Stronger together: comparing and integrating camera trap, visual, and dung survey data in tropical forest communities

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Abstract. Accurate estimations of animal populations are necessary for management, conservation, and policy decisions. However, methods for surveying animal communities disproportionately represent specific groups or guilds. For example, transect surveys can provide robust data for large arboreal species but underestimate cryptic or small-bodied terrestrial species, whereas camera traps have the inverse tendency. The integration of information from multiple methodologies would provide the most complete inference on population size or responses to putative covariates, yet a simple, robust framework that allows integration and comparison of multiple data sources has been lacking. We use 27,813 counts of 35 species or species groups derived from concurrent visual transects, dung transects, and camera trap surveys in tropical forests and compare them within a generalized joint attribute modeling framework (GJAM) that both compares and integrates field-collected dung, visual, and camera trap data to quantify the species- and trait-specific differences in detection for each method. The effectiveness of survey method was strongly dependent on species, as well as animal traits. These differences in effectiveness contributed to meaningful differences in the reported strength of a known important covariate for animal communities (distance to nearest village). Data fusion through GJAM allows clear and unambiguous comparisons of the counts provided from each different methodology, the incorporation of trait information, and fusion of all three data streams to generate a more complete estimate of the effects of an anthropogenic disturbance covariate.

Research and conservation resources are extremely limited, which often means that field campaigns attempt to maximize the amount of information gathered especially in remote, hard-to-access areas. Advances in these understudied areas will be accelerated by analytical methods that can fully leverage the total body of diverse biodiversity field data, even when they are collected using different methods. We demonstrate that survey methods vary in their effectiveness for counting species based on biological traits, but more importantly that generative models like GJAM can integrate data from multiple sources in one cohesive statistical framework to make improved inference in understudied environments.

Key words: data fusion; joint species distribution modeling; population estimation; survey comparison.

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INTRODUCTION

Wildlife populations are in flux worldwide, with some species disappearing at alarming rates (Dirzo et al. 2014) while others are becoming overabundant or invasive (Didham et al. 2007, Doherty et al. 2016). Scientists employ an array of non-invasive survey methods to estimate

Choosing appropriate survey methods is particularly important when the goal is to survey entire wildlife communities, rather than a single species or guild. Overlooking methodological differences can lead to misinterpretations of the effect of human and natural disturbances on populations and communities, leading to poor management and conservation decisions (Fragoso et al. 2016). This is of particular concern in tropical forests as dense vegetation exaggerates differences in the detection ability of different methods (Espotosa et al. 2011), and biodiverse communities harbor many rare and data-deficient species.

Visual transects, dung transects, and camera trap surveys are most commonly used in tropical environments because of their cost efficiency (De Bondi et al. 2010), and non-invasive nature (Silveira et al. 2003). These characteristics also permit consistent replicability in survey design, helping establish statistically representative survey design (Buckland et al. 2010). In visual transects, observers record direct observations of animals while walking straight lines of a predetermined length (Plumptre 2000). Visual transects can be used to inexpensively and repeatedly sample relatively open environments for non-cryptic mammals (Silveira et al. 2003), but tend to underestimate cryptic and small animals as they are more difficult to detect (Fragoso et al. 2016). Dung transects involve recording observations of dung along transects and using estimates of dung production and decay rates to quantify populations. Dung surveys can effectively detect cryptic and nocturnal species because they do not require direct observation of an animal (Snyder 1961, Koh and Kim 2005). However, this method is only appropriate for detecting species that defecate frequently and with uniquely identifiable dung shapes and sizes (Plumptre 2000, Jenkins and Manly 2008). Camera trap surveys allow consistent observation of a limited view for up to months at a time and can detect terrestrial species regardless of activity pattern, body size, or human avoidance (Burton et al. 2015). However, terrestrial camera traps under represent arboreal species, can malfunction in humid climates, must be deployed and re-collected, and are relatively expensive compared to other methods, limiting their practicality for large scale studies (Snyder 1961, Burton et al. 2015).

Previous studies have examined how the choice of survey method affects the interpretation of community composition by comparing popular wildlife survey methods such as camera trapping (Rovero et al. 2013), visual surveys (Silveira et al. 2003), and dung surveys (Eggert et al. 2003). These studies evaluated both the relative effectiveness of these methods in detecting certain species and guilds and their implementation costs. While comparative studies of survey methods are less common in tropical forests, several studies have compared animal counts across different methods for one species or within a group of species with shared traits (Rovero and Marshall 2004, Fragoso et al. 2016, Whitworth et al. 2016, Kamgaing et al. 2018). These studies generally agree that using multiple complementary approaches for surveying is most appropriate for a broad assessment of the wildlife community given the relative strengths and weaknesses of each method.

Despite the consensus that multiple survey techniques should be used when censusing diverse wildlife communities, accessible analysis frameworks which allow simultaneous modeling of count data from different methodologies (from here onwards referred to as “data fusion”) are lacking to date (but see D. E. Bowler et al. 2019 for a single species example). As such, researchers choose to either focus on a single methodology or consider the data from different methods in separate analyses. The potential power of data fusion methods is highlighted by the recent analytical advancements in species distribution modeling where data fusion has improved the accuracy and precision of distribution models through the incorporation of multiple, non-standardized data streams (e.g., Zipkin et al. 2017, Miller et al. 2019). In this paper, we quantify the relative detection rates of 35 wildlife species or species groups derived from concurrent visual
transects, dung transects, and camera trap surveys in tropical forests and compare them within a cohesive statistical framework. We employ a generalized joint attribute modeling framework (GJAM; Clark et al. 2017) approach that incorporates observations of live mammals, dung, and camera trap photos from the same study area to estimate community composition and the effectiveness of each survey type. This framework explicitly quantifies the association between animal traits (e.g., animals that are nocturnal vs. diurnal, large vs. small bodied, terrestrial vs. arboreal, etc.) and survey method (i.e., camera, visual, or dung), allowing us to identify the survey type best suited for assessing a specific subset of a community. We present three suites of inference: the effect of method on mammal species counts, the effect of method on community-weighted traits, and a comparison of the ecological inference derived from using a single data source when compared to an analysis that fuses our three disparate data sources into a single, cohesive model.

**METHODS**

**Study location**

We conducted the study over 8000 km² in Ogooué-Ivindo Province near the regional capital of Makokou in northeastern Gabon. The study area is relatively flat (450–600 m above sea level) and characterized by continuous broadleaf tropical forest with a mosaic of cropland and herbaceous vegetation cover near human settlements. A majority of the ~1700 mm of annual precipitation falls during two wet seasons (September–December, April–May), which are interspersed between two relatively dry periods (January–March, June–August). The mean annual temperature near Makokou is 23.9°C with higher temperatures between March and April (average maximum temperature 30.6°C), and lower temperatures in July (average maximum temperature 26.7°C). The study area is intersected by three main roads and includes ~60 small villages (ranging in population from 22 to 335) and three active forest concessions under sustainable management agreements (Koerner et al. 2017). Before the study, we visited all villages within 10–60 km of Makokou to explain the goals of the study and to assess their interest in participating. We then randomly selected 10 villages out of the 27 villages that agreed to participate, maintaining an equal representation of small, medium, and large villages.

**Transect creation**

We established 60 2-km transects within the vicinity of the 10 focal villages to test the effect of distance from villages on species richness and relative abundance using our three survey methods (Fig. 1). Two of the six transects per village were located within 4 km of the village, and the remaining four were located between 4 and 8 km away. We limited the study to an 8 km radius around villages because conversations with villagers and previous studies suggest that most hunting and foraging occur within 8–10 km from villages (Abernethy et al. 2013, Abrahams et al. 2017, Koerner et al. 2017). Camera trap, visual, and dung surveys were conducted concurrently along each transect. We recruited two paraecologists from each of the ten study villages and trained them in data collection (details below) for each method. Each paraecologist participated in a mandatory three-day training program and practiced each of the methods under supervision of an expert ecologist in the field before beginning the study to ensure that methods were applied consistently across villages. We also conducted a refresher training after six months of data collection and the expert ecologist walked roughly 10% of the transects with the paraecologists (Beirne et al. 2019).

**Visual and dung survey data**

Paraecologists surveyed each transect an average of 32 times (range 24–36) for 1941 transect walks (3737 km) between August 2015 and January 2017. Paraecologists recorded all visual observations of mammals on each transect walk, following the mammalian transect methods in Koerner et al. (2017). Dung was recorded as encountered and marked to avoid double-counting. For each observation, paraecologists recorded the species, group size, observation time, distance along the transect, and the perpendicular distance from the transect centerline to the observation (either estimated by eye for live observations or measured with a measuring tape for dung). Groups of conspecific animals were considered independent if they occurred more
than 50 m apart. On average, paraecologists started transect walks at 08:30 and surveyed at an average speed of 0.9 km/h. Observations were made at the species level, except when similarities between species warranted a more general class. For example, the medium duiker multi-species group represents all mid-sized duikers: bay duiker (*Cephalophus dorsalis*), Ogilby’s duiker (*Cephalophus ogilbyi*), Peter’s duiker (*Cephalophus callipygus*), white-bellied duiker (*Cephalophus leucogaster*), black-fronted duiker (*Cephalophus nigrifrons*), etc. In rare cases, difficult to identify mammals that spanned multiple genera were aggregated into multi-genera groups (e.g., group named Squirrel represents genera *Heliosciurus*, *Epixerus*, *Funisciurus*, etc.). Table 1 lists all species and species groups.

**Camera trap survey data**

Between January 2015 and January 2017, the paraecologists set four camera traps per village, for a total of 40 un-baited camera traps. Camera
traps were located 50 cm above the ground and 500 m apart on each transect and were rotated monthly among the six transects per village. Paraecologists deployed camera traps near fruiting trees or signs of animal activity (e.g., game trails, footprints, scratch marks, scat) returning every two weeks to ensure that the equipment remained operational. Camera traps were programmed to collect 60 s of video within one-second of detecting animal movement. Bushnell 8MP trophy cam HD trail camera (model number: 119676C) was used because of its high-quality image quality, fast trigger speed, relatively low cost, and extensive use in other camera trap studies (Yoburn et al. 1981, Rovero et al. 2013, Howe et al. 2017).

**Data processing**

Six trained research technicians watched all collected videos and sorted them into directories based on the village, transect, and camera trap at which the observation occurred as well as the species name and number of individuals. Printed animal guides for the area were used to identify species. Observations that could not be definitively identified were labeled as unidentified (UID) and removed from analyses. We derived the Euclidean distance between the centroid of

Table 1. Cumulative counts of all species and species groups.

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Common name</th>
<th>Camera</th>
<th>Visual</th>
<th>Dung</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atherurus africanus</td>
<td>Brush-tailed porcupine</td>
<td>369</td>
<td>69</td>
<td>229</td>
</tr>
<tr>
<td>Multiple genera</td>
<td>Bat</td>
<td>8</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Syncerus caffer</td>
<td>Buffalo</td>
<td>0</td>
<td>15</td>
<td>2</td>
</tr>
<tr>
<td>Philantomba monticola</td>
<td>Blue duiker</td>
<td>1309</td>
<td>325</td>
<td>1039</td>
</tr>
<tr>
<td>Cercopithecus neglectus</td>
<td>De Brazza monkey</td>
<td>14</td>
<td>26</td>
<td>0</td>
</tr>
<tr>
<td>Cephalophus silviculorum</td>
<td>Yellow-backed duiker</td>
<td>62</td>
<td>21</td>
<td>86</td>
</tr>
<tr>
<td>Profelis aurata</td>
<td>Golden cat</td>
<td>17</td>
<td>5</td>
<td>8</td>
</tr>
<tr>
<td>Pan troglodytes</td>
<td>Chimpanzee</td>
<td>114</td>
<td>159</td>
<td>37</td>
</tr>
<tr>
<td>Hyemoschus aquaticus</td>
<td>Water chevrotain</td>
<td>23</td>
<td>11</td>
<td>0</td>
</tr>
<tr>
<td>Civettictis civetta</td>
<td>African civet</td>
<td>5</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Cephalophus spp.</td>
<td>Medium duiker</td>
<td>605</td>
<td>203</td>
<td>642</td>
</tr>
<tr>
<td>Colobus spp.</td>
<td>Black and white colobus</td>
<td>0</td>
<td>36</td>
<td>0</td>
</tr>
<tr>
<td>Cercopithecus pogonias</td>
<td>Crowned guenon</td>
<td>0</td>
<td>1528</td>
<td>1</td>
</tr>
<tr>
<td>Multiple genera</td>
<td>Squirrel</td>
<td>737</td>
<td>3693</td>
<td>2</td>
</tr>
<tr>
<td>Loxodonta cyclotis</td>
<td>Elephant</td>
<td>345</td>
<td>253</td>
<td>2326</td>
</tr>
<tr>
<td>Sciurocherirus gabonensis</td>
<td>Squirrel galago</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Genetta spp.</td>
<td>Genet</td>
<td>95</td>
<td>4</td>
<td>13</td>
</tr>
<tr>
<td>Arctocebus aureus</td>
<td>Golden angwantibio</td>
<td>4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Gorilla gorilla</td>
<td>Gorilla</td>
<td>15</td>
<td>33</td>
<td>15</td>
</tr>
<tr>
<td>Cercopithecus nictitans stomfii</td>
<td>White-nosed guenon</td>
<td>5</td>
<td>3611</td>
<td>10</td>
</tr>
<tr>
<td>Hydrictis spp.</td>
<td>Otter</td>
<td>1</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Mandrillus sphinx</td>
<td>Mandrill</td>
<td>420</td>
<td>574</td>
<td>44</td>
</tr>
<tr>
<td>Herpestes spp.</td>
<td>Mongoose</td>
<td>101</td>
<td>36</td>
<td>6</td>
</tr>
<tr>
<td>Lophocebus albigena</td>
<td>Grey-cheeked mangabey</td>
<td>1</td>
<td>613</td>
<td>0</td>
</tr>
<tr>
<td>Cercopithecus sclateri</td>
<td>Moustached monkey</td>
<td>0</td>
<td>5144</td>
<td>0</td>
</tr>
<tr>
<td>Civettictis civetta</td>
<td>African palm civet</td>
<td>0</td>
<td>1</td>
<td>18</td>
</tr>
<tr>
<td>Orycteropus after</td>
<td>Aardvark</td>
<td>4</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Panthera pardus</td>
<td>Leopard</td>
<td>13</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Multiple genera</td>
<td>Pangolin</td>
<td>50</td>
<td>7</td>
<td>6</td>
</tr>
<tr>
<td>Potamochoerus porcus</td>
<td>Red forest hog</td>
<td>170</td>
<td>823</td>
<td>222</td>
</tr>
<tr>
<td>Perodicticus potto</td>
<td>Potto</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Multiple genera</td>
<td>Rat</td>
<td>953</td>
<td>75</td>
<td>14</td>
</tr>
<tr>
<td>Tragelaphus spekii</td>
<td>Sitatunga</td>
<td>2</td>
<td>9</td>
<td>36</td>
</tr>
<tr>
<td>Miopithecus ogouensis</td>
<td>Talapoin</td>
<td>93</td>
<td>828</td>
<td>0</td>
</tr>
<tr>
<td>Mellivora capensis</td>
<td>Honey badger</td>
<td>0</td>
<td>2</td>
<td>3</td>
</tr>
</tbody>
</table>
each transect and the centroid of the nearest village using ArcGIS Pro 2.0.1 (ArcGIS Pro 2018). We analyzed data from 52 of the 60 transects; excluding eight transects from the analysis because camera trapping was unsuccessful due to poor camera positioning or battery failure, etc.).

**Data analysis**

To provide accurate forecasts of community change, we employ a generative model that predicts at the scale and context used to fit the model (Clark et al. 2017). This generalized joint attribute model (GJAM) fits individual species jointly, that is, at the community scale. Probabilistic inference in GJAM also resolves three characteristics of biodiversity data that often make forecasting difficult: (1) Data are multivariate—multiple predictors are introduced to explain abundances of species; (2) data are observed on different scales and using different methods; and, (3) data include many zeros—rare species are infrequently observed. Unlike traditional generalized linear models, GJAM does not use link functions that distort the scale of the response variable; thus, GJAM can be interpreted on the scale of the observation, accounting for sample effort.

Using a generic bracket notation (where \([A, B]\) is the joint distribution or density of \(A\) and \(B\), and \([A|B]\) is the conditional distribution or density of \(A\) given \(B\)), GJAM is based on a joint distribution \([0, X, Y]\) of parameters \(0\), predictors \(X\), and species responses \(Y\). Parameters \(0\) in the model include matrices of coefficients \(B\) relating \(X\) to \(Y\) and the residual covariance matrix for all species pairs in \(Y\) (\(\Sigma\)). In effect, \(\Sigma\) represents the covariance between species beyond what has already been explained by the environmental covariates. It can include interactions between species, unaccounted for environmental gradients, and other unexplained sources of error. In the generative model, all elements, including estimates and prediction, are part of one analysis. The likelihood is: \([Y_1, \ldots, Y_S | 0, X]\), where subscripts refer to species 1 through 5. Model fitting is done on the prediction scale, which is also the observation scale (i.e., all species jointly), based on the posterior distribution, \([0 | X, Y] \propto [Y_1, \ldots, Y_S | 0, X][0]\). The right-hand term is the likelihood and the prior distribution, \([0]\), which is non-informative. Full model specifications can be found in (Clark et al. 2017).

**Accounting for effort across methods**

Effort in GJAM is equivalent to an offset in generalized linear models and is an essential element allowing us to relate the counts coming from our three methods. Whereas effort for visual and dung transects is traditionally measured in distance, we instead used observation time on transect to relate them to stationary camera trap hours. Although not a perfect corollary, both visual and dung transects already dictate a standardized walking pace to account for inter-observer variability in effort. This standardized approach allows us to use camera traps as a reference category in GJAM, meaning positive posterior parameter estimates indicate a method was more effective at capturing a given species than camera traps, whereas negative posterior parameter estimates and estimates with 95% CIs that overlap zero indicate that the method is less and equally as effective as camera trapping.

**Species analysis**

Our first analysis assesses how survey methods affect the counts of each of the observed species. The response is the total number of counts of 35 vertebrate species collected by camera traps, visual transects, and dung surveys from 52 of our original 60 transects. We included survey method (visual transect, dung transect, camera trap survey) as a factorial predictor variable with camera trapping (the most popular contemporary method) as our reference category, acknowledging that not all methods are appropriate for all mammals.

**Trait analysis**

Our second analysis seeks to generalize the findings beyond the specific species in our study area. We therefore used the community-weighted mean trait values in place of species in the nxS response matrix, \(Y\), and kept the survey method type as the predictor. Trait data were obtained by collating available species-specific trait information from Elton Traits V1 archive, a global species-level compilation of these key traits for 5400 mammal species derived from literature sources (Wilman et al. 2014). These included strata usage (arboreal, terrestrial, or both), activity pattern (Nocturnal vs. diurnal), group living (yes or no: binary), protected status (binary), frugivory (binary), and body mass (kg).
Ecological inference

Our third analysis investigates how ecological inferences differ between each survey type compared to a data fusion approach. This involved creating four separate models. Three models had, as the response variable, count data for the eight most common species (which were present in at least 15% of transects regardless of survey method) from one of the data types (camera, visual, dung). The fourth model incorporated data from all three survey methods to predict the same eight most common species. In all models, we included distance to nearest village and distance to nearest road (in kilometers, taken from the midline of the transect) as predictors because they serve as uncorrelated proxies for hunting pressure ($r = 0.35$), with distance to nearest village known to have a strong effect on animal communities in our study area (Beirne et al. 2019, Koerner et al. 2017).

RESULTS

Species analysis

We recorded 27,813 counts of 35 species, including 5537 counts of 29 species in 111,792 camera trap hours; 17,512 counts of 30 species with visual surveys over 3769 h, and 4764 counts of 24 species with dung surveys over 3769 h (Table 1). The survey method employed strongly affected the counts obtained for many species (Fig. 2; Appendix S1: Tables S1–S3). Camera traps positively affected the counts for nine terrestrial species (Fig. 2; Appendix S1: Table S1). Visual surveys positively affected the counts for 11 primarily arboreal species and negatively affected the counts for 10 cryptic terrestrial species (Fig. 2; Appendix S1: Table S2). Dung surveys positively affected the counts for 6 species (Fig. 2; Appendix S1: Table S3).

Trait analysis

The effectiveness of a method was strongly influenced by community-weighted trait values; of the 30 posterior densities generated by our second model (the three methods for each of our 10 traits), 24 had posterior parameter estimates that did not overlap with the null effect of 0 (Fig. 3; Appendix S1: Table S4). Visual transects captured more counts of diurnal and arboreal species, and fewer counts of fully terrestrial species. Dung transects captured more counts of large species and fewer counts of diurnal species. Camera traps captured fewer counts of arboreal species and species that live in groups. Interestingly, visual transects captured fewer counts of protected species than other methods.

Ecological inference analysis

Our third suite of three models demonstrated that the effect of distance to village on counts of the eight most common species (i.e., counts becoming more or less abundant as distance increased) was generally consistent across methods (Fig. 4; Appendix S1: Table S5). However, the strength of the effect changed according to the survey method. For example, distance to village was negatively related to the encounter rate of the brush-tailed porcupine according to camera trap data, but had no effect on encounter rate according to the other methods. The effect of distance to village was markedly stronger for elephants when dung transects were used and markedly stronger for mandrill when visual transects were used. Our final fusion model for the most common species generally showed trends consistent with the individual models. One exception was the chimpanzee (Pan troglodytes), which had no meaningful relationship with distance to village in the individual models but a significantly negative relationship in the fusion model.

DISCUSSION

Data fusion methodologies have the potential to provide more robust inference on the factors influencing biological communities, but accessible analysis frameworks are currently lacking. Here, we employ the GJAM framework to compare and fuse wildlife count data from three sources: visual encounter, dung, and camera trap surveys. Our work allows clear and unambiguous comparisons of the counts provided from each different methodology, the incorporation of trait information, and fusion of all three data streams to generate a more complete estimate of the effects of an anthropogenic disturbance covariate. It is important to stress that we do not recommend that researchers always use multiple methodologies when surveying biological communities. When research is focused on a single
species or a suite of similar species, the best single method should be employed. However, where multiple data sources are available they should be exploited, particularly in under-surveyed locations or ecosystems such as tropical forests where habitat structure makes direct observations difficult.

The GJAM framework facilitates comparison of methodologies to identify that which most productively surveyed species in the community. Significant differences between survey techniques were detected for 29 of 35 species classifications (83%), with no single method clearly outperforming the others for all species. Information on species-specific survey bias will be useful for researchers or organizations looking to design focal species surveys or monitor conservation interventions. Crucially, the high proportion of species showing markedly better representation in one of the three methods highlights the potential

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**Fig. 2.** Comparison of posterior parameter estimates for all species (y-axis) by survey method (x-axis). Each square is colored according to the mean of its posterior distribution. The symbols (+/−) indicate that the 95% credible interval does not intersect 0. Survey method strongly affected the counts obtained for many species.
danger in using a single methodology to characterize diverse biological communities. Although most studies select the survey methodology that best accommodates their focal species or guild, our study demonstrates that researchers should be cautious when reporting results of ancillary data concurrently collected on non-focal species.

Incorporation of trait information on animals highlights how species-level variation in life-history characteristics underpins the species-level specificity of different survey methods. Visual encounter surveys more effectively accrued counts of arboreal, group living, diurnal, and unprotected species, consistent with findings of
previous authors (e.g., Whitworth et al. 2016). The under-counting of protected species by visual transects is consistent with human avoidance behavior (either fleeing humans or even shifting activity patterns from diurnal to nocturnal), as species with protected status are often under the strongest pressure from poaching (Poulsen et al. 2017). Protected, large-bodied, and terrestrial species are most productively surveyed through dung counts, a census technique less susceptible to human disturbance effects (Fragoso et al. 2016). However, the effectiveness of dung transect observations must be balanced with the sources of error introduced by converting number of dung to numbers of animals. That camera traps were more productive in the detection of smaller bodied, terrestrial species is also consistent with the current literature (e.g., Rowcliffe et al. 2011, Burton et al. 2015), as small animals usually produce small dung and both can be difficult to detect in forest environments. Interestingly, group-living species appeared to be relatively underrepresented by camera traps. This likely arises from underestimation of group sizes due to the limited field of view of camera traps and/or the limited capture duration of videos, although our average one-minute video lengths were longer than in many other studies. The general patterns observed here again suggest that caution should be used when making

Fig. 4. Comparison of posterior parameter estimates for eight most common species (y-axis) by individual survey method or ensemble of all methods (x-axis). Each square is color according to its mean. Symbol (+/−) indicates a 95% credible that does not intersect with 0. Effects are generally consistent across methods, but with varying strengths and notable exceptions.
community-level inferences from single methodologies.

The unique method-specific patterns of detection reported here should be generalizable to other forested ecosystems, with the caveat that hunting is highly prevalent in this region and may accentuate the patterns observed, particular for visual observations. The trait level information can be used to predict the methodology that is most productive for species outside of our study region. These results, however, may be less generalizable to other ecosystems (such as savanna) where the detection processes may differ markedly from forests.

Informed management decisions rely on understanding how biological communities respond to putative covariates of interest (such as hunting pressure or anthropogenic disturbance). Here, we compared the effect of village distance, a covariate known to markedly affect the observation of mammals in this study area (Beirne et al. 2019). Reassuringly, for six of nine species assessed, the directional effect of the covariate was consistent across all survey methodologies, suggesting that the same conclusions would be reached regardless of survey method. Where different methods showed idiosyncratic responses to distance to village, such as the brush-tailed porcupine, the fusion model reflected the ambiguity and reported a neutral coefficient. For a species showing consistent non-significant, negative effects for each individual method, such as the chimpanzee, the fusion model reported a significant effect of the parameter. Consequently, where there is weak support for a model (due to low sample size or due to a small effect size), data fusion can integrate the information across different methods to give a consensus result. We take this as evidence that data fusion can lead to more complete inference than single methodologies alone.

The multiple method approach could also reveal novel ecological information. For example, a species exhibiting behavioral avoidance of humans may move away from villages during the day when anthropogenic disturbance is typically high (e.g., Gaynor et al. 2018), but return at night. Such behavioral shifts could result in a disparity between the effect of a given covariate on visual encounter survey counts (e.g., strong reduction in counts in close proximity to villages) and the effect of the covariate on other round the clock survey techniques such as dung surveys or camera trapping (e.g., no change in counts with village distance). Consequently, a lack of congruence between the effects of covariates for different survey methods may not be due to poor study design, but rather reveal an important ecological response.

Resources for research and conservation are limited in the tropics, which often means that field campaigns attempt to maximize the amount of information gathered particularly in remote, hard-to-access areas. Advances in these understudied areas will be accelerated by analytical methods that can fully leverage the fully body of diverse biodiversity field data, even when they are collected using different methods. We demonstrate that survey methods vary in their effectiveness for counting species based on biological traits, but more importantly that generative models like GJAM can integrate data from multiple sources in one cohesive statistical framework to make improved inference in understudied environments.

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