generally less abundant (Figure 2), possibly inducing low precision in our estimates. The camera trap distance sampling (CTDS, Howe et al., 2017), which uses almost all detections, was probably more suitable for these species. However, this model did not suit our objectives because its current formula cannot incorporate habitat covariates. Further extensions to explain spatial variations, such as REST, are indispensable for alternative models to be used for large-scale camera trap studies.

Another issue in our camera trap density estimation was that, despite careful testing in an outside environment, the detection probabilities of our focal species did not reach 100% in the field (Nakashima et al., 2022; see also Methods). Although they were very high (87%–97%), the imperfect detections violate an assumption of the REST model, and the densities may have been underestimated by 3%–13%. This result implies the need for pre-testing to be carried out in the same location and time as the survey area and period. More importantly, most of the current density estimation models using camera traps, including CTDS, assume perfect detection at

a given point; therefore, further model refinements to incorporate the imperfect detection are critically required for more accurate estimation.

4.2 | Predictive performance of indicators for bushmeat biomass

The R/B ratio showed the highest performance regarding the three critical criteria (Table 4). It requires only three parameters, and their correlations with bushmeat biomass were reliably positive and nearly linear (Figure 3a), suggesting that the relationships could be formulated as simple linear equations. Moreover, its generality was moderately good, implying that the observed relationships might be generalised across the study area. The D/R ratio, which requires the capture data of all five species, also exhibited a correlation with a reliable monotonic increase and high linearity (Figure 3c). But its correlation slopes were considerably different between the sites, which may complicate information sharing between adjacent communities. Furthermore, both ratios had a relatively high uncertainty, indicating that precise prediction requires a large sample size.

The other indicators also clearly met the monotonic increase criterion and outperformed the R/B and D/R ratios in generality and precision (Table 4). However, their correlations with the biomass were not linear but logarithmic, depicting that the sensitivity of these

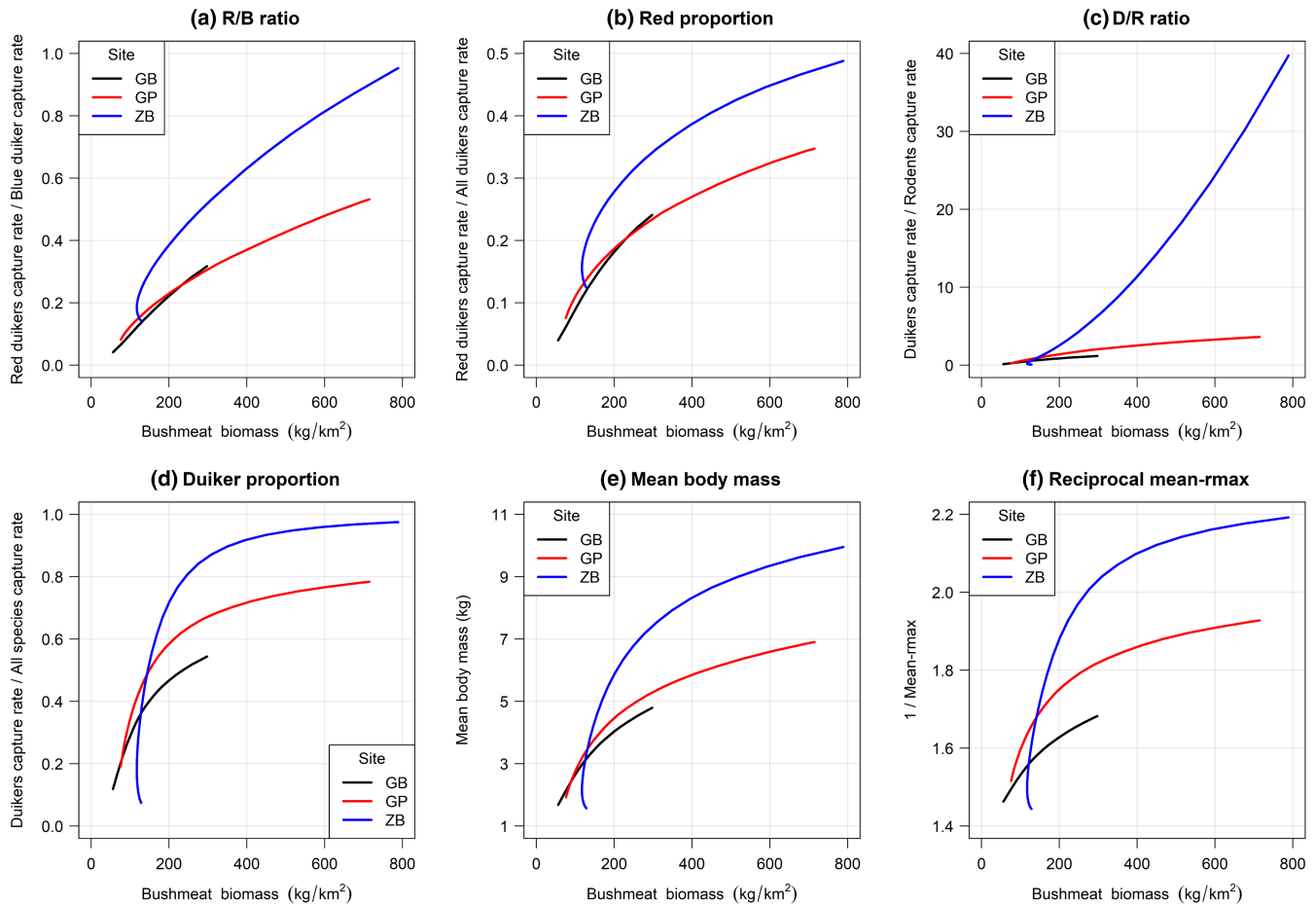


FIGURE 3 Relationships in the posterior median estimates between bushmeat biomass and indicators.

indicators to the biomass changes is inconsistent. This logarithmic relationship will be problematic when comparing the indicators in multiple locations with substantially different biomass or predicting large temporal changes in the biomass from the indicators.

Collectively, our results suggest that the two species-ratio indicators can effectively predict bushmeat biomass given a reasonably large sample size. The R/B ratio is recommended as a first choice. On the other hand, the D/R ratio can be a good alternative when information sharing is not essential.

The positive linear-like correlations between the total biomass and the ratios of larger to smaller animals are probably underpinned by the biological relationship between body size and reproductive rates (Fenchel, 1974). Multiple duiker species with varied body sizes coexist almost throughout the Congo Basin (Kingdon et al., 2013). Further, ungulates and rodents both enjoy high species diversity but suffer from hunting in many parts of the tropics worldwide (Peres, 2000; Rowcliffe et al., 2003; Wright, 2003). Given these, capture species ratios similar to the R/B or D/R are possibly applicable across tropical forests as biomass indicators. Nevertheless, this may be not the case when a particular group is selectively hunted than the others by active hunting techniques such as nets and firearms (Yasuoka, 2014). Careful investigation will also be required for other systems, such as grasslands and temperate zones, where animal community structure and hunting patterns are considerably

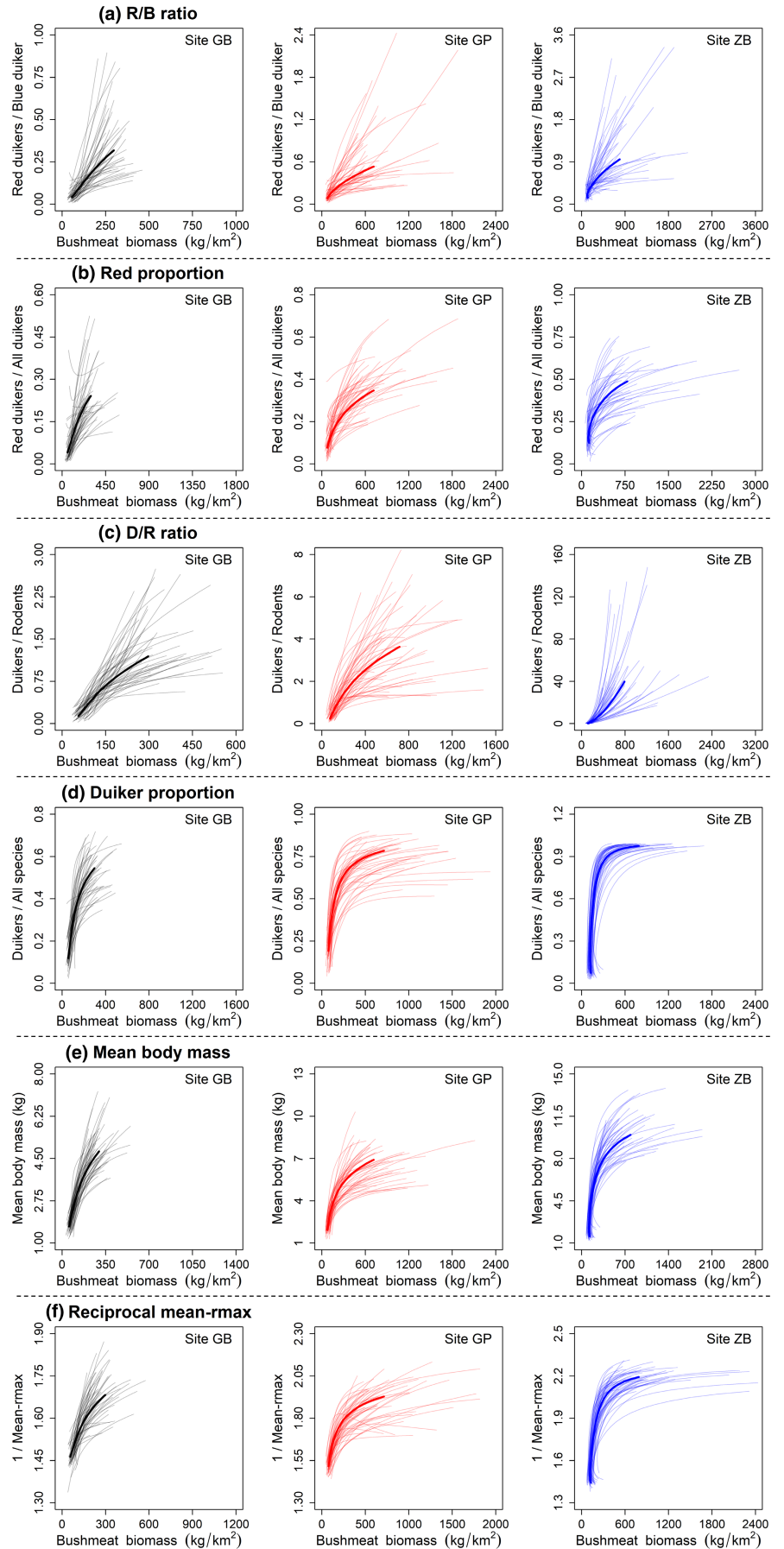
different from those in tropical forests. Future research needs to reveal the generalisability of our findings and the conditions under which they hold.

4.3 | Implications for locally based monitoring

In this study, the design and protocol of camera trap surveys were planned by scientists, and the camera trapping was also scientist-led. People in the local community only guided the scientists in the forest, helping them set up and retrieve cameras. Through our fieldwork together, however, we exchanged both local and scientific knowledge and skills. For example, local people gave the scientists geographic information on landmarks used when they practice activities in the forest (e.g., names of rivers, routes of human trails, and activity areas by settlements); meanwhile, scientists provided some locals with instructions on how to operate the cameras and GPS. Such interactions should provide an essential basis for scientists and local communities to work together in the planning and implementation of bushmeat monitoring on equal footing.

More importantly, the R/B and D/R ratios can be calculated simply by adding and dividing the number of animals taken at a hunting camp. Assuming that snare hunting is, as is often considered, an unselective method (Nielsen, 2006), the species composition of hunting

FIGURE 4 Uncertainty in the biomass-indicator relationships. Bold lines exhibit the posterior medians (as in [Figure 3](#)), and finer lines represent 50 alternative relationships drawn from randomly selected MCMC samples. For all indicators except the D/R ratio, the scale ratio between the x-axis and the y-axis is the same across sites.



catches should follow the relative captures by camera traps. If this is the case, these hunting-based ratios may also predict the total bushmeat biomass and its spatiotemporal changes without quantifying hunting effort or using expensive technology and complicated statistics. Moreover, local people are often keenly aware of spatial and temporal changes in bushmeat species composition, including the decline of larger species due to intense hunting (Kamgaing et al., 2019), so these indicators are likely to gain people's acceptance.

In this way, snare trap hunting—one of the essential livelihood activities of local people—would simultaneously become a monitoring activity for faunal resource amounts. Such locally based monitoring could even overcome the weakness of low precision in the species-ratio indicators by many hunters collaborating to collect large datasets. Nevertheless, challenges remain in applying the indicators to wildlife monitoring. Particularly, the non-selectivity of snare hunting is subject to be adequately examined. For example, Yasuoka et al. (2015) reported that Baka snare hunters harvested considerably more red duikers than blue duikers, which contradicts our density estimates. Snare hunters have different trapping techniques (Hayashi, 2008) and may choose one according to their preference. To fully implement the potential indicators in hunter-self monitoring, therefore, we should investigate local hunting techniques and compare hunting harvests with camera trap estimates. This perspective undoubtedly underpins coproduction research with local and scientific knowledge.

AUTHOR CONTRIBUTIONS

Shun Hongo, Yoshihiro Nakashima, Champlain Djiéto-Lordon and Hirokazu Yasuoka conceived the study; Shun Hongo, Zeun's C. B. Dzefack, Latar N. Vernyuy, Sosuke Minami and Hirokazu Yasuoka conducted the field surveys; Kaori Mizuno and Yukiko Hiroshima analysed camera trap videos; Shun Hongo and Ryoma Otsuka performed the statistical analyses; Shun Hongo managed the writing of the manuscript; and all authors contributed critically to the drafts and gave final approval for publication. Our study brings together the authors from Cameroon, the country where the fieldwork was conducted, and Japan. Scientists in the two countries collaboratively developed the study and conducted the fieldwork. However, the data analysis was principally performed by the Japanese authors, and local stakeholders were not fully involved in the discussion about the present study. We are planning to address these issues in future research.

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CONFLICT OF INTEREST

We declare there is no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.g4f4qrfr8> (Hongo, 2022). Camera trap videos are available on a case-by-case basis on request to the corresponding author, and some examples are available on our YouTube channel (<https://www.youtube.com/channel/UCFuAzBctF-gTiovcvKbNDA0g>).

ORCID

Shun Hongo  <https://orcid.org/0000-0001-8167-1348>

Ryoma Otsuka  <https://orcid.org/0000-0002-5147-1916>

Yoshihiro Nakashima  <https://orcid.org/0000-0002-2415-5555>

Hirokazu Yasuoka  <https://orcid.org/0000-0001-5066-1534>

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SUPPORTING INFORMATION

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