



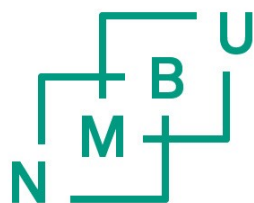
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Spatial and temporal distributions and interactions in a neotropical ground-dwelling animal community

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Acknowledgements

This thesis serves as the end product of my 60 ECST Master of Science in Ecology at the University of Life Sciences in Ås. My original project left me with only a lesson in naivety and misfortune, but the bad ending was far outweighed by the thrill and learning experience of the journey. I owe thanks to everyone involved; my supervisor Torbjørn Haugaasen, who made it possible to conduct fieldwork at one of the most pristine tropical research locations on earth, and my fellow students and the researchers, locals and wilderness at Cocha Cashu Biological Station, who made my stay among the most memorable months of my life.

When the deceitful weather gave the final blow and all things failed, the rescue came in the form of camera trap images provided by Whaldener Endo and Torbjørn Haugaasen. I am thankful for this additional opportunity to finalise my master's degree.

The completion of this thesis relied on the help of several people that deserve my gratitude. Using camera traps for research purposes involve interpretation of thousands of images, some of lesser quality to others. Several more experienced researchers provided aid in the identification process: Torbjørn Haugaasen and Whaldener Endo with obscure images of large mammals, Carla Bantel with the troublesome smaller mammals and Alexander Lees and Martin Austad with the diversity of birds. Turning snapshots into results required implementation of statistical methods not mentioned in any of my previous courses. Supervisor Richard Bischof came to my rescue on several occasions when the boundless amount of information on the internet left me in confusion.

Writing a coherent story about broad results, narrow findings and treacherous statistics proved challenging. The constructive feedback provided by my supervisors, Martin Austad, Marte Sofie Søreide, Petter Lillengen and my father helped turning preliminary drafts into a, hopefully, readable thesis. If not, there are images.

Ås 15.12.2016

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Jørgen Sand Sæbø

Abstract

Distribution in time and space are central parts of a species' niche, and linking these to environmental and anthropogenic factors are common objectives in ecological research. However, the observed distributions are inextricably linked to the complex array of interactions among members of a community. Disentangling these interactions and their effects on species distributions is a challenging task, but may improve our understanding of community structure and forecasting of distribution changes. In this thesis, I explored the spatial and temporal distribution of large ground-dwelling vertebrates in a Brazilian rainforest using a collection of camera trap images, using occupancy models and kernel density analysis. Pair-wise co-occupancy models and density overlap were applied to explore interactions among the species. The results indicated that the effect of hunting by local villagers on the spatial distributions of the observed species were limited. However, the black agouti (*Dasyprocta fuliginosa*) and spotted paca (*Cuniculus paca*) used fewer sites near human settlements, while the opposite was shown for the pale-winged trumpeter (*Psophia leucoptera*). The models indicated few relationships among predators and prey. However, the carnivorous puma (*Puma concolor*), jaguar (*Panthera onca*) and ocelot (*Leopardus pardalis*) seem to show cathemeral activity patterns and behavioural versatility, while other species are limited to shorter and more rigid activity periods. This could indicate a low potential for prey to escape in time, and rather a bottom-up control of predator activity according to prey availability. Both convergent and divergent patterns were observed between pairs of species utilizing similar feeding resources. Overall, there was a lack of significant and consistent results arising from the pair-wise models. I suggest that this could be a consequence of the complexity of interactions in diverse communities, but also point out some analytical challenges.

Sammendrag

Utbredelse i tid og rom er sentrale deler av en arts nisje, og forsøk på å knytte disse til miljømessige og antropogene faktorer har vært typiske formål for økologisk forskning. De observerte fordelingene er uløselig knyttet til de komplekse interaksjonene mellom artene i et økologisk samfunn. Å skille disse interaksjonene og deres effekter på arters utbredelse er en utfordrende oppgave, men kan øke vår forståelse av samfunnsstruktur og forbedre våre anslag av utbredelsesendringer. I denne avhandlingen utforsket jeg utbredelse i tid og rom for bakkelevende vertebrater, ved analyse av en samling viltkamerabilder innhentet i et regnskogsområde i Brasil, og anvendelse av «occupancy»-modeller og «kernel density» analyse. Parvise «co-occupancy»-modeller og overlapp mellom tetthetsfordelingene ble anvendt for å undersøke interaksjoner mellom artene. Resultatene indikerte at lokale innbyggers jakt hadde begrenset påvirkning utbredelsen til de observerte artene. Aguti (*Dasyprocta fuliginosa*) og paka (*Cuniculus paca*) brukte imidlertid færre områder nær landsbyer, mens den motsatte effekten ble vist for hvitvingetrompetfugl (*Psophia leucoptera*). Modellene indikerte få sammenhenger mellom predatorer og byttedyr. De kjøttetende artene puma (*Puma concolor*), jaguar (*Panthera onca*) og ocelot (*Leopardus pardalis*) viser allsidig atferd og aktivitet døgnet gjennom, mens andre arter er begrenset til kortere og mer rigide aktivitetsperioder. Dette kan indikere et lavt potensiale for byttedyr til å rømme i tid, og heller at predatoraktivitet kontrolleres av byttetilgang. Både konvergerende og divergerende mønstre ble observert mellom par av arter som utnytter lignende matressurser. Samlet sett viste de par-vise modellene begrenset med signifikante og konsistente resultater. Jeg foreslår at dette kan forekomme av de komplekse interaksjonene i diverse økologiske samfunn, men påpeker også enkelte analytiske utfordringer.

Table of Contents

Acknowledgements.....	iii
Abstract.....	v
Sammendrag	v
1. Introduction.....	1
2. Methods	3
2.1 Study site	3
2.1.1 Area description.....	3
2.1.2 Human population and hunting	3
2.2 Data collection.....	4
2.2.1 Camera trapping	4
2.2.2 Species identification.....	4
2.3 Statistical analysis.....	5
2.3.1 Occupancy analysis of spatial patterns	5
2.3.2 Kernel density analysis of temporal patterns	7
3. Results.....	8
3.1 Data summary	8
3.2 Activity patterns and temporal relationships	10
3.3 Occupancy estimates, anthropogenic impacts, and spatial relationships.....	14
4. Discussion.....	16
4.1 The ground-dwelling animal community along Xerua River	16
4.1.1 Temporal distribution of ground-dwelling animals	16
4.1.2 Relationships among competing species	17
4.1.3 Relationships among predators and prey	18
4.1.4 Effects of human settlements.....	19
4.2 The analytical framework	19
4.3 Conclusions	20
5. References.....	21
Appendix 1: Hierarchical occupancy model	I
Appendix 2: Choice of bandwidth for kernel density estimation	II
Appendix 3: Additional captures	VI
Appendix 4: Camera trap sites included in the study.....	VII
Appendix 5: Occupancy model selection.....	VIII

1. Introduction

The “ecological niche” is a long-standing concept in ecology, encompassing a species’ requirements and use of its abiotic and biotic environment (Grinnell 1917, Elton 1926, Hutchinson 1957). Following Hutchinson’s definition, the niche is commonly treated theoretically as a distribution within a multi-dimensional space, where the axes refer to specific environmental conditions (Hutchinson 1957). Distribution in time and space are central parts of a species’ niche, both as independent resources and as axes over which other environmental conditions and resources can be quantified (Schoener 1974, Carothers and Jakzić 1984, Kronfeld-Schor and Dayan 2003).

The niche term is inextricably linked to the complex array of interactions among species existing in the same community. The abstract “fundamental niche” of a species is defined quantitatively as the range of environmental conditions that can allow a population to persist in the absence of interspecific interactions (Hutchinson 1957). The observable “realized niche” is the product of the fundamental niche shaped by natural selection, and adjustments of behaviour and resource utilizations induced by interactions with the surrounding community (Hutchinson 1957, Bruno et al. 2003). Space and time thus provides axes along which species can move, by adaptation or behaviour, to maximise their fitness in the presence of interacting sympatric organisms (Schoener 1974, Kronfeld-Schor and Dayan 2003). Temporal and spatial distribution can be classified on different scales. In this text, the temporal niche relates to the 24h environmental cycle, and the use of space refers to distribution within one continuous habitat.

Hutchinson’s quantitative definition of the ecological niche provided a reformulation of the competitive exclusion principle, stating that two species occupying identical niches cannot coexist (Hutchinson 1957, Schoener 1974). This sparked an abundance of papers examining patterns of segregation between competitors along niche dimensions (Schoener 1974). Space and time may act as independent axes over which species can segregate to avoid detrimental effects of direct confrontation in interference competition relationships (Kronfeld-Schor and Dayan 2003). Resource competition may also be reduced by differentiating the use of space (Schoener 1974) or time, if the shared and limited resources differ throughout time (Carothers and Jakzić 1984, Kronfeld-Schor and Dayan 2003), or is renewed in the time that separates the species (Kronfeld-Schor and Dayan 2003). Thus, adaptational or plastic displacement of the inferior competitor in time or space are likely outcomes of competition.

Predator-prey relationships present conflicting interaction effects for the species involved. Predation is a beneficial interaction and an indispensable part of the niche for the predator (Lima 2002), while prey must counteract with defence, escape or avoidance to prevent lethal or injuring encounters (Kronfeld-Schor and Dayan 2003, Wirsing et al. 2010). Predicting evolutionary and behavioural patterns arising from these discordant interaction effects is not straightforward. Predators rely on some degree of spatial and temporal overlap, and their patterns should track those of their prey (Lima 2002, Kronfeld-Schor and Dayan 2003). Contrastingly, variations in predation risk in space and time could lead to reduced activity and spatial and temporal displacement for the prey (Lima and Dill 1990, Kronfeld-Schor and Dayan 2003). Thus, the outcome could depend on the relative strength of the interaction effects for the participants, the presence of other interacting predators and prey species (Wirsing et al. 2010), the costs related to niche changes (Lima 1998, Creel and Christianson 2008), prey escape behaviour (Wirsing et al. 2010) and constraints applied by physiological traits, energetic demands (Bennie et al. 2014) and evolutionary histories (Wiens and Graham 2005).

Beyond well-known mutualistic relationships, the role of facilitative interactions through habitat or resource enhancement or provision of predation refuge are increasingly acknowledged as forces behind community structure (Bruno et al. 2003, Bronstein 2009). In contrast to the narrowing effect of detrimental interactions, facilitation can represent an expansion of the realized niche, or even the fundamental niche, if allowing species to persist in areas outside that allowed by the abiotic environment alone (Bruno et al. 2003). There is clearly a spatial component in many facilitative interactions (Arsenault and Owen-smith 2002, du Toit and Olff 2014), suggesting that some degree of spatial association between the species can be expected. Convergence in time could also be advantageous to ensure overlap for species enjoying benefit from direct

interaction. However, little information exists on the importance and effects of such interactions among mammalian species.

Most populations must additionally adjust to the pervasive presence of humans. Resembling the behavioural effects of predation pressure, human presence and hunting have been shown to affect the use of space (Djagoun et al. 2014, Wang et al. 2015) and time (Pagon et al. 2013, Wang et al. 2015) by some species. Local changes in community structure through discordant behavioural reactions to human activities (Wang et al. 2015) could thus add to the direct effects of local depletion. Selective hunting of large game species can lead to shifts in community structure favouring smaller species and lower total biomass (Peres and Palacios 2007), alter prey availability for predators (Foster et al. 2014) and cause further community changes through cascading effects on tree recruitment (Terborgh et al. 2008, Kurten 2013).

As an alternative to traditional survey techniques (e.g. direct observation, sign counts, tracking), automatically triggered cameras are now deployed for population and community surveys in a range of environments (Mccallum 2013). Although the first wild animals had captured their own images when stepping on George Shiras III's trip wire system almost a century before (Sanderson and Trolle 2005), the explosion in scientific use of camera traps has followed the rapid technological development and their increased accessibility during the 21st century (Mccallum 2013). They provide some obvious advantages as a tool for population sampling; compared to traditional methods they are low-invasive, remove the human observer from the survey process and generate reviewable documentation for other researchers (O'Connell et al. 2011). They provide standardized spatial replication, effortless and continuous temporal replication and a timestamp of trigger events, making them suitable tools for studying spatial and temporal distribution of species (Trolliet et al. 2014).

This study provides an analysis of camera trap images collected in a lowland rainforest area in western Amazonia, Brazil. The western Amazon rainforest is home to a diverse mammal community (Ceballos and Ehrlich 2006) and several ground-dwelling birds (Schulenberg et al. 2007, IUCN 2015). However, distributional, taxonomic and ecological knowledge is inadequate for several species in the region (Patton et al. 2000). Apart from its value in a natural history perspective, reliable descriptions of spatial and temporal patterns can prove relevant for making effective management decisions, facilitating further research associated with the species (Gómez et al. 2005), and to provide data for large-scale reviews of general patterns (e.g. Bennie et al. 2014). Further, evaluating the effect of interactions between species is crucial for our understanding of community structure. Neotropical mammal communities typically consists of several medium- and large-sized carnivores, a range of insectivorous species of superorder *Xenarthra* largely feeding on ants and termites, and multiple ungulates and large rodents (Eisenberg and Redford 2000). Considering the range of vertebrate-feeders, insectivores and the importance of fruits and seeds within several taxa (Haugaasen and Peres 2005), predator-prey relationships and competitive interactions arising from scarcity of any of these resources is likely to exist within the community. Lastly, subsistence hunting is persistent in accessible areas of the Amazon basin, often being the main form of protein acquisition for local villagers (Peres 2000a, Jerozolinski and Peres 2003). Several of the focal species of this study are subject to varying degrees of hunting pressure throughout the basin (Peres and Palacios 2007, Endo et al. 2010, Constantino 2015), and understanding the effect on populations and communities is essential for management decisions.

As an attempt to fill knowledge gaps and strengthen previous findings, the study had four fundamental objectives, namely to (O1) provide descriptions of the temporal and spatial distribution of the resident species and (O2) assess the spatial and temporal relationships among them, (O3) evaluate the impact of the local indigenous settlements on species presence, and (O4) discuss the utility of the presented methodological and analytical procedures. Rooted in the previous introduction to niche segregation, I predicted that (P1) spatial and/or temporal avoidance should be seen among ecologically similar species and that (P2) dynamic predator-prey relationships to be evident in divergent or convergent spatial and temporal patterns. Based on a premise of local depletion or active avoidance, I further predicted that (P3) human presence would induce lower occurrence estimates of the most commonly hunted species near permanent settlements.

2. Methods

2.1 Study site

2.1.1 Area description

The study was conducted along a ~110 km stretch of Rio Xeruã (6°37'20"S 68°14'18"W), a relatively small side river to the lower central part of Rio Juruá in the state of Amazonas, Brazil. The area is classified with a tropical rainforest climate (Alvares et al. 2013), with stable average temperatures around 25°C and a high average precipitation of 2196 mm/yr (Instituto Nacional de Meteorologia n.d.). Although there is no proper dry season, the yearly variation in mean rainfall is pronounced, being lowest in August with 58.2 mm and peaking in April at 263.9 mm (Instituto Nacional de Meteorologia n.d.).

Being a relatively small river, Rio Xeruã is bordered by a narrow tract of seasonally flooded várzea forests on its flat banks, progressing into unflooded terra firme forests in higher terrain. These lowland neotropical rainforests are characterised by a tall and evergreen forest cover providing habitat for a rich epiphyte assemblage and vertically structured plant- and animal communities (Corlett and Primack 2011). Protected by altitude from the annual rise of the rivers, terra firme forests show compositional differences and higher diversity than flooded forests in terms of floristic, mammalian and avian taxa (Haugaasen and Peres 2005, 2006, 2008). Relative abundance of species between the forest types may oscillate with season, and as vertebrates utilize phenological differences to actively pursue peaks in fruit availability (Haugaasen and Peres 2007, Hawes and Peres 2014).

2.1.2 Human population and hunting

The study area runs along the edges of two regularized traditionally occupied indigenous territories, a classification that implies legal recognition of land possession and exclusive use of natural resources for subsistence or economical exploitation (Lei 6001 1973). The 596.433 ha Terra Indígena Kanamarí do Rio Juruá was demarcated in 1997 to encompass part of the area inhabited by the Kanamarí people. The neighbouring Terra Indígena Dení consists of 1.531.300 ha of land possessed by the Dení people since 2004 (Peres and Ricardo 2011). The population sizes of the inhabiting indigenous groups are expanding within both territories; estimates have increased from 496 to 867 Kanamarí and 492 to 1422 Dení between 1984 and 2010 (Ricardo et al. 1984, IBGE 2012).

The study area contains six permanent villages with a total population of around 875, spanning from 39 to 274 inhabitants in each village (Conselho Indigenista Missionário 2009, 2011). The lifestyle of the local villagers is semi-traditional, and subsistence hunting is an important form of protein acquisition. Georeferencing of hunting forays in the local villages showed that very few trips extended beyond 10 km from the permanent settlements (Whaldener Endo, unpublished data). However, the area held several additional settlements before demarcation (Whaldener Endo, personal communication), with relics of historical impact potentially remaining in now uninhabited areas.

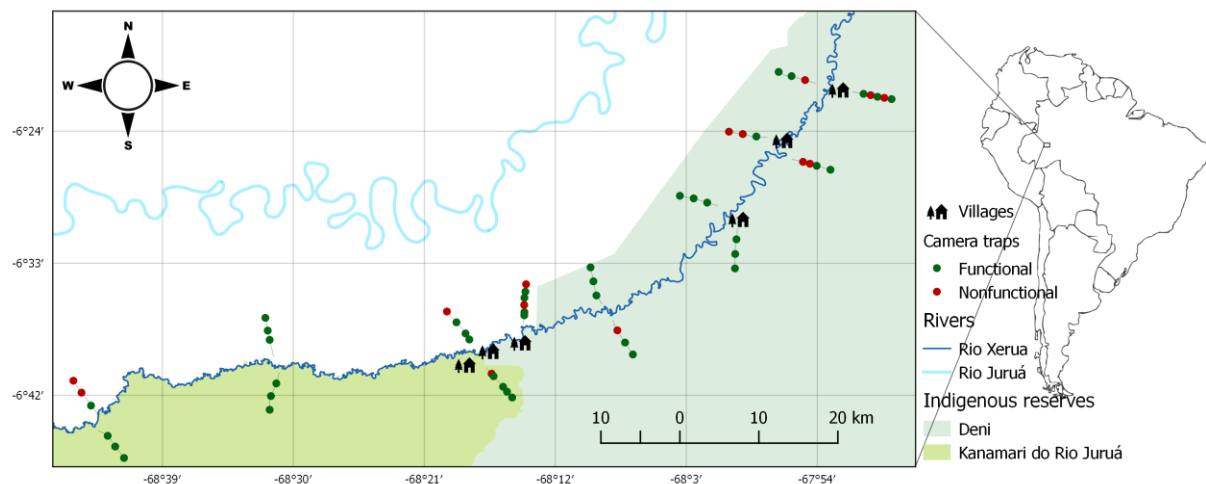


Figure 1. Map showing the study area and distribution of camera.

2.2 Data collection

2.2.1 Camera trapping

Fifty motion sensitive (45 Reconyx HC500 Hyperfire and five Reconyx RM45 Rapidfire) cameras were deployed in a continuous terra firme forest along 15 transects on both sides of Xerua River (Figure 1), between June 2011 and June 2012. Due to the remoteness of the study area, frequent checks of the cameras during their deployment period were not feasible, and the moisture of the tropical forest environment and manipulation by jaguars (Figure 2) took its toll on some of the cameras. Thus, fourteen cameras were removed from the analysis due to early failure, near-absence of triggers or clouded images. For some toppled cameras, the period after position change was removed from the dataset and subtracted from the total duration of camera functionality. Further, some cameras were devoid of images during a suspiciously long period before retrieval. As a compromise between over- and underestimation of the functional period, the last functional date was estimated by adding the mean number of days between images during the certain functional period to the date of the last image. The remaining 36 functional camera stations were operated from 52 to 235 days (mean = 145, SD = 50.2) amounting to 5219 active camera days (Appendix 4). Transects on the same side of the river had a minimum distance of 7 km between them, while functional cameras within transects were separated by 1.2 to 1.9 km (mean = 1.74, SD = 0.15). Camera placements ranged from 2.7 to 47.6 km (mean = 14.12, SD = 13.45) to the nearest village and from 1.2 to 7.7 km (mean = 3.87, SD = 1.55) to the river.

2.2.2 Species identification

Species identification from the camera trap images relied on available field guides (Emmons and Feer 1997, Schulenberg et al. 2007), species distribution maps (IUCN 2015) and help from experienced field biologists. Due to the infrequent appearance of arboreal species at camera height and difficulties with accurately identifying small rodents and marsupials (Figure 2), only medium- and large-sized ground-dwelling species were included in the analysis. The readily photographed and easily distinguishable green acouchi (*Myoprocta pratti*) was included despite its relatively small size. Information on average body size was retrieved for each species from Smith et al. (2003), and mammal feeding guilds from Peres (2000b).



Figure 2. A curious jaguar gets intimate with a camera trap, and leaves it toppled (top). The arboreal great black hawk (*Buteogallus urubitinga*), white-fronted capuchin (*Cebus albifrons*) and margay (*Leopardus wiedii*) descends from the canopy (middle). Relatively uncomplicated photos of the small brown four-eyed opossum (*Metachirus nudicaudatus*), black-eared opossum (*Didelphis marsupialis*) and *Philander* sp. (bottom).

2.3 Statistical analysis

All analyses were conducted in the statistical software R (R Core Team 2015) with the RStudio interface (RStudio Team 2015) and the associated packages and software mentioned below. For the full set of images, timestamps were extracted from the metadata using Exiftool (Harvey 2016). To remove the effect of individuals pausing or repassing in front of the camera, a capture event was defined as images separated by at least one hour. Figure 2 depicts a conceptual diagram of the analytical procedure described below.

2.3.1 Occupancy analysis of spatial patterns

Acknowledging the difficulties of producing reliable abundance estimates from count- or detection/non-detection data, researchers often evade density estimation altogether, instead adopting occupancy (i.e. the probability that a site is occupied by a species) as an alternative population parameter (Burton et al. 2015). The occupancy model framework provides methods for estimating the probability of species occurrence while accounting for imperfect detection, based on detection/non-detection data collected at repeated visits to multiple sites (Mackenzie et al. 2002, Bailey et al. 2013). In this study, individual camera traps provided detection/non-detection data from multiple sites, additionally conflated into detection/non-detection data from multiple transects. The required repeated visits to each site were imitated by partitioning the continuous camera trap data into detection/non-detection data for 24-hour intervals. Note that when individual sites are limited to the area monitored by the camera sensor, they are likely to encompass only a small portion of a specie's home range. In such cases, the assumption that the population is closed (i.e. no changes in site occupancy status) during the survey fails due to only random temporary presence at the site. Thus, the occupancy parameter is more safely interpreted as site "use" (i.e. probability of a site being occupied at some point during the study period) rather than site occupation (Mackenzie and Royle 2005).

Occupancy modelling was used to assess the spatial patterns of all species with more than ten capture events throughout the study period. The ambiguity of non-detections in the data was solved by fitting hierarchical occupancy models in a Bayesian estimation framework, with latent transect use ($z[t]$) and site use ($z[s]$) state variables, indicating estimated presence ($z = 1$) or absence ($z = 0$) at each transect and site (see Nichols et al. 2008). In each iteration of the model, the latent state variables were drawn from a Bernoulli distribution with a probability of transect use (ψ ; probability that a transect is used by the target species) and probability of site use (θ ; probability that a site is used by the target species) fitted with uniform (0,1) priors:

$$\begin{aligned} z[t] &| \psi \sim \text{Bernoulli}(\psi) \\ z[s] &| \theta, z[t] \sim \text{Bernoulli}(\theta) * z[t] \end{aligned}$$

The number of events at each site (y) was modelled as a binomial response dependent on site use state variable, a detection probability (p ; probability of detection given the site is used) fitted with uniform (0,1) priors, and the number of replication surveys (N ; the number of days the camera was active):

$$y | p, z[s] \sim \text{Binomial}(z[s] * p, N)$$

Potential spatial covariates were extracted from GPS data using the open source geospatial information system QGIS 2.8.1 Wien (QGIS Development Team 2015), and the associated plugin NNJoin 1.2.2 (Tveite 2015). After testing potential measures for independence using Pearson's rank correlations, anova and chi-square tests, the side of river and the distance to the river and nearest village were included as spatial covariates in the study. The continuous distance covariates were standardized by subtracting the mean and dividing by the standard deviation. A covariate structure for detection probability was determined for each species by fitting models with all eight potential combinations of the covariates as linear predictors of the log-odds of the detection probability.

$$\text{logit}(p_i) = \alpha + \beta * \text{Cov}_i + \dots$$

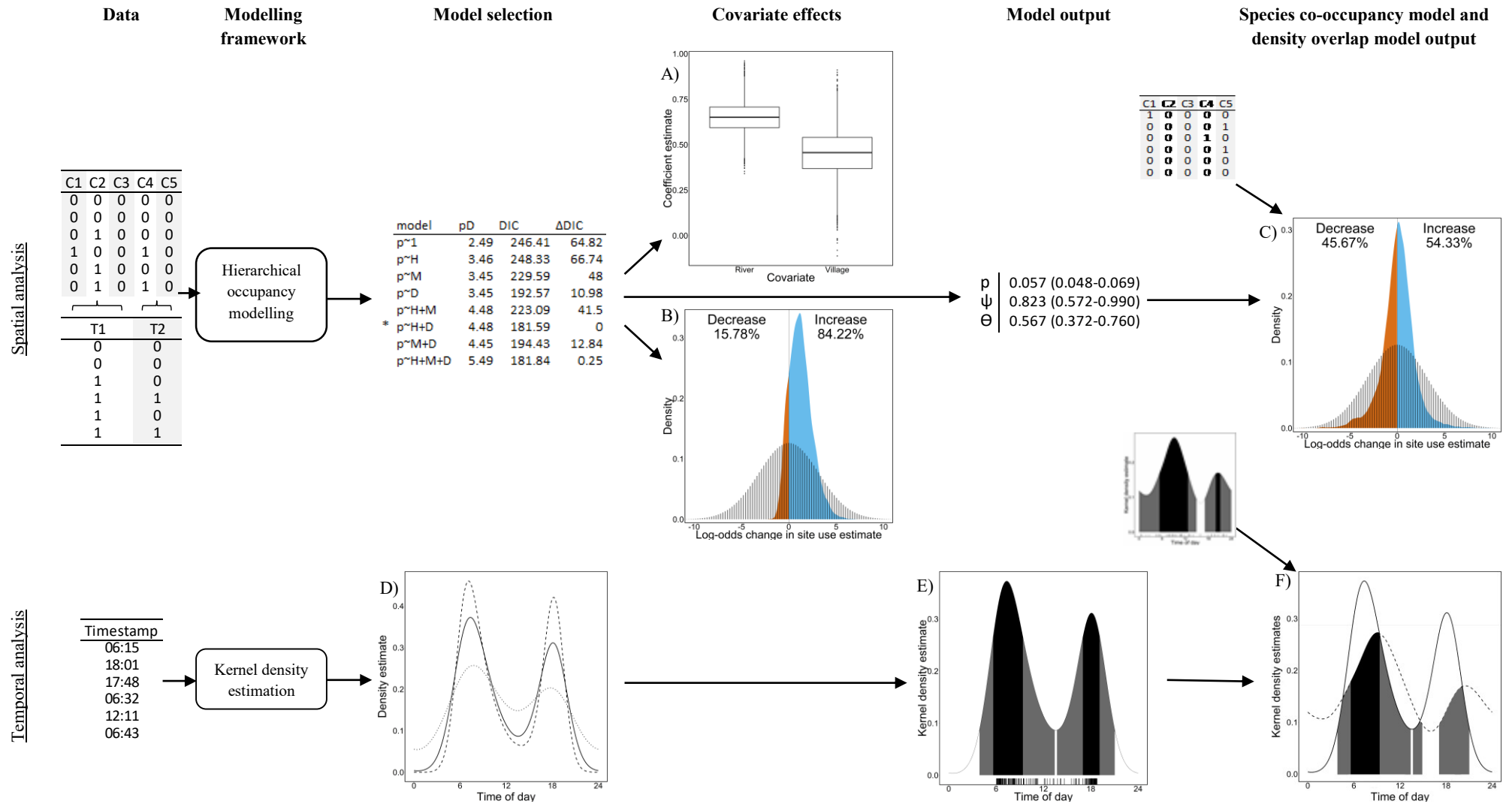


Figure 3. Conceptual diagram depicting the spatial and temporal analysis as described in the main text. Figures for green acouchi is shown: A) Boxplot of posterior point estimates of detection probability covariate coefficients from the chosen model. B) and C) Prior (black) and posterior (red < 0 > blue) distribution of site use covariate coefficient, with distance to the nearest village (B) and ocelot site use (C) as covariates. D) Activity density estimates for a medium bandwidth of 5 (—), a high bandwidth of 10 (---), and the bandwidth estimated using the Taylor method. (····). E) Activity density estimate with a bandwidth of 5, with 95% of the density estimate (black and grey) and 50% of the density estimate (black) indicated. F) Density overlap plot with ocelot, with overlap of their 95% regions (black and grey) and 50% regions (grey) indicated.

where α is the intercept for all sites, β is the coefficient for the first covariate and Cov_i is the value of the first covariate at site i . All covariate effect parameters were fitted with uniform $(-10,10)$ priors. Model selection was based on deviance information criterion (DIC) values calculated from the monitored and posterior estimates of deviance using the original definition by Spiegelhalter et al. (2002), by marginalizing out the latent occupancy state variable from the hierarchical likelihood function. When multiple models were within five DIC-units of the highest ranked model (i.e. with lowest DIC value), the simplest model was used for further analysis (Lunn et al. 2012).

Estimation of covariate effects on transect and site use was regarded as unfeasible due to the failure of the model to discriminate between high parameter estimates when the inverse of the log-odds response reaches one, evident in posterior parameter estimates pushed against the boundaries of the flat priors. Remaining heterogeneity in occupancy parameters does not have the same biasing effects as for the detection probability however, and it is still a valid estimate of the mean across sites. Thus, although an absolute value for the effect of covariates was not assessed, a measure of evidence for the effect of a single covariate and its relative strength between species could be assessed, adapting the method from Bischof et al. (2014). The log-odds of site use was modelled with a flat-prior intercept and a zero-centred normal prior with precision 0.1 for the effect of the covariate in question. The strength and direction of the coefficient posterior distributions deviance from zero was interpreted as evidence for impact. This method was used to assess the effect of villages on the site use estimate of each species, and spatial interaction between each pair of species. The latter utilized the co-occurrence models as parametrized by Waddle et al. (2010), modelling the site use estimate of one species as dependent on the other, and proceed to estimate their parameters simultaneously:

$$\text{logit}(\theta_{1i}) = \alpha + \beta * z[s]_{2i}$$

where θ_{1i} denotes the site use probability of the affected species at site i , α is the intercept for all sites, β is the covariate coefficient, and $z[s]_{2i}$ is the site use state parameter of the second species.

All occupancy models were implemented in the BUGS language, and model parameters were estimated using Gibbs sampling executed in the statistical software JAGS (Plummer 2003) through the ‘R2Jags’ R package (Su and Yajima 2015). Posterior estimates consisted of 12.000 samples from three parallel chains, each with 50.000 iterations with 10.000 burn-ins and a thinning factor of 10. Trace plots and the Gelman-Rubin statistic (Gelman and Rubin 1992) provided by JAGS was used to assess model convergence. The general BUGS model specification and its mathematical counterpart can be found in Appendix 1.

2.3.2 Kernel density analysis of temporal patterns

Dividing species into three activity modes (i.e. “diurnal”, “nocturnal” and “crepuscular”) is a simplification of a reality where species can show divergence in peak activity and sudden bursts in activity following environmental ques. More detailed descriptions of activity patterns are thus desired for more specific inference regarding the temporal niche. Kernel density estimation circumvents the conflation of data required for histograms, and enable extraction of related statistics (Ridout and Linkie 2009, Oliveira-Santos et al. 2013). The method is a non-parametric statistical framework to estimate probability density functions from random samples in cases where assuming a parametric description of the population density is unsuitable. It derives the density estimate directly from the data by wrapping an assumed kernel function (i.e. a non-negative function with a mean of zero and area of one) around each point, placing them on the scale according to distances between data points and an arbitrary point within the range of the distribution’s scale, and summing across the scale:

$$\hat{f}_h(x) = \frac{1}{n} \sum_{i=1}^n K_h(x - x_i)$$

where K_h is the kernel function with smoothing parameter h . The smoothing parameter is called the bandwidth of the function, and determines the shape of the distribution around the data points, and thus ultimately the density function (Silverman 1986). The von Mises distribution resembles a linear normal distribution wrapped around the unit circle, and is typically used for the purpose of describing activity patterns (Ridout and Linkie 2009, Oliveira-Santos et al. 2013, Rowcliffe et al. 2014). The choice of bandwidth has strong influence over the results, and thus clear implications for inference. Ridout and Linkie (2009) suggested using the method developed by Taylor (2007), which aims to provide automated smoothing by choosing the bandwidth that minimizes the asymptotic mean squared error of the estimated function. However, Oliveira-santos et al. (2013) advocate using ad hoc approaches to bandwidth selection in order to maintain better control over assumptions, particularly regarding the significance of narrow gaps in small-sampled biological data.

In this thesis, an ad-hoc sensitivity analysis was conducted to choose a collective bandwidth for all species that did not produce any extreme outcomes (Appendix 2). For each species with more than ten capture events, timestamp data were pooled for the full study period and converted to radian time with origin at midnight. The von Mises kernel densities were estimated for a range of bandwidths between 0.1 and 15.1 and for the Taylor-method in particular, utilizing the R packages ‘circular’ (Agostinelli and Lund 2013) and ‘overlap’ (Meredith and Ridout 2016). In accordance with the results of Oliveira-Santos et al. (2013), the Taylor-method seemed to produce highly unreliable estimates, while a bandwidth of five fell within regions of relatively stable estimates of activity proportions (Appendix 2) and was chosen for further analysis.

The R package ‘circular’ (Agostinelli and Lund 2013) was utilized to estimate the final von Mises probability density functions (PDF) with a bandwidth of five, and their respective 95% and 50% modal regions (i.e. the narrowest region that contains a given proportion of the PDF). The activity range (AR; i.e. the total duration of estimated activity) was derived from the PDFs, conditional on both the 95% and 50% isopleths (i.e. the limits of the given modal regions on the time-axis). Further, the coefficient of overlap (OVL; i.e. the joint area of two density distributions) was calculated for all species pairs according to the method outlined in Oliveira-santos et al. (2013), conditional on both the 95% and 50% isopleths. Recalculation from 200 bootstrap samples provided 95% confidence intervals of the activity range and overlap estimates.

3. Results

3.1 Data summary

The 36 functional camera stations produced 2151 capture events. This included 1197 captures of ground-dwelling mammals and 429 captures of ground-dwelling birds (Table 1). The remaining captures consisted of 30 captures of non-terrestrial birds, 96 captures of arboreal mammals, 39 captures of *Squamata*, 306 captures of unidentified animals and 54 captures of passing humans (Appendix 3). Additionally, 6484 images were devoid of any visible animal (Appendix 3).

Among the ground-dwelling animals, some sympatric species with similar morphology were pooled into genus to avoid false detections; *Mazama* sp. comprise Red brocket (*Mazama americana*) and Amazonian brown brocket (*Mazama nemorivaga*), *Dasyopus* sp. includes Nine-banded armadillo (*Dasyopus novemcinctus*) and Greater long-nosed armadillo (*Dasyopus kappleri*), while *Tinamus* sp. and *Crypturellus* sp. are two genera of birds belonging to the family *Tinamidae*. Thus, the total dataset on ground-dwelling animals includes 18 species and two unseparated genera of mammals, and three species and two unseparated genera of birds (Table 1).

The photo-captured community of medium and large mammals consisted of four obligate carnivores, four mixed-feeding carnivores incorporating fruits and invertebrates in their diet, five insectivores all feeding to a large degree on ants and termites (Peres 2000b, Da Silveira Anacleto 2007), three frugivorous-granivorous large rodents, the frugivorous-folivorous deer and lowland tapir, and two species of mainly granivorous-frugivorous peccaries (Table 1).

Table 1. Summary of ground-dwelling animals captured during the study period, number and frequency (/1000 days) of capture events, and proportion of cameras that photographed the species.

Mammalia							Capture events	Capture frequency (events/1000 days)	Camera proportion
Order	Family	Genus	Species	Common name	Guild ¹	Size ² (kg)			
Carnivora	Felidae	Panthera	onca	Jaguar	Vp	100.0	41	7.47	0.44
Carnivora	Felidae	Puma	concolor	Puma	Vp	51.6	14	2.55	0.28
Carnivora	Felidae	Herpailurus	yagouaroundi	Jaguarundi	Vp	6.7	4	0.73	0.11
Carnivora	Felidae	Leopardus	pardalis	Ocelot	Vp	11.9	51	9.3	0.53
Carnivora	Canidae	Atelocynus	microtis	Short-eared dog	Vp/Fr	7.8	15	2.73	0.25
Carnivora	Mustelidae	Eira	barbara	Tayra	Fr/In/Vp	3.9	13	2.37	0.31
Carnivora	Procyonidae	Nasua	nasua	South American coati	In/Vp	3.8	5	0.91	0.08
Carnivora	Procyonidae	Procyon	cancrivorus	Crab-eating raccoon	In/Vp/Fr	6.9	5	0.91	0.14
Cingulata	Dasypodidae	Cabassous	unicinctus	Southern naked-tailed armadillo	In	4.8	5	0.91	0.11
Cingulata	Dasypodidae	Dasyus		Dasyus spp.	In		66	12.03	0.67
Cingulata	Dasypodidae	Priodontes	maximus	Giant armadillo	In	45.4	19	3.46	0.42
Pilosa	Myrmecophagidae	Myrmecophaga	tridactyla	Giant anteater	In	22.3	25	4.56	0.36
Pilosa	Myrmecophagidae	Tamandua	tetradactyla	Southern Tamandua	In	5.5	5	0.91	0.14
Rodentia	Cuniculidae	Cuniculus	paca	Spotted paca	Gr/Fr	8.0	74	13.49	0.5
Rodentia	Dasyproctidae	Dasyprocta	fuliginosa	Black agouti	Gr/Fr	3.5	380	69.27	0.92
Rodentia	Dasyproctidae	Myoprocta	pratti	Green acouchi	Gr/Fr	0.6	192	35	0.5
Cetartiodactyla	Cervidae	Mazama		Brocket deer	Fr/Fo		171	31.17	0.83
Cetartiodactyla	Tayassuidae	Pecari	tajacu	Collared peccary	Gr/Fr/Vp	21.3	90	16.41	0.69
Cetartiodactyla	Tayassuidae	Tayassu	pecari	White-lipped peccary	Gr/Fr	32.2	1	0.18	0.03
Perissodactyla	Tapiridae	Tapirus	terrestris	Lowland tapir	Fr/Fo	207.5	21	3.83	0.25
Aves							Capture events	Capture frequency (events/1000 days)	Camera proportion
Order	Family	Genus	Species	Common name	Guild	Size (kg)			
Galliformes	Cracidae	Mitu	tuberosum	Razor-billed curassow			124	22.6	0.81
Galliformes	Cracidae	Penelope	jacquacu	Spix's guan			58	10.57	0.61
Gruiformes	Psophiidae	Psophia	leucoptera	Pale-winged trumpeter			136	24.79	0.75
Struthioniformes	Tinamidae	Crypturellus		Crypturellus sp.			47	8.57	0.39
Struthioniformes	Tinamidae	Tinamus		Tinamus sp.			64	11.67	0.58

¹Information on general feeding guild was taken from Peres (2000b). Notations indicate: Vp = Vertebrate predator, Fr = Frugivore, In = Insectivore, Gr = Granivore, Fo = Folivore

²Information on average body size was taken from Smith et al. (2003)

3.2 Activity patterns and temporal relationships

The three felids with sufficient captures for analysis seem to retain long activity periods (Table 2) and some activity throughout most of the day and night (Figure 4), evident in their high overlap in the 95% modal regions (Table 4). However, there is a striking divergence between the distribution peaks (Figure 4). The ocelot is primarily night-active with the full 50% modal region falling between sunset and sunrise, but there is a significant right-skewed peak around noon, separated from the nocturnal captures by periods devoid of observations. The diurnal peaks of the two apex predators fall chiefly within these periods; jaguar activity peaks in the morning and the activity of puma in late afternoon. Further, their night-time activity peaks show the same divergent skew around midnight. This pattern is confirmed for the two apex predators by the large decline in overlap between their 95% and 50% modal regions, but for ocelot the peak overlap estimates were vastly uncertain (Table 4).

Aside from the cathemeral obligate carnivores, species activity ranges were generally shorter (Table 2) and divided among three patterns: unimodal diurnal or nocturnal, or bimodal crepuscular (Figure 4). The long activity periods and cathemeral behaviour estimated from the kernel densities of the lowland tapir and giant armadillo are exceptions among the non-carnivores. Note however that they both show unimodal nocturnal behavior compared to the obligate predators in terms of proportion of captures, disrupted by a few mid-day observations (Figure 4, Table 2).

The estimates of activity overlap generally reflected this division between activity patterns (Table 4). Within groups of similar foraging strategies, the mixed-feeding carnivores (short-eared dog and tayra) and the birds (Spix's guan, pale-winged trumpeter and razor-billed curassow) showed significant convergence in activity patterns. The mixed-feeding carnivores retained the overlap in their 50% overlap estimates, while no evidence was found for convergence or divergence among the activity peaks of the birds. On the contrary, the insectivorous giant anteater and giant armadillo showed significant divergence between activity peaks but not overall activity. Two of the large rodents, black agouti and green acouchi, show convergence in their crepuscular activity patterns, but a significant decline to their 50% overlap estimates, owing to a stronger crepuscular affinity for the green acouchi. They both show a strong divergence from the nocturnal spotted paca, which abstain from any crepuscular activity.

The long and cathemeral activity patterns of the obligate carnivores generally induced intermediate overlap with all non-carnivorous species (Table 4). Only the short-eared dog shows significant divergence from the ocelot. All other exceptions are species showing convergence towards carnivore activity patterns; the black agouti with both jaguar and puma, green acouchi with jaguar and Spix's guan with puma. No species show significant convergence with the obligate predators in the 50% modal regions, but several show strong divergence (Table 4). The nocturnal peaks of giant armadillo and spotted paca diverge from the pre-midnight peak of the jaguar. A similar divergence is seen between the pre-noon peaks of the short-eared dog, tayra, collared peccary and razor-billed curassow and the evening-peak of the puma. The 50% modal region of the ocelot were confined within the nocturnal hours, leading to peak divergence from mainly diurnal species.

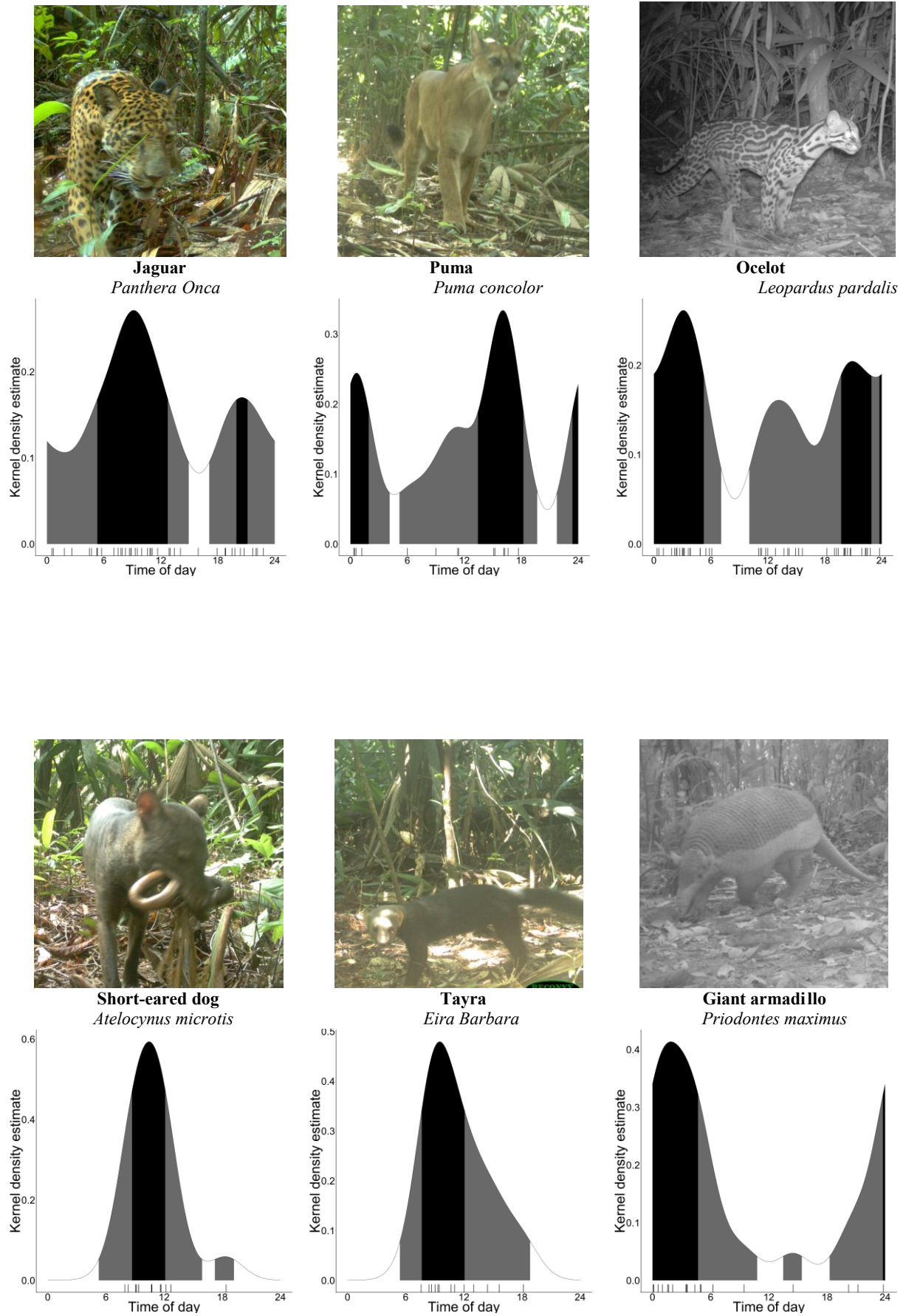
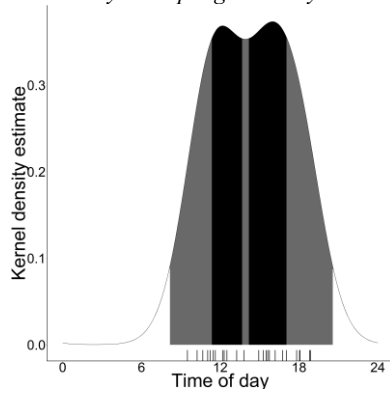


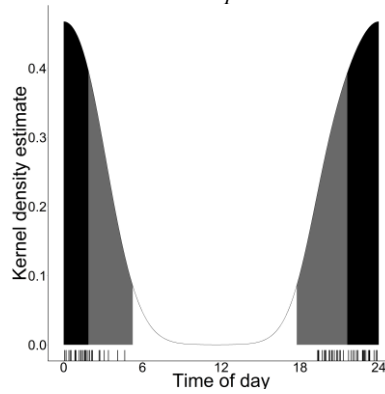
Figure 4. Example photographs captured during camera trapping (top) and plots of kernel densities of activity estimated with a bandwidth of five, including rug plots indicating temporal dispersion of captures (bottom).



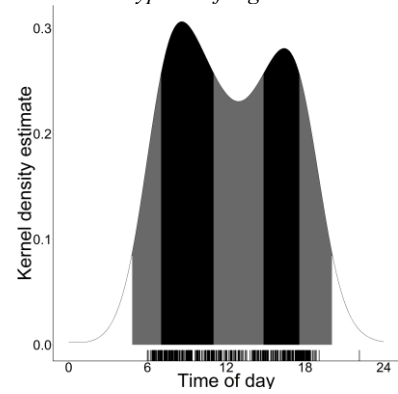
Giant anteater
Myrmecophaga tridactyla



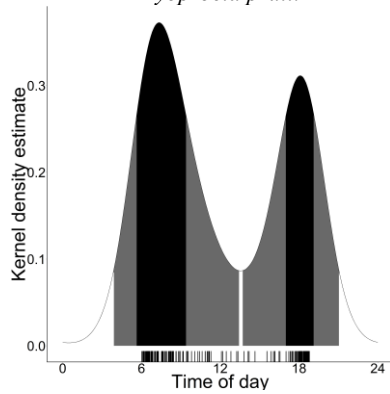
Spotted paca
Cuniculus paca



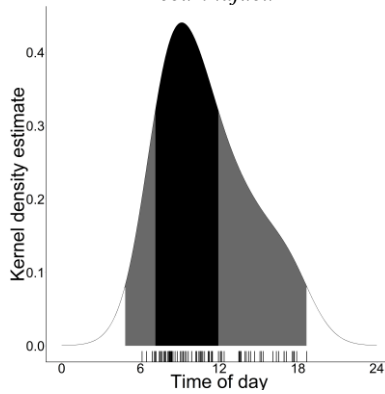
Black agouti
Dasyprocta fuliginosa



Green acouchi
Myoprocta pratti



Collared peccary
Pecari tajacu



Lowland tapir
Tapirus terrestris

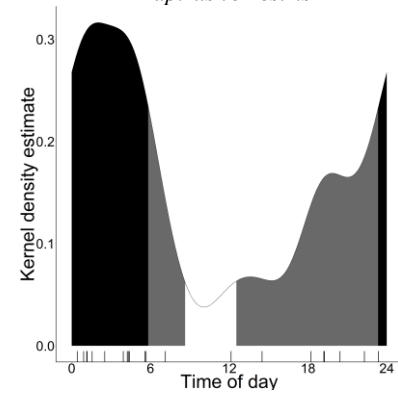


Figure 4 cont.

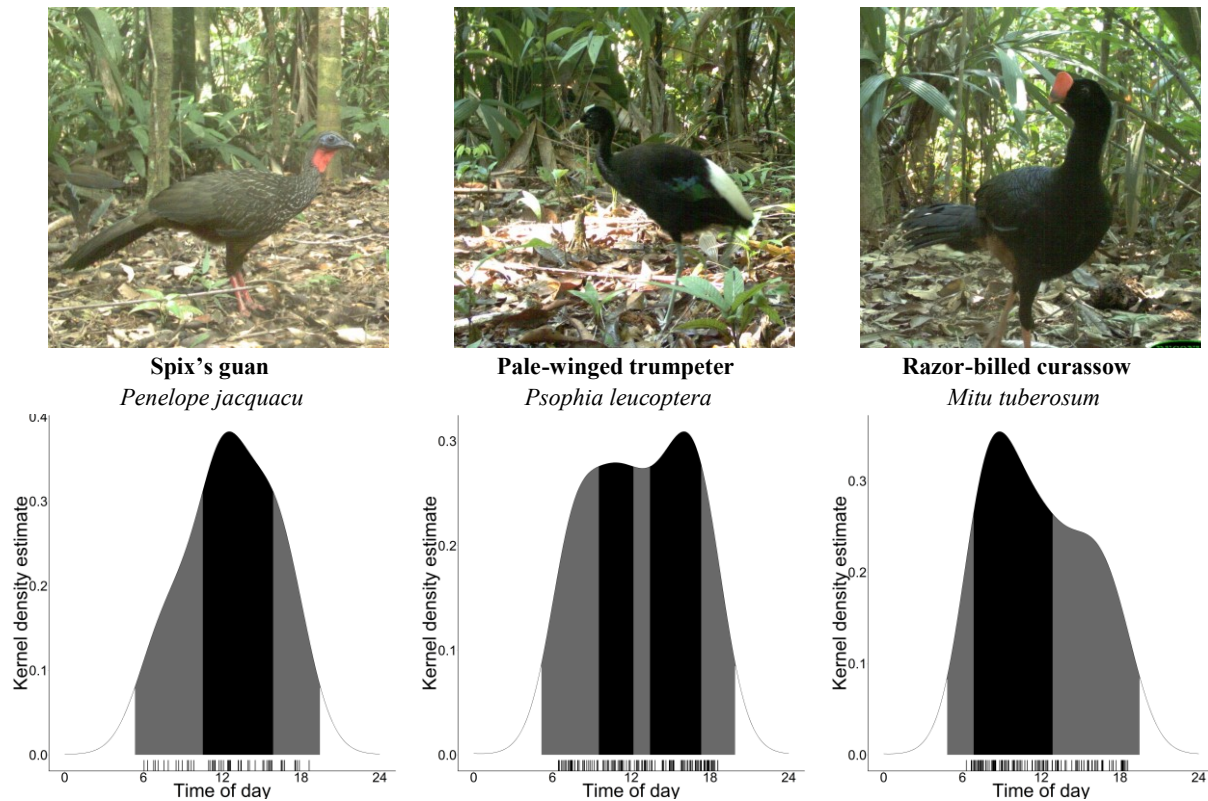


Figure 4 cont.

Table 2. Dispersion of captures among the day, night and the crepuscular period, and estimated activity ranges for all species.

	Capture proportion ¹ [N (%)]			Activity range ² (h)	
	Day	Night	Crepuscular	95% isopleth	50% isopleth
Jaguar	21 (51%)	18 (44%)	2 (5%)	21.81 (21.29-22.95)	8.67 (7.54-11.8)
Puma	8 (57%)	4 (29%)	2 (14%)	20.92 (20.47-23.21)	7.43 (6.36-11.65)
Jaguarundi	3 (75%)	0 (0%)	1 (25%)		
Ocelot	14 (27%)	34 (67%)	3 (6%)	20.96 (20.2-22.03)	8.78 (8.02-11.39)
Short-eared dog	14 (93%)	0 (0%)	1 (7%)	12.72 (10.88-16.78)	3.47 (2.79-4.16)
Tayra	12 (92%)	0 (0%)	1 (8%)	13.46 (11.88-17.08)	4.49 (3.44-6.50)
South American Coati	4 (80%)	0 (0%)	1 (20%)		
Crab-eating raccoon	1 (20%)	4 (80%)	0 (0%)		
Southern naked-tailed armadillo	2 (40%)	2 (40%)	1 (20%)		
Dasyus spp.	0 (0%)	65 (98%)	1 (2%)		
Giant armadillo	2 (11%)	16 (84%)	1 (5%)	18.46 (16.12-22.46)	4.99 (3.53-6.75)
Giant anteater	20 (80%)	3 (12%)	2 (8%)	12.44 (11.7-13.56)	5.24 (4.89-6.76)
Southern tamandua	3 (60%)	2 (40%)	0 (0%)		
Spotted paca	0 (0%)	74 (100%)	0 (0%)	11.46 (10.79-12.22)	4.32 (3.92-4.85)
Black agouti	312 (82%)	9 (2%)	59 (16%)	15.27 (14.97-15.59)	6.79 (6.63-7.15)
Green acouchi	105 (55%)	20 (10%)	67 (35%)	16.92 (16.75-17.21)	5.99 (5.63-6.48)
Collared peccary	83 (92%)	1 (1%)	6 (7%)	13.89 (13.23-14.94)	4.82 (4.16-5.68)
White-lipped peccary	0 (0%)	0 (0%)	1 (100%)		
Lowland tapir	3 (14%)	15 (71%)	3 (14%)	20.03 (18.13-22.84)	6.52 (4.60-9.25)
Brocket deer	113 (66%)	38 (22%)	20 (12%)		
Razor-billed curassow	113 (91%)	2 (2%)	9 (7%)	14.68 (14.21-15.42)	6.06 (5.54-7.00)
Spix's guan	51 (88%)	1 (2%)	6 (10%)	14.15 (13.37-15.60)	5.39 (4.74-6.47)
Pale-winged trumpeter	116 (85%)	2 (1%)	18 (13%)	14.76 (14.28-15.30)	6.62 (6.37-7.64)
Crypturellus sp.	35 (74%)	1 (2%)	11 (23%)		
Tinamus sp.	47 (73%)	4 (6%)	13 (20%)		

¹The number and percentage of images captured during the day (06:30-17:30), night (18:30-05:30) and crepuscular periods (05:30- 06:30 and 17:30-18:30)

²The estimated total duration of daily activity (the extent of the 95% and 50% modal regions on the time-axis)

3.3 Occupancy estimates, anthropogenic impacts, and spatial relationships

For eight species (puma, short-eared dog, tayra, giant armadillo, giant anteater, spotted paca, collared peccary, lowland tapir and Spix's guan), none of the models including covariates on the detection probability proved better than the model with constant detection (Appendix 5). The best model included distance to the nearest village as a significant covariate for the jaguar and the ocelot. The distance to the river was a significant covariate in the best model for the razor-billed curassow and the pale-winged trumpeter. Both distance to the nearest village and distance to the river were significant covariates in the best model for the black agouti and the green acouchi (Appendix 5).

The model-estimated occupancy and detection probabilities represented considerable adjustments of the naïve estimates (capture frequency and proportion of cameras that captured the species), indicating potentially severe underestimation of presence of up to almost 50% (Table 1 and 3). The black agouti was both the most spatially widespread and readily detected of the species, while the green acouchi had an almost equally high detection rate but was restricted to fewer transects and sites. All other species were far less likely to be captured, in particular short-eared dog, giant armadillo, puma and tayra. All species were widespread throughout the area with high estimates of use at the scale of transects. Within occupied transects, the lowland tapir emerged with a low estimate of use. The puma, short-eared dog, giant anteater, spotted paca and green acouchi were also using relatively few sites (Table 3).

Few species showed significant model-predicted probabilities of covariate effects on occupancy estimates (Table 3 and 4). The spotted paca and black agouti site use parameter decreased towards villages, while the pale-winged trumpeter site use parameter increased (Table 3). Only the jaguar and giant anteater showed significant spatial divergence, while five pairs showed significant positive affiliation; jaguar with lowland tapir, puma and spotted paca with Spix's guan, green acouchi with pale-winged trumpeter and collared peccary with lowland tapir (Table 4).

Table 3. Occupancy model outputs from the best-fitting detection covariate model, and the effect of villages on site use.

Species	Covariates ¹	p ²	ψ ²	Θ ²	Log-odds change in occupancy ³
Jaguar	p ~ V	0.013 (0.009-0.017)	0.730 (0.459-0.957)	0.779 (0.514-0.978)	54.55% (+), 0.18
Puma	p ~ 1	0.005 (0.002-0.010)	0.800 (0.475-0.992)	0.658 (0.329-0.972)	84.22% (+), 2.36
Ocelot	p ~ V	0.013 (0.009-0.016)	0.741 (0.489-0.943)	0.884 (0.658-0.996)	51.01% (+), 0.30
Short-eared dog	p ~ 1	0.007 (0.003-0.013)	0.758 (0.405-0.988)	0.563 (0.260-0.937)	71.22% (+), 1.21
Tayra	p ~ 1	0.004 (0.002-0.007)	0.861 (0.591-0.996)	0.785 (0.449-0.991)	57.30% (+), 0.61
Giant armadillo	p ~ 1	0.005 (0.003-0.009)	0.844 (0.564-0.994)	0.822 (0.529-0.992)	72.67% (-), 1.64
Giant anteater	p ~ 1	0.010 (0.006-0.016)	0.806 (0.510-0.990)	0.577 (0.334-0.872)	65.85% (+), 0.70
Spotted paca	p ~ 1	0.027 (0.021-0.033)	0.871 (0.639-0.995)	0.572 (0.388-0.757)	96.53% (+), 1.52
Black agouti	p ~ V + D	0.067 (0.060-0.074)	0.942 (0.795-0.999)	0.871 (0.749-0.957)	99.33% (+), 3.36
Green acouchi	p ~ V + D	0.057 (0.048-0.069)	0.823 (0.572-0.990)	0.567 (0.372-0.760)	84.70% (+), 1.25
Collared peccary	p ~ 1	0.024 (0.019-0.029)	0.941 (0.794-0.998)	0.721 (0.557-0.864)	72.48% (+), 0.48
Lowland tapir	p ~ 1	0.013 (0.007-0.021)	0.814 (0.491-0.993)	0.380 (0.184-0.648)	86.90% (+), 0.85
Razor-billed curassow	p ~ D	0.022 (0.018-0.026)	0.927 (0.750-0.998)	0.870 (0.726-0.969)	87.08% (+), 1.45
Spix's guan	p ~ 1	0.015 (0.011-0.020)	0.849 (0.638-0.985)	0.814 (0.604-0.975)	70.35% (+), 1.24
Pale-winged trumpeter	p ~ D	0.027 (0.022-0.031)	0.940 (0.791-0.998)	0.793 (0.636-0.918)	98.40% (-), 0.98

¹Covariates of the detection probability is indicated by: 1 = no covariates, V = distance to the nearest village and D = distance to the river.

²Detection probability (p), transect use probability (ψ) and site use probability (Θ) is shown for the best-fitting occupancy model with no covariates of estimates of use.

³Column indicates the estimated probability, direction and magnitude of the effect of the distance to nearest village on the log-odds of the site use estimate. Negative directions indicate an increase towards villages. Significant (i.e. probability > 0.95) effects are shown in bold.

	Jaguar (a) 0.614 (0.463-0.805) (b) 0.002 (0-0.003) * (c) 92.76% (-), -2.81								
Puma		Puma							
	0.691 (0.59-0.821) 0.108 (0.017-0.954) 91.83% (-), -2.4	0.663 (0.591-0.847) 0.236 (0.079-0.99) 74.17% (+), 1.71							
Ocelot			Ocelot						
	0.547 (0.406-0.716) 0.444 (0.273-0.93) 78.96% (-), -1.42	0.412 (0.248-0.742) 0.002 (0-0.007) * 67.52% (+), 1.19	0.284 (0.185-0.467) 0.002 (0-0.004) * 59.03% (-), -0.48		Short-eared dog				
Short-eared dog									
	0.571 (0.38-0.711) 0.583 (0.348-0.945) 65.18% (-), -0.95	0.531 (0.306-0.787) 0.001 (0-0.007) * 62.82% (+), 0.97	0.363 (0.261-0.559) 0.001 (0-0.004) * 57.32% (+), 0.51	0.852 (0.75-0.954) 0.78 (0.55-0.97) 85.35% (+), 2.66		Tayra			
Tayra									
	0.541 (0.398-0.748) 0.003 (0-0.003) * 53.46% (-), -0.16	0.454 (0.247-0.786) 0.265 (0.082-0.994) 52.78% (+), 0.28	0.646 (0.445-0.791) 0.607 (0.391-0.979) 64.28% (-), -0.86	0.174 (0.085-0.051) 0.003 (0.002-0.003) * 55.07% (+), 0.39	0.174 (0.086-0.447) 0.003 (0.001-0.002) * 56.77% (+), 0.57		Giant armadillo		
Giant armadillo									
	0.453 (0.296-0.615) 0.144 (0.027-0.975) 95.97% (-), -2.55	0.639 (0.391-0.866) 0.494 (0.128-0.997) 60.5% (+), 0.75	0.396 (0.276-0.579) 0.003 (0-0.004) * 81.53% (+), 1.82	0.525 (0.29-0.706) 0.152 (0.012-0.953) 73.32% (-), -1.09	0.631 (0.272-0.842) 0.142 (0.01-0.958) 61.78% (+), 0.88	0.119 (0.044-0.861) 0.003 (0.002-0.008) * 66.14% (+), 1.16		Giant anteater	
Giant anteater									
	0.421 (0.3-0.648) 0.003 (0-0.003) * 62.72% (+), 0.32	0.35 (0.149-0.681) 0.304 (0.087-0.996) 66.18% (+), 0.94	0.607 (0.5-0.723) 0.377 (0.188-0.852) 87.82% (+), 2.15	0.023 (0.005-0.352) 0.003 (0.002-0.003) * 61.56% (+), 0.59	0.028 (0.006-0.445) 0.003 (0.001-0.002) * 64.73% (+), 1.05	0.667 (0.466-0.822) 0.436 (0.131-0.969) 57.8% (+), 0.59	0.112 (0.07-0.237) 0.003 (0.002-0.008) * 82.16% (+), 1.11		Spotted paca
Spotted paca									
	0.655 (0.519-0.771) 0.541 (0.331-0.878) 87.57% (+), 1.71	0.683 (0.521-0.875) 0.393 (0.134-0.791) 78.97% (+), 2.18	0.444 (0.339-0.577) 0.002 (0-0.004) * 88.32% (+), 2.06	0.656 (0.52-0.75) 0.359 (0.199-0.682) 51.52% (-), -0.17	0.789 (0.588-0.897) 0.526 (0.345-0.888) 56.1% (+), 0.49	0.23 (0.133-0.427) 0.002 (0.002-0.007) * 64.72% (+), 1.07	0.74 (0.648-0.829) 0.002 (0.003-0.004) * 57.33% (+), 0.16	0.094 (0.071-0.136) 0.002 (0.003-0.004) * 86.62% (+), 1.38	Black agouti
Black agouti									
	0.659 (0.513-0.752) 0.469 (0.303-0.85) 54.78% (-), -0.15	0.537 (0.362-0.712) 0.162 (0.056-0.934) 54.83% (-), -0.1	0.485 (0.436-0.569) 0.002 (0-0.003) * 52.94% (+), 0.13	0.514 (0.372-0.616) 0.114 (0.026-0.906) 83.82% (+), 1.61	0.617 (0.443-0.772) 0.306 (0.141-0.993) 66.8% (+), 1.19	0.322 (0.196-0.521) 0.002 (0-0.006) * 61.85% (+), 0.87	0.572 (0.48-0.671) 0.017 (0.001-0.194) * 50.39% (+), 0.05	0.185 (0.147-0.241) 0.002 (0.003-0.004) * 93.25% (+), 1.11	0.763 (0.694-0.814) 0.446 (0.321-0.624) * 82.4% (+), 1.19
Green acouchi									
	0.599 (0.41-0.728) 0.628 (0.349-0.914) 69.48% (+), 0.56	0.53 (0.323-0.786) 0.001 (0-0.006) * 53.03% (-), -0.04	0.384 (0.289-0.528) 0.001 (0-0.004) * 85.52% (-), -2.07	0.806 (0.728-0.896) 0.684 (0.461-0.882) 52.61% (-), -0.09	0.944 (0.94-0.992) 0.904 (0.836-0.997) 75.49% (+), 1.96	0.203 (0.102-0.383) 0.001 (0.002-0.007) * 53.13% (+), 0.33	0.609 (0.465-0.742) 0.104 (0.011-0.919) 54.69% (-), -0.27	0.035 (0.017-0.146) 0.001 (0.003-0.004) * 86.82% (+), 1.11	0.816 (0.711-0.887) 0.597 (0.39-0.803) 75.78% (+), 0.82
Collared peccary									
	0.626 (0.49-0.803) 0.055 (0.004-0.822) 96.08% (+), 2.83	0.54 (0.35-0.802) 0.306 (0.081-0.996) 53.94% (-), -0.06	0.797 (0.67-0.92) 0.662 (0.431-0.958) 91.86% (-), -2.4	0.194 (0.082-0.476) 0.002 (0.002-0.003) * 71.65% (+), 1.18	0.242 (0.137-0.576) 0.002 (0-0.002) * 51.41% (-), 0.01	0.834 (0.748-0.954) 0.795 (0.538-0.982) 63.42% (+), 0.94	0.226 (0.126-0.502) 0.002 (0-0.002) * 58.53% (-), -0.17	0.666 (0.518-0.818) 0.002 (0.003-0.004) * 84.82% (+), 0.97	0.329 (0.211-0.518) 0.002 (0-0.002) * 50.43% (-), -0.07
Lowland tapir									
	0.63 (0.446-0.76) 0.739 (0.483-0.961) 50.94% (+), -0.08	0.63 (0.466-0.829) 0.001 (0-0.007) * 57.92% (-), -0.42	0.417 (0.323-0.528) 0.001 (0-0.004) * 59.05% (-), -0.7	0.728 (0.635-0.827) 0.584 (0.34-0.836) 51.18% (-), -0.15	0.865 (0.761-0.96) 0.769 (0.636-0.973) 63.97% (+), 1.07	0.217 (0.108-0.396) 0.001 (0.002-0.007) * 59.02% (+), 0.67	0.695 (0.57-0.807) 0.224 (0.056-0.985) 90.3% (+), 2.69	0.065 (0.043-0.131) 0.001 (0.003-0.004) * 64.17% (-), -0.93	0.917 (0.82-0.964) 0.612 (0.281-0.821) 66.44% (-), -1.18
Razor-billed curassow									
	0.548 (0.397-0.692) 0.249 (0.072-0.989) 92.44% (-), -2.37	0.675 (0.517-0.874) 0.345 (0.063-0.989) 96.56% (+), 4.34	0.39 (0.292-0.552) 0.001 (0-0.004) * 74.8% (+), 1.34	0.676 (0.545-0.816) 0.303 (0.094-0.991) 72.46% (+), 1.28	0.779 (0.542-0.916) 0.292 (0.048-0.991) 72.88% (+), 1.78	0.18 (0.096-0.5) 0.001 (0.002-0.007) * 70.05% (+), 1.47	0.842 (0.737-0.929) 0.743 (0.382-0.983) 82.32% (+), 1.69	0.054 (0.031-0.192) 0.001 (0.003-0.004) * 96.02% (+), 2.25	0.836 (0.689-0.901) 0.229 (0.062-0.566) * 90.72% (+), 1.96
Spix's guan									
	0.624 (0.475-0.733) 0.332 (0.079-0.994) 77.62% (-), -1.53	0.704 (0.498-0.884) 0.571 (0.293-0.998) 67.55% (-), -1.02	0.423 (0.314-0.546) 0.002 (0-0.004) * 68.77% (+), 0.86	0.657 (0.529-0.774) 0.389 (0.234-0.995) 50.48% (+), 0.05	0.786 (0.599-0.915) 0.384 (0.113-0.997) 61.32% (+), 0.82	0.207 (0.099-0.418) 0.002 (0.002-0.006) * 53.89% (+), 0.35	0.796 (0.705-0.892) 0.615 (0.383-0.947) 79.57% (-), -1.47	0.078 (0.054-0.126) 0.002 (0.003-0.004) * 77.05% (+), 0.84	0.937 (0.865-0.975) 0.591 (0.218-0.852) * 67.54% (-), -1.17
Pale-winged trumpeter									

Table 4 cont.

	Green acouchi				
Collared peccary	0.666 (0.584-0.734)		Collared peccary		
	0.397 (0.243-0.595)				
	92.59% (+), 1.33				
	0.437 (0.307-0.606)		0.27 (0.148-0.481)		
Lowland tapir	0.032 (0.003-0.363)		0.002 (0-0.002) *	Lowland tapir	
	65.37% (+), 0.35		99.47% (+), 3.71		
Razor-billed curassow	0.721 (0.636-0.79)	0.895 (0.724-0.954)	0.304 (0.178-0.495)	Razor-billed curassow	
	0.42 (0.259-0.759)	0.824 (0.63-0.961)	0.001 (0-0.005) *		
	77.28% (+), 0.98	93.34% (+), 2.63	93.24% (+), 2.73		
	0.607 (0.494-0.691)	0.759 (0.602-0.863)	0.264 (0.153-0.492)	0.842 (0.692-0.914)	
Spix's guan	0.001 (0-0.002) *	0.255 (0.061-0.989)	0.001 (0-0.004) *	0.363 (0.094-0.797)	Spix's guan
	64.62% (+), 0.56	67.49% (+), 0.55	68.7% (-), -0.63	88.84% (-), -2.38	
Pale-winged trumpeter	0.706 (0.627-0.774)	0.785 (0.621-0.879)	0.303 (0.178-0.48)	0.889 (0.692-0.954)	0.892 (0.781-0.954)
	0.057 (0.004-0.643)	0.36 (0.111-0.996)	0.002 (0-0.005) *	0.392 (0.05-0.812)	0.622 (0.248-0.914)
	98.66% (+), 2.42	85.5% (+), 1.17	59.63% (-), -0.42	80.65% (-), -1.85	92.04% (-), -2.61

4. Discussion

4.1 The ground-dwelling animal community along Xerua River

The camera traps uncovered a diverse community of medium- and large-sized ground-dwelling mammals and birds in the studied tract of terra firme forest along Xerua River. All species were estimated to occur throughout most of the area. With most species sharing either vertebrate prey, ants and termites or fallen fruits as important dietary components, they are all likely to be subject to some degree of resource competition. Considering the wide range of vertebrate feeders and cathemeral activity behaviour of the top predators, most species are also prone to encounters with predators. In addition to these ecological interactions, several of the resident species provides an important protein source for more than 800 local villagers, thus making them susceptible to hunting pressure.

Having to share their environment, species must waive their potential niche breadth and conform to a reality where humans are pervading, predators are lurking, and competitors are plundering. Time and space provides axes over which they can converge to strengthen beneficial interactions and diverge to lessen detrimental ones. This thesis aimed to (O1) describe the use of these niche axes for the resident species, (O2) assess the spatial and temporal relationships among them and (O3) evaluate the impact of local indigenous settlements on species presence. The following summary of the diverse findings and comparison with previous literature allow some insight into niche use, community interactions and human influence on the community.

4.1.1 Temporal distribution of ground-dwelling animals

Apart from the obligate carnivores, species were mostly constrained to specific diurnal, nocturnal or crepuscular activity patterns. These were generally consistent with previously published empirical work. A similar study from the Ecuadorian Amazon reports highly congruent patterns for the diurnal giant anteater, nocturnal giant armadillo, and diurnal-crepuscular green acouchi and black agouti (Blake et al. 2012), while several studies confirms the strictly nocturnal pattern of the spotted paca (Gómez et al. 2005, Harmsen et al. 2011, Michalski and Norris 2011, Blake et al. 2012). Similar mainly diurnal patterns of the collared peccary is reported in several studies from rainforest areas in Mexico and South America (Gómez et al. 2005, Tobler et al. 2009, Harmsen et al. 2011, Santos-Moreno and Pérez-Irinea 2016), while others report diurnal patterns but with some nocturnal captures (Cortés-Marcial and Briones-Salas 2014, Galetti et al. 2015, Hofmann et al. 2016). All acquired studies on the lowland tapir confirms it's nocturnal behaviour with infrequent diurnal captures (Gómez et al. 2005, Tobler et al. 2009, Harmsen et al. 2011, Wallace et al. 2012, Cruz et al. 2014). The mixed-feeding tayra and short-eared dog both showed strictly diurnal patterns in this study, while a previous study reports a few nocturnal captures for both species (Gómez et al. 2005). In accordance with this study, the pale-winged trumpeter, razor-billed curassow and Spix's guan have previously been mentioned as

diurnal, although allegedly with a somewhat stronger affinity towards the early and late hours of the day for the latter two (Strahl et al. 1997, Delacour and Amadon 2004, Sherman and Eason 2016).

In contrast, the carnivorous jaguar, puma and ocelot retain some degree of activity throughout the day-night cycle, and less congruence was found among previously published studies. The puma and jaguar show highly different patterns among studies, although contrary to this study there seems to be some general affinity towards night- and crepuscular activity for both species (e.g. Gómez et al. 2005, Bitetti et al. 2010, Harmsen et al. 2011, Foster et al. 2013). The pattern of ocelot activity is equally conflicting with previous literature, which generally show more distinct night-time dominance (e.g. Gómez et al. 2005, Bitetti et al. 2010, Kolowski and Alonso 2010, Blake et al. 2015).

Some morphologically similar species were only identified to genus to avoid misidentification, and were not included in the analysis. However, all images of *Dasypus* sp. was captured during night, confirming that both the nine-banded armadillo and greater long-nosed armadillo show nocturnal behaviour (Emmons and Feer 1997, Blake et al. 2012, Cortés-Marcial and Briones-Salas 2014, Soria-Díaz et al. 2016). More variation was found in the patterns of *Mazama* sp., *Crypturellus* sp., and *Tinamus* sp., and it is unclear to what degree this reflects cathemerality or behavioural differences between species. Indeed, previous studies from neotropical rainforests have indicated that the sympatric brocket deer show both cathemerality and some degree of temporal divergence, with red brocket deer being mainly nocturnal and the brown brocket deer mainly diurnal (e.g. Tobler et al. 2009, Harmsen et al. 2011, Ferreguetti et al. 2015).

Other species were observed to exist in the area, but the effort failed to yield sufficient quantity of data for the activity analysis. Previous camera trap studies spanning multiple seasons have successfully provided descriptions of diurnal behaviour in the jaguarundi and South American coati (Gómez et al. 2005, Maffei et al. 2007, Bitetti et al. 2010), and mainly nocturnal behaviour in the crab-eating raccoon (Gómez et al. 2005). The little studied southern tamandua has only been mentioned as nocturnal with some crepuscular patterns (Montgomery 1985 & Wetzel 1985 cited in Hayssen 2011), while the southern naked-tailed armadillo has been reported as nocturnal in the rainforest (Emmons and Feer 1997), and largely diurnal in an observational study from the Brazilian Cerrado where fieldwork was limited to 06:00 to 02:00 (Bonato et al. 2008). Extended camera trap studies could provide clarifications on the temporal distributions of these species.

4.1.2 Relationships among competing species

The results indicated that some species with similar diets are divided among diurnal and nocturnal behaviour. Resource competition and related confrontations may be reduced by displacement of the inferior competitor in time or space (Kronfeld-Schor and Dayan 2003). If the competition is mediated through limited resources alone, such divergence provides a mean to differentiate their use of resources available in different areas or at different times (e.g. prey with different activity patterns) or that is continually renewed in time (e.g. fallen fruit or a wide range of potential prey) (Schoener 1974, Carothers and Jakzić 1984, Kronfeld-Schor and Dayan 2003). In particular, the giant anteater showed mainly diurnal behaviour and significantly diverged in peak activity from the nocturnal armadillos, all feeding mainly on termites and ants (Eisenberg and Redford 2000, Da Silveira Anacleto 2007, Ferreira et al. 2015). The three large rodents also share similar diets composed mainly of fruits and seeds (Eisenberg and Redford 2000, Dubost and Henry 2006). The black agouti and green acouchi were both strongly affiliated with the crepuscular period but showed a significant decline between overlap estimates. The spotted paca was the most nocturnal species in this study, diverging strongly from the agouti and acouchi by avoiding day, dusk and dawn altogether.

Contrastingly, this study also revealed some positive affiliations on both the temporal and spatial scale, including species utilizing similar food resources. Coarse similarity in diet does not necessarily imply competition for food resources, however. Resource and interference competition may be limited between short-eared dog and tayra, considering that they occur solitarily at low densities, with highly omnivorous diets including small vertebrates, invertebrates and fruits (Presley 2000, Pitman and Williams 2004). The three species of large birds all rely heavily on consumption of seeds and fruits, but show differences in their foraging behaviour and use of the vertical forest strata. Both the pale-winged trumpeter and razor-billed

curassow largely forage on the forest floor (Delacour and Amadon 2004, Sherman and Eason 2016). However, the latter have been alleged to avoid the abundant *Ficus* fruits, that provides an important food source for the Trumpeters (Delacour and Amadon 2004). Although regularly descending, the Spix's guan is the species least bound to the ground in this study, mainly feeding on fruit in the mid-storey (Delacour and Amadon 2004). In contrast to the divergence expected to arise from competition relationships, benefits from spatial or temporal overlap due to positive interactions could explain these convergent patterns. However, with limited knowledge on species and their ecological relationships, attempting to link convergence to any specific hypothesis on facilitation is a speculative exercise.

The dietary overlap is very high between the two apex predators (de Oliveira 2002), and while the other mesopredators keeps to smaller prey and fruits (Presley 2000, Pitman and Williams 2004, Rocha-mendes et al. 2010), the ocelot competes among both these groups (Moreno et al. 2006). However, the overlap estimates gave few indications of competition release on the temporal scale; their activity periods span day and night, resulting in high overlap between the 95% isopleths, while the divergent peak overlap with ocelot was highly uncertain for both the jaguar and puma. The jaguar and puma showed a strong and significant decline between their overlap estimates, indicating that they focus their activity peaks in different periods. However, acknowledging the low sample sizes, noisy sample patterns and wide activity ranges, one may argue that the estimated kernel densities are unreliable, and that care should be taken when interpreting very specific differences among patterns. Little clarification is found in the literature; although lacking any statistical effort to support the claim, the fluctuating activity patterns between studies seem to vary in their degree of overlap (e.g. Gómez et al. 2005, Bitetti et al. 2010, Harmsen et al. 2011), indicating that competition may not be the main force behind the pattern variations.

4.1.3 Relationships among predators and prey

While predators depend on spatial and temporal association to catch their prey (Lima 2002), prey must react with escape or avoidance to prevent capture (Wirsing et al. 2010). In this study, the occupancy models indicated that jaguar and giant anteater diverge on the spatial scale. The jaguar is likely to be the main predator of the giant anteater, and the felid has been shown to affect anteater density across its distribution (Quiroga et al. 2016). Contrastingly, the anteater constitutes only a small part of the jaguar diet in rainforest environments (de Oliveira 2002), potentially generating a stronger urgency for reducing encounter probability in the prey than for the predator to ensure encounter. Predation risk is indeed spatially heterogeneous and may affect the habitat choice of prey species (Brown et al. 1999, Brown and Kotler 2004). However, avoidance may carry fitness costs (Creel and Christianson 2008) and the spatial response of prey depend on their escape behaviour (Wirsing et al. 2010). Although possessing a similar relationship with the jaguar as the giant anteater in terms of their relative importance as predator and prey (Padilla and Dowler 1994, de Oliveira 2002), the occupancy model indicated that lowland tapir converged with the felid in space. These contrasting findings could reflect the complex and flexible behavioural dynamics arising from the opposing interests in predator-prey relationships (Brown et al. 1999, Lima 2002, Wirsing et al. 2010). The puma showed both temporal and spatial association with Spix's guan. Both the puma and jaguar hold generalist feeding patterns, and are known to prey on birds (de Oliveira 2002). However, consumption of birds is sporadic and considered as opportunistic behaviour (de Oliveira 2002), and Spix's guan is only partially terrestrial (Delacour and Amadon 2004). Adaptational or behavioural convergence of the predator to the prey is thus an unlikely explanation for their observed convergent spatial patterns.

In equivalence to theories of spatial heterogeneity in predation risk and prey abundance, time acts as an additional axis where predators and prey can move in relation to each other to maximise encounter probabilities or mitigate predation risk (Lima 2002, Kronfeld-Schor and Dayan 2003). The neotropical felids in this study occur in diverse habitats throughout wide geographic ranges (Emmons and Feer 1997), exposing them to diverse prey community compositions with varying congregations of available prey biomass across the temporal scale. Their broad and spatially varied diets (de Oliveira 2002), long activity periods and lack of ubiquitous temporal patterns are possibly adaptations to this challenge. Regardless of the cause of these patterns, their incessant activity and apparent behavioural plasticity could limit the potential of their prey to

escape in time. Indeed, these patterns were not seen in other species; apart from the lowland tapir and giant armadillo, they were mostly limited to either day or night, and showed more consistent behaviour across studies. This discordance in perceived potential for temporal adjustments could indicate that relative patterns of time use between the sympatric predator and prey communities are, in ecological time, more strongly controlled bottom-up by temporal prey availability.

4.1.4 Effects of human settlements

Black agouti and spotted paca seemed to suffer from depletion or avoid areas close to human settlements. These large rodents are among the species most frequently consumed by Amazonian hunters (Peres 2000a), and black agouti have shown density declines in response to hunting pressure (Peres and Palacios 2007). However, any absolute effect of decline in site use was not given in the thesis due to the choice of model priors, leaving the severity of anthropogenic impact unknown. In favour of sustainability, the black agouti was overall the most widespread and frequently captured species. Contrastingly, the pale-winged trumpeter was estimated to have a higher site use probability close to humans, despite being frequently targeted by hunters (Peres 2000a, Peres and Palacios 2007). This could be explained by release from competitor or predators, or affiliations with anthropogenic habitats, but note that a previous review has shown a weak but significant decline in density when exposed to hunting pressure (Peres and Palacios 2007).

Several of the focal species occurring in the area are highly sought after by hunters, and show density declines in accessible areas throughout the Amazon basin (Peres 2000a, Peres and Palacios 2007). Yet, few species in this study showed any significant relationship between site use probability and distance to settlements, including the particularly sensitive large ungulates lowland tapir and collared peccary (Peres and Palacios 2007). This could indicate that the hunting pressure in the area is limited. The total area within a 10 km radius from the villages is indeed small compared to the surrounding unhunted region. Thus, spillover effects into the hunted areas from surrounding populations could act to reduce any effect of game outtake. Alternatively, patterns of absence could be obscured by a historically different distribution of hunting pressure, in particular for these large species with slow generation turnover.

4.2 The analytical framework

In addition to the ecological objectives, this thesis aimed to (O4) discuss the utility of the presented methodological and analytical procedure. The framework used proved capable of specifying species distributions and assessing temporal and spatial relationships among species, but it is accompanied by required model assumptions that needs to be addressed when used in a scientific setting. The occupancy models assume that (1) there is no temporal and spatial heterogeneity in detection probability that are not accounted for through covariates, (2) there are no systematic changes in presence/absence or movement patterns, and (3) survey outcomes and (4) sites are independent (Mackenzie 2006). In particular, as several neotropical vertebrates display seasonal changes in abundance (Haugaasen and Peres 2007), the long and continuous timespan of data collection could connote sensitivity to the first two assumptions, depending on species-specific population dynamics. The non-random distribution of cameras along transects could oppose the fourth assumption, especially for highly mobile species.

When using kernel density analysis, the conflation of the data implies an assumption of consistent behaviour in time and space, or at least that a relevant description of average behaviour is captured by the merged sample. Studies on some species of neotropical mammals indicate changes in activity patterns across seasons (e.g. lowland tapir; Oliveira-Santos et al. 2010, and peccaries; Hofmann et al. 2016) and among individuals (e.g. captive ocelots; Weller and Bennett 2001). Further, unlike the occupancy models for spatial analysis, the described model for activity estimation is naïve in regards to detection, assuming that the chance of capturing an animal is equal whenever it is active. Detection rate could potentially vary according to activity type (e.g. affecting movement speed; Rowcliffe et al. 2014) or camera trigger sensitivity (e.g. affected by temperature or weather events; Meek et al. 2015).

Some recognized methodological and statistical shortcomings could also serve as an alternative to ecological explanations for the lack of strong findings arising from the occupancy models. The posterior

probability distribution of the site use parameters is wide for most species and approach estimated use of all sites (i.e. $\theta=1$), as evident in their 95% credibility intervals. This uniformity and lack of precision could hamper the model's ability to recognize covariates affecting the estimated parameter. Simulating the sampling and modelling process with similar data (Mackenzie and Royle 2005, Guillera-Arroita et al. 2010) showed that this exercise could have provided a warning of insufficient site replication if performed pre-fieldwork. Further, effective assessment of covariate effects requires the covariate in question to be strongly defined in the methodology and model. Notably, the covariates of the co-occupancy models are derived from high and uncertain estimates of site use.

Another weakness of occupancy modelling is its inability to detect changes in population densities. The detrimental effects of hunting on neotropical mammal communities have commonly been inferred from decreases in population densities as indicated by encounter rates in line-transect surveys (Peres and Palacios 2007, Endo et al. 2010). Long-term absence at a site is a drastic outcome compared to such changes in abundance, which are absorbed by the detection probability parameter in occupancy models. However, comparison of detection by sight and sign have indicated underestimation of occurrence from encounter rate methods (Fragoso et al. 2016), and behavioural responses to hunting pressure (e.g. Ciuti et al. 2012, Thurfjell et al. 2013) could induce exaggerated differences in density estimates. Complementing previous efforts to assess the impacts of hunting with alternative methods and analytical frameworks incorporating detection probabilities could thus be worthwhile.

The results of the sensitivity analysis indicated that the kernel density method fails to capture sudden changes in activity (e.g. as seen for the strongly crepuscular green acouchi), and that the model outcome is highly sensitive to the choice of bandwidth (Appendix 2). Results from Oliveira-santos et al. (2013) demonstrate that the choice of bandwidth have even more severe influence on the coefficient of overlap between a species pair, than on the estimated activity range of the individual species. The overlap estimates have the potential to be both exaggerated and obscured depending on the accuracy of the kernel densities of the species pairs. Empirical validation of the method would better indicate the suitability for describing real activity patterns, and further statistical development could improve estimations by accounting for method- and activity-type specific detection probabilities (e.g. weighed kernel density distributions, Rowcliffe et al. 2014) and patterns that are not captured by the currently assumed distribution (e.g. directional log-spline distributions, Ridout and Linkie 2009).

4.3 Conclusions

Several independent pair-wise species relationships were discussed in the first section of this discussion. I predicted to see (P1) avoidance among ecologically similar species. Some pairs of species utilizing similar general feeding resources did show diverging temporal patterns, but others converged in time or space. I further predicted that (P2) predator-prey relationships should be evident in diverging or converging patterns. On the spatial scale, the jaguar showed opposite relationships with two large and assumedly equally important prey. On the temporal scale, comparison with previous literature indicated that the obligate predators retain long activity periods that vary between areas, while other species are restricted to more narrow and invariable patterns. Under such a scenario, observed predator patterns could be controlled by prey availability, and the potential for prey to escape from predation pressure in time limited. Lastly, I predicted that (P3) commonly hunted species should show lower occurrence estimates near permanent settlements. The occupancy models indicated impacts on some species; the site use estimates of black agouti and spotted paca was negatively affected by human inhabitation, while the estimate for pale-winged trumpeter opposed the prediction and previous literature. Most species showed no effect, indicating either that hunting pressure is low, patterns of absence are obscured by historical hunting pressure, or the analytical framework failed to capture effects.

Although some relationships between species were identified within the data, significant results were generally scarce and inconsistent, and only partly reflected the predicted patterns. Previous camera trap studies utilizing similar analytical approaches have provided more comprehensive descriptions of community relationships, comparing spatial and temporal patterns to draw inference on responses to

sympatric species (e.g. Schuette et al. 2013, Bischof et al. 2014, Wang et al. 2015). The lack of congruence between species pairs showing significant relationships on the temporal and spatial scale hindered such comparisons in this study. Species are exposed to a range of interactions submitting them to various and potentially opposing pressures. Thus, the general predictions may appear as simplistic, considering the extent of resident species included in the analysis and the myriad of interactions likely to exist among them. Other studies on community interactions often focus on one species and some known predators and competitors, with the potential to create more specific predictions based on known interactions (e.g. Schuette et al. 2013, Bischof et al. 2014, Wang et al. 2015). This is particularly relevant for competition interactions; “ecologically similar” is indeed a vague term. Including measures of actual overlap on niche axes where limitations may occur (e.g. trophic niches, Petrov et al. 2016) may allow drawing more robust descriptions of community structure.

A major weakness of the analytical procedure applied here is the descriptive nature of the results used to draw inferences. The previous discussion focused entirely on examining the identified patterns within a framework of interspecific interactions. However, diel activity and spatial preferences are linked to physiological traits and tolerances, energetic constraints, resource availabilities and evolutionary histories (Wiens and Graham 2005, Kearney and Porter 2009, Bennie et al. 2014). This may limit the behavioural and adaptational plasticity of the spatial and temporal niche axis. Perceived non-random patterns between species may thus be epiphenomena of unrelated convergent or divergent adaptations or behaviour. Being unable to distinguish between potential causes for the observed patterns, the initial predictions are not rooted in any falsifiable scientific hypotheses and can only be discussed in a speculative manner. Thus, although providing valuable insights into community structure, the demonstrated methodological and analytical procedure only leave room for ad-hoc explanations of patterns, and are more suitably treated as a form of hypothesis generation. Utilizing natural experiment settings to study ecological interactions would provide more robust evidence of causality.

Nevertheless, the range of species captured in this study demonstrates the potential of camera traps as a cost-effective tool to provide ecological data for several species simultaneously, including rare and elusive species that are difficult to monitor by direct observation or live-trapping (Voss and Emmons 1996). With proper methodological planning and strongly defined covariates, the presented analytical approach can produce valuable descriptions of complex community patterns.

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Appendix 1: Hierarchical occupancy model

The general single-species model defined in the methods section models the detection/non-detection data as a binomial function dependent on the transect use (ψ), site use (θ) and detection (p) probability. Mathematically, the ambiguity of apparent species absence is solved by implementing an indicator function in the likelihood:

$$L(\psi, \theta, p | D_{tsv}) = \prod_{t=1}^T \psi \prod_{s=1}^S \left[\theta \binom{n_s}{o_s} p^{o_s} (1-p)^{n_s-o_s} + I(o_s = 0)(1-\theta) \right] + I(o_t = 0)(1-\psi)$$

where D_{tsv} is a three-dimensional observation array for v visits to s sites within t transects, merged into a vector n for number of visits to each site and vector o for the total number of observations for each site. $I(.)$ denotes an indicator function taking the value 1 if true or 0 if untrue. To account for heterogeneity, the log-odds of occupancy and detection probabilities can be modelled as linearly dependent on spatial or temporal covariates, replacing them by the inverse of their logit-functions in the original likelihood function:

$$\text{logit}^{-1}(p_{ts}/\psi_{ts}) = \frac{1}{1 + e^{-(\alpha + \beta * \text{Cov}_{ts} + \dots)}}$$

where α is the intercept, β is a regression coefficient indicating covariate effect and Cov represents a site- or transect-specific covariate. Bayesian hierarchical modelling of this likelihood function is achieved by introducing a latent occupancy state variable, denoted as a vector z . The two-species model iterates values for two species simultaneously, and models the site use parameter of one species as dependent on the latent occupancy state variable z of the other species. A general single-species model and the two-species model were defined in the BUGS language as follows:

```
model {
  #SINGLE-SPECIES LIKELIHOOD MODEL
  for(t in 1:T){
    zT[t] ~ dbern(psiT)
    for(s in 1:S[t]){
      logit(p[s,t]) <- alphap + betap * Covariate[s,t] + ...
      logit(psiS[s,t]) <- alphaS + betaS * Covariate[s,t] + ...
      zS[s,t] ~ dbern(psiS * zT[t])
      count[s,t] ~ dbinom(zS[s,t] * p, ndays[s,t])
    }
  }
  #PRIORS
  psiT ~ dunif(0,1)
  # If no covariates:
  psiS ~ dunif(0,1)
  p ~ dunif(0,1)

  # If covariates:
  alphap ~ dunif(-10,10)
  betap ~ dunif(-10,10)
  ...
  alphaS ~ dunif(-10,10)
  betaS ~ dunif(0,0.1)
  ...
}
```

```
model {
  #TWO-SPECIES LIKELIHOOD MODEL
  for(t in 1:T){
    zT1[t] ~ dbern(psiT1)
    zT2[t] ~ dbern(psiT2)
    for(s in 1:S[t]){
      logit(p1[s,t]) <- alphap1 + betap1 * Covariate1[s,t] + ...
      logit(p2[s,t]) <- alphap2 + betap2 * Covariate2[s,t] + ...
      logit(psiS2[s,t]) <- alphaS2 + betaS1 * zS2[s,t]
      zS1[s,t] ~ dbern(psiS1 * zT1[t])
      zS2[s,t] ~ dbern(psiS2[s,t] * zT2[t])
      count[s,t] ~ dbinom(zS[s,t] * p, ndays[s,t])
    }
  }
  #PRIORS
  psiT1 ~ dunif(0,1) ; psiT2 ~ dunif(0,1)
  alphaS1 ~ dunif(-10,10)
  betaS1 ~ dunif(0,0.1)
  psiS2 ~ dunif(0,1)

  # If covariates on detection:
  alphap1 ~ dunif(-10,10) ; alphap2 ~ dunif(-10,10)
  betap1 ~ dunif(-10,10) ; betap2 ~ dunif(-10,10)
  ...
  # If no covariates on detection:
  p1 ~ dunif(0,1) ; p2 ~ dunif(0,1)
}
```

Appendix 2: Choice of bandwidth for kernel density estimation

The sensitivity analysis depicted in figure A2 indicates that the estimated activity proportions declines rapidly until bandwidths around three to six for most species, where the rate of decline decreases. For most of these, the Taylor-bandwidth fall within the relatively stable region, producing very similar density estimates for the three depicted choices of bandwidth. However, for the three felids, green acouchi and to some degree the lowland tapir, the Taylor-bandwidth produced highly smoothed density curves seemingly discarding the sample distribution. Thus, in an attempt to acknowledge higher belief in the sample than a flat activity curve, while removing the effect of potentially biologically irrelevant narrow gaps, a medium bandwidth of five was selected for further analysis.

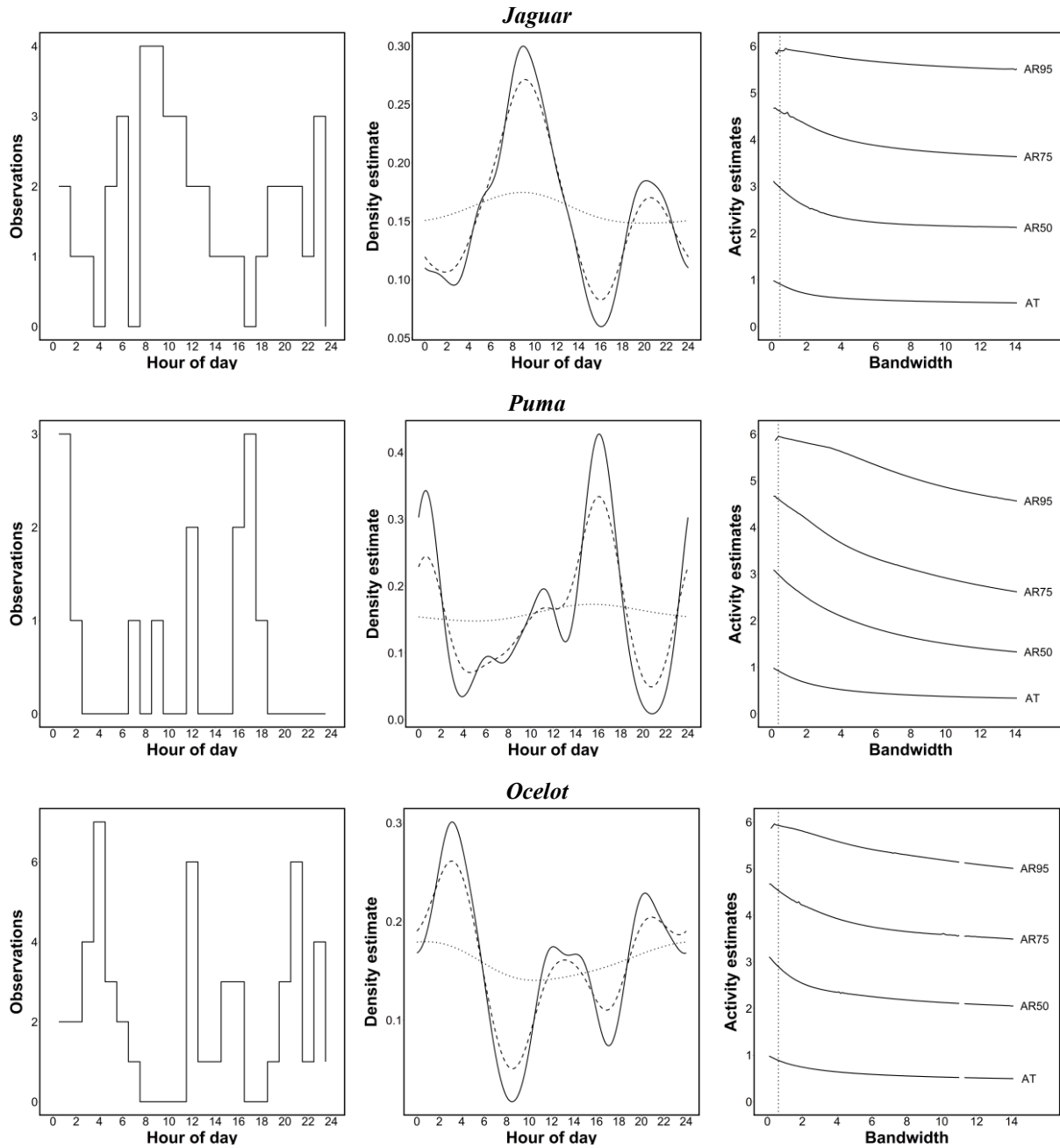


Figure A2. The first column shows the hourly distribution of captures throughout the day. The second column depicts density estimates for a medium bandwidth of 5 (····), a high bandwidth of 10 (—), and the bandwidth estimated using the Taylor method. (---). Column 3 shows the effect of bandwidth choice on estimated activity proportion estimates, with the Taylor bandwidth indicated by a horizontal line.

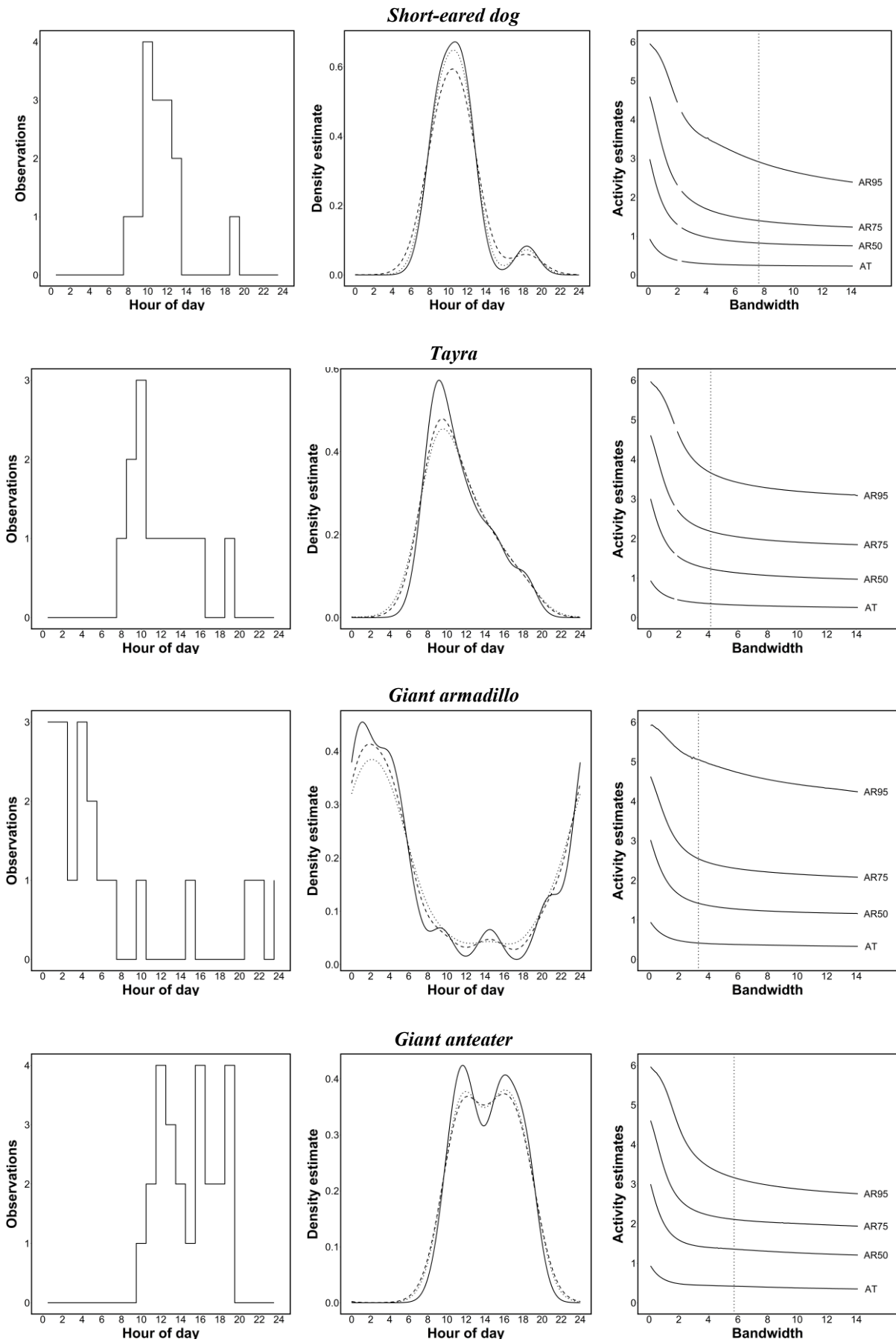


Figure A2 cont.

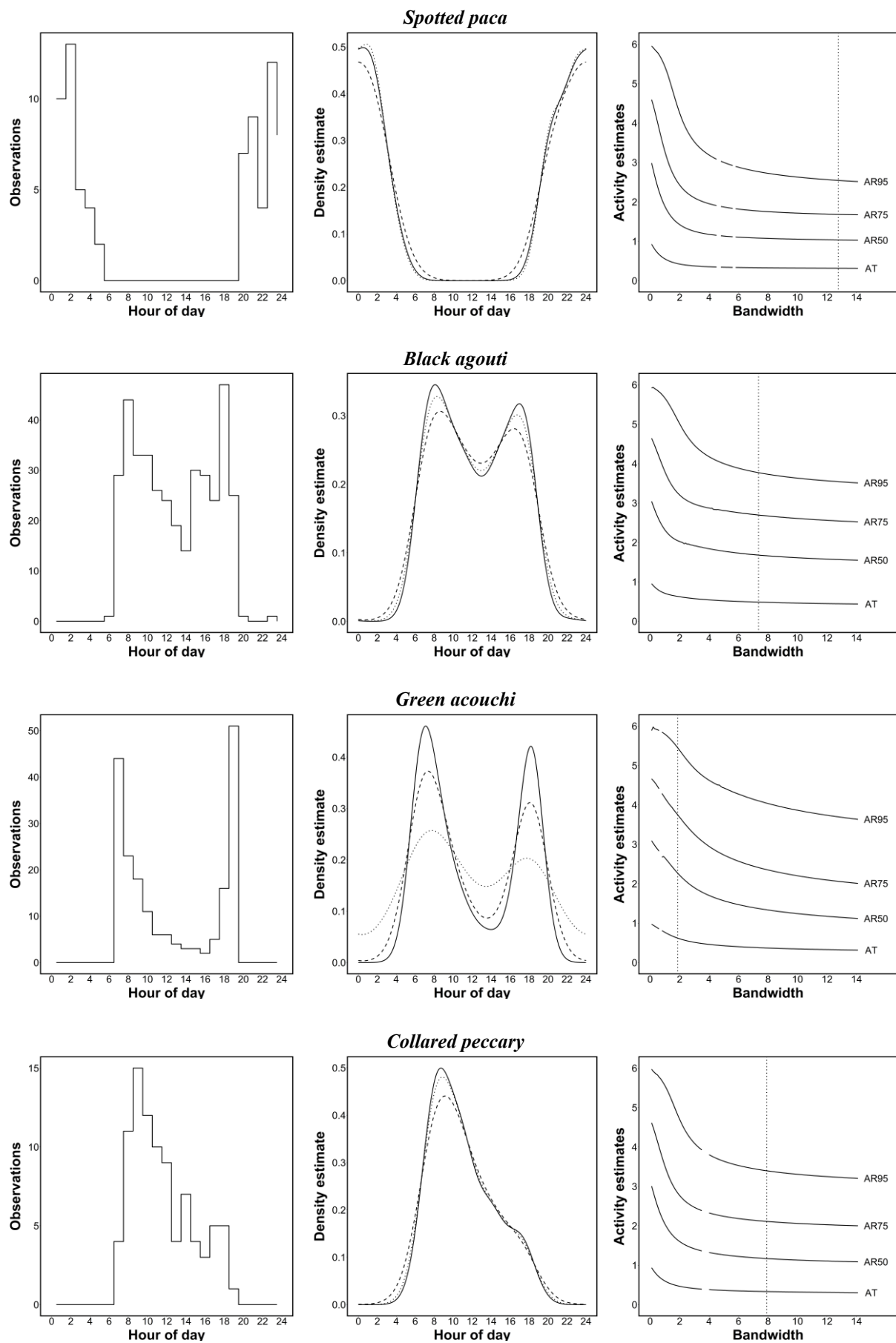


Figure A2 cont.

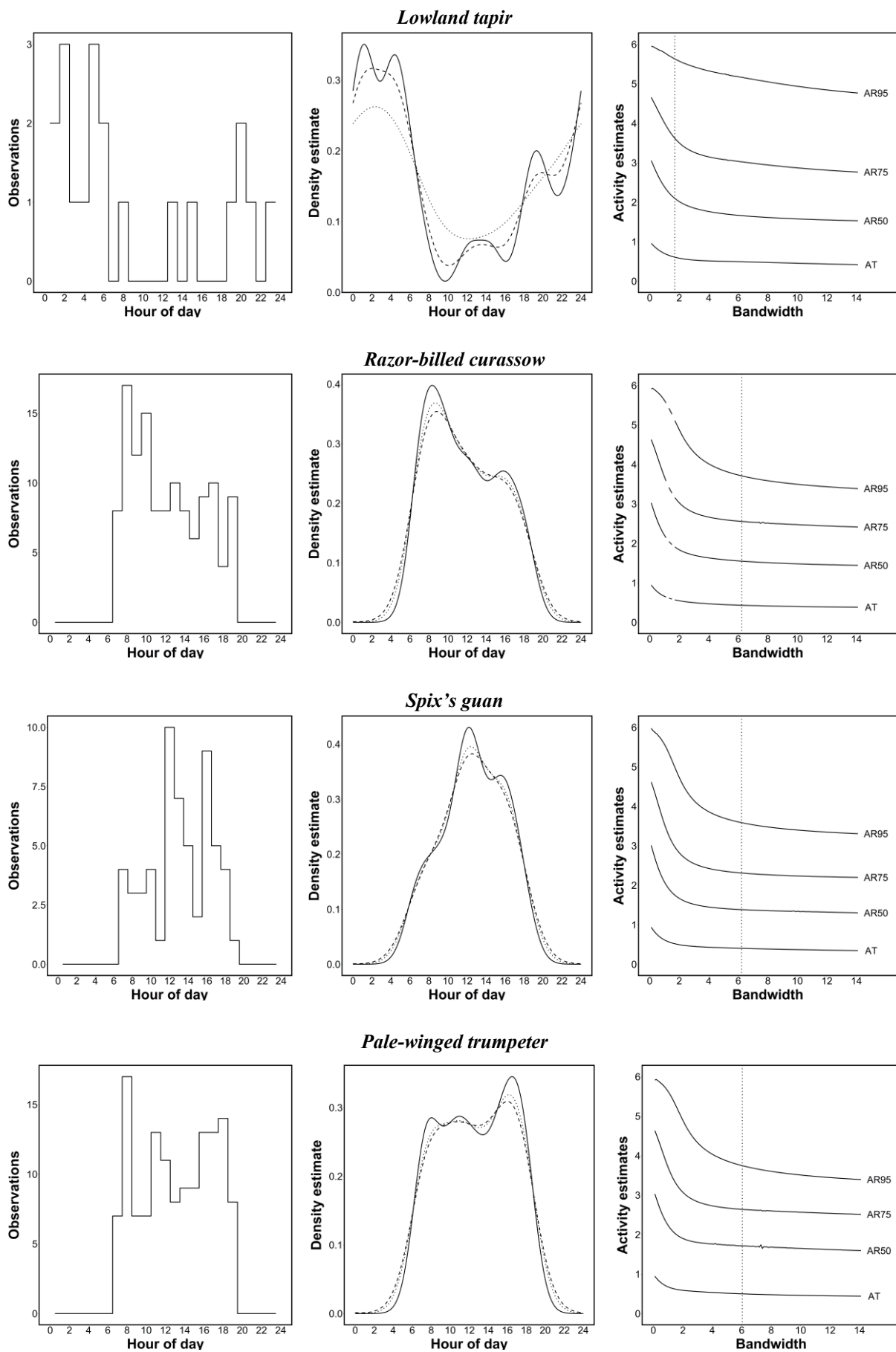


Figure A2 cont.

Appendix 3: Additional captures

This appendix summarizes species and other image types removed from the analysis. Some genera were hard to separate to species; *Scirius* sp. are likely to consist mainly of the Northern and Southern Amazon red squirrels (*S. igniventris* and *S. spadiceus* respectively), *Philander* sp. is represented in the area by Gray four-eyed opossum (*P. opossum*) and McIlhenny's four-eyed opossum (*P. mcilhennyi*) while *Proechimys* sp. is a large genus of South American spiny rats. For birds, *Formicarius* sp. is a genus of anthruses, while *Turdus* sp. is a large genus of true thrushes.

Table A3. Full list of images produced by the cameras in the study. The number of images and events (i.e. images separated by more than one hour) is summarized for each species and other image types.

Mammalia						
Order	Family	Genus	Species	Common	Images	Events
<i>Medium and ground-dwelling mammals (see main text)</i>					10796	1197
Carnivora	Felidae	Leopardus	wiedii	Margay	127	2
Primates	Cebidae	Cebus	albifrons	White-fronted capuchin	89	12
Didelphimorphia	Didelphidae	Didelphis	marsupialis	Black-eared opossum	25	6
Didelphimorphia	Didelphidae	Metachirus	nudicaudatus	Brown four-eyed opossum	39	9
Didelphimorphia	Didelphidae	Philander		Philander sp.	9	3
Rodentia	Echimyidae	Proechimys		Proechimys sp.	226	31
Rodentia	Sciuridae	Sciurus		Squirrels	95	33
Aves						
Order	Family	Genus	Species	Common	Images	Events
<i>Ground-dwelling birds (see main text)</i>					4719	429
Accipitriformes	Accipitridae	Buteogallus	urubitinga	Great black-hawk	6	1
Accipitriformes	Accipitridae	Leucopternis	kuhli	White-browed hawk	3	1
Columbiformes	Columbidae	Geotrygon	montana	Ruddy quail-dove	20	5
Cuculiformes	Cuculidae	Neomorphus	pucheranii	Red-billed ground-cuckoo	27	3
Galliformes	Odontophoridae	Odontophorus	stellatus	Starred wood-quail	36	6
Gruiformes	Rallidae	Aramides	cajanea	Gray-necked wood-rail	3	1
Passeriformes	Formicariidae	Chamaeza	nobilis	Striated antthrush	12	1
Passeriformes	Formicariidae	Formicarius		Formicarius sp.	3	1
Passeriformes	Formicariidae	Formicarius	colma	Rufous-capped antthrush	7	3
Passeriformes	Rhinocryptidae	Liosceles	thoracius	Rusty-belted tapaculo	4	2
Passeriformes	Thamnophilidae	Gymnopathys	salvini	White-throated antbird	6	1
Passeriformes	Thamnophilidae	Phlegopsis	nigromaculata	Black-spotted bare-eye	3	1
Passeriformes	Turdidae	Turdus		Turdus sp.	3	1
Passeriformes	Turdidae	Turdus	albicollis	White-necked thrush	3	1
Pelecaniformes	Ardeidae	Cochlearius	cochlearius	Boat-billed heron	3	1
Strigiformes	Strigidae	Lophotrix	cristata	Crested owl	9	1
Other					Images	Events
Image type						
Empty					6484	1529
Human					852	54
Squamata					152	39
Unidentified						
Unknown					360	209
Small mammal					225	75
Large mammal					44	18
Small cat					26	4

Appendix 4: Camera trap sites included in the study

Table A4. Camera traps included in the study, their functional period and capture information

Transect ¹	Position	Village (km) ²	River (km) ²	Start date	End date	Events	Species	Days ³
Morada nova								
North	S6 20.240 W67 55.758	6.19	4.31	10/08/2011	07/12/2011	18	11	120
North	S6 19.954 W67 56.645	7.90	5.85	10/08/2011	14/12/2011	39	12	127
South	S6 21.450 W67 50.809	3.21	4.15	09/08/2011	14/01/2012	14	5	159
South	S6 21.649 W67 49.848	5.02	5.92	09/08/2011	12/03/2012	33	12	217
South	S6 21.808 W67 48.882	6.82	7.70	09/08/2011	12/03/2012	258	19	217
Boiador								
North	S6 24.358 W67 58.178	3.34	2.25	12/08/2011	18/12/2011	14	7	129
South	S6 26.355 W67 54.031	5.45	4.08	29/07/2011	18/12/2011	18	9	143
South	S6 26.624 W67 53.083	7.17	5.90	29/07/2011	19/03/2012	100	13	235
Itauba								
North	S6 28.867 W68 01.555	4.44	2.45	16/08/2011	25/11/2011	72	13	102
North	S6 28.580 W68 02.485	6.22	3.81	11/10/2011	22/03/2012	29	11	164
North	S6 28.402 W68 03.432	7.96	5.21	16/08/2011	22/03/2012	14	7	220
South	S6 31.368 W67 59.546	2.66	2.14	14/08/2011	08/01/2012	8	7	148
South	S6 32.369 W67 59.631	4.51	2.62	14/08/2011	25/11/2011	26	10	104
South	S6 33.351 W67 59.646	6.32	3.79	14/08/2011	25/11/2011	17	6	104
Belo Horizonte								
North	S6 35.199 W68 09.170	11.20	1.72	16/10/2011	28/02/2012	30	13	136
North	S6 34.233 W68 09.378	11.92	3.45	16/10/2011	29/04/2012	31	13	197
North	S6 33.281 W68 09.574	12.86	5.19	16/10/2011	29/04/2012	34	10	197
South	S6 38.406 W68 07.200	13.22	3.81	23/08/2011	13/10/2011	22	7	52
South	S6 39.217 W68 06.662	14.30	5.59	23/08/2011	19/12/2011	22	10	119
Santa Luzia								
North	S6 36.332 W68 14.118	3.74	1.72	20/08/2011	23/12/2011	17	11	126
North	S6 35.355 W68 14.118	5.53	3.51	20/08/2011	26/03/2012	49	12	220
São Joao								
North	S6 37.788 W68 18.165	3.62	2.20	20/11/2011	06/02/2012	39	13	78
North	S6 37.028 W68 18.790	5.33	3.57	19/08/2011	05/04/2012	36	11	231
Flexal								
South	S6 40.699 W68 16.238	3.32	3.10	18/08/2011	07/02/2012	55	14	173
South	S6 41.420 W68 15.584	4.94	4.81	18/08/2011	11/02/2012	63	15	178
South	S6 42.154 W68 14.956	6.65	6.55	18/08/2011	01/01/2012	46	12	137
Lower camping site								
North	S6 38.223 W68 31.626	24.91	2.46	31/10/2011	18/01/2012	18	9	80
North	S6 37.591 W68 31.759	25.32	3.56	31/10/2011	09/04/2012	166	15	162
North	S6 36.721 W68 31.921	25.93	5.13	31/10/2011	09/04/2012	67	13	162
South	S6 41.190 W68 31.169	24.01	1.90	01/11/2011	24/12/2011	14	3	54
South	S6 42.052 W68 31.538	24.90	3.52	01/11/2011	18/02/2012	24	10	110
South	S6 42.986 W68 31.628	25.39	5.25	01/11/2011	19/01/2012	54	14	80
Upper camping site								
North	S6 42.702 W68 43.904	47.63	1.20	06/11/2011	24/02/2012	28	10	111
South	S6 44.763 W68 42.758	46.13	1.98	05/11/2011	16/04/2012	27	9	164
South	S6 45.491 W68 42.242	45.48	3.58	05/11/2011	16/04/2012	112	14	164
South	S6 46.271 W68 41.636	44.75	5.38	05/11/2011	13/02/2012	14	7	101

¹Transects ordered from east to west.

²Shortest distance estimated using GIS.

³Total duration of camera operation, with potential down-periods subtracted.

Appendix 5: Occupancy model selection

Jaguar												
Model ¹	p ²	ψ ²	θ ²	α ³	β[Village] ³	β[River] ³	β[Side] ³	\bar{D} ⁴	\hat{D} ⁴	pD ⁵	DIC ⁶	ΔDIC ⁶
p~1	0.015 (0.003)	0.704(0.137)	0.705(0.13)					109.51	106.93	2.59	112.1	7.07
* p~V	0.013 (0.003)	0.729(0.132)	0.777(0.123)	-4.71 (-5.29 - -4.21)	-1.09 (-1.93 - -0.36)			101.51	97.98	3.52	105.03	0
p~M	0.014 (0.004)	0.71(0.141)	0.713(0.128)	-4.09 (-4.53 - -3.68)			-0.39 (-1.16 - 0.33)	109.61	106.01	3.59	113.2	8.17
p~D	0.015 (0.004)	0.713(0.141)	0.707(0.129)	-4.25 (-4.64 - -3.9)		-0.25 (-0.68 - 0.21)		109.39	105.82	3.57	112.96	7.94
p~V+M	0.012 (0.004)	0.734(0.132)	0.785(0.119)	-4.6 (-5.2 - -4.05)	-1.16 (-2.06 - -0.4)		-0.48 (-1.25 - 0.24)	100.95	96.55	4.41	105.36	0.33
p~V+D	0.013 (0.004)	0.735(0.132)	0.777(0.122)	-4.74 (-5.31 - -4.24)	-1.09 (-1.99 - -0.34)	-0.04 (-0.54 - 0.47)		102.39	97.99	4.4	106.79	1.76
p~M+D	0.014 (0.005)	0.727(0.143)	0.702(0.123)	-4.11 (-4.56 - -3.71)		-0.29 (-0.72 - 0.17)	-0.46 (-1.22 - 0.29)	108.89	104.42	4.46	113.35	8.32
p~V+M+D	0.013 (0.005)	0.743(0.132)	0.781(0.119)	-4.61 (-5.21 - -4.07)	-1.14 (-2.07 - -0.35)	-0.08 (-0.58 - 0.44)	-0.5 (-1.28 - 0.22)	101.79	96.46	5.33	107.12	2.09
Puma												
Model	p	ψ	θ	α	β[Village]	β[River]	β[Side]	\bar{D}	\hat{D}	pD	DIC	ΔDIC
* p~1	0.005 (0.002)	0.803(0.14)	0.658(0.18)					59.01	57.25	1.76	60.77	4.32
p~V	0.004 (0.002)	0.814(0.135)	0.711(0.17)	-5.52 (-6.26 - -4.81)	0.27 (-0.29 - 0.77)			58.46	55.71	2.76	61.22	4.77
p~M	0.005 (0.002)	0.821(0.133)	0.697(0.174)	-5.7 (-6.89 - -4.55)			0.37 (-0.9 - 1.68)	59.4	56.65	2.75	62.15	5.7
p~D	0.004 (0.002)	0.839(0.127)	0.774(0.158)	-5.86 (-6.72 - -5.01)		0.49 (-0.07 - 1.03)		55.81	53.24	2.58	58.39	1.94
p~V+M	0.005 (0.003)	0.812(0.14)	0.71(0.17)	-5.62 (-6.86 - -4.43)	0.28 (-0.29 - 0.84)		0.12 (-1.36 - 1.5)	59.38	55.67	3.71	63.09	6.64
p~V+D	0.003 (0.002)	0.847(0.121)	0.814(0.142)	-6.13 (-7.05 - -5.28)	0.49 (-0.06 - 1.01)	0.69 (0.09 - 1.31)		53.06	49.68	3.39	56.45	0
p~M+D	0.004 (0.002)	0.833(0.129)	0.766(0.158)	-5.82 (-7.02 - -4.7)		0.53 (-0.07 - 1.14)	-0.12 (-1.52 - 1.3)	56.87	53.33	3.54	60.41	3.96
p~V+M+D	0.004 (0.003)	0.823(0.131)	0.798(0.144)	-5.72 (-7.02 - -4.51)	0.64 (0.02 - 1.26)	0.87 (0.18 - 1.61)	-0.82 (-2.57 - 0.88)	53.69	49.23	4.46	58.16	1.71
Ocelot												
Model	p	ψ	θ	α	β[Village]	β[River]	β[Side]	\bar{D}	\hat{D}	pD	DIC	ΔDIC
p~1	0.015 (0.002)	0.739(0.128)	0.775(0.111)					117.48	114.9	2.58	120.06	7.43
* p~V	0.013 (0.003)	0.741(0.119)	0.883(0.093)	-4.57 (-5.01 - -4.17)	-0.76 (-1.4 - -0.23)			109.56	106.48	3.08	112.63	0
p~M	0.015 (0.003)	0.741(0.129)	0.774(0.109)	-4.12 (-4.6 - -3.69)			-0.21 (-0.84 - 0.41)	117.99	114.44	3.56	121.55	8.91
p~D	0.015 (0.003)	0.738(0.129)	0.776(0.11)	-4.22 (-4.57 - -3.89)		-0.06 (-0.4 - 0.26)		118.39	114.86	3.53	121.92	9.28
p~V+M	0.013 (0.003)	0.741(0.12)	0.877(0.096)	-4.47 (-5.01 - -3.96)	-0.78 (-1.44 - -0.22)		-0.22 (-0.82 - 0.38)	110.14	106.03	4.11	114.25	1.62
p~V+D	0.014 (0.003)	0.738(0.119)	0.881(0.092)	-4.55 (-4.99 - -4.15)	-0.76 (-1.37 - -0.23)	-0.1 (-0.42 - 0.2)		110.12	106.07	4.05	114.17	1.54
p~M+D	0.015 (0.004)	0.749(0.129)	0.776(0.109)	-4.12 (-4.62 - -3.68)		0.02 (-0.41 - 0.43)	-0.25 (-1.05 - 0.54)	118.91	114.44	4.47	123.38	10.75
p~V+M+D	0.013 (0.004)	0.744(0.12)	0.875(0.095)	-4.48 (-5.04 - -3.96)	-0.77 (-1.42 - -0.23)	-0.04 (-0.41 - 0.34)	-0.19 (-0.93 - 0.55)	111.05	105.98	5.07	116.12	3.49
Short-eared dog												
Model	p	ψ	θ	α	β[Village]	β[River]	β[Side]	\bar{D}	\hat{D}	pD	DIC	ΔDIC
* p~1	0.007 (0.002)	0.758(0.159)	0.564(0.177)					59.19	57.22	1.97	61.16	1.58
p~V	0.006 (0.003)	0.763(0.159)	0.594(0.18)	-5.18 (-5.92 - -4.5)	0.05 (-0.53 - 0.55)			60.09	57.11	2.98	63.08	3.51
p~M	0.006 (0.003)	0.782(0.152)	0.621(0.178)	-5.81 (-7.18 - -4.6)			0.85 (-0.47 - 2.25)	58.53	55.58	2.95	61.47	1.9
p~D	0.005 (0.003)	0.802(0.147)	0.636(0.165)	-5.57 (-6.46 - -4.73)		0.64 (-0.05 - 1.38)		56.59	53.61	2.98	59.57	0
p~V+M	0.006 (0.003)	0.783(0.151)	0.628(0.177)	-5.83 (-7.22 - -4.53)	-0.01 (-0.6 - 0.5)		0.83 (-0.57 - 2.29)	59.61	55.64	3.96	63.57	4
p~V+D	0.005 (0.003)	0.803(0.145)	0.644(0.164)	-5.64 (-6.53 - -4.8)	0.17 (-0.43 - 0.67)	0.7 (-0.01 - 1.47)		57.01	53.09	3.92	60.93	1.36
p~M+D	0.006 (0.004)	0.802(0.145)	0.632(0.167)	-5.64 (-7.14 - -4.22)		0.64 (-0.23 - 1.64)	0.09 (-2.03 - 1.93)	57.51	53.55	3.96	61.47	1.9
p~V+M+D	0.007 (0.006)	0.8(0.147)	0.627(0.162)	-5.48 (-7.1 - -3.9)	0.21 (-0.44 - 0.78)	0.84 (-0.19 - 1.99)	-0.29 (-2.73 - 1.8)	57.89	53.18	4.71	62.6	3.02
Tayra												
Model	p	ψ	θ	α	β[Village]	β[River]	β[Side]	\bar{D}	\hat{D}	pD	DIC	ΔDIC
* p~1	0.004 (0.001)	0.859(0.115)	0.785(0.15)					54.05	52.61	1.44	55.48	1.51
p~V	0.003 (0.001)	0.866(0.111)	0.804(0.144)	-5.82 (-6.5 - -5.17)	-0.15 (-0.89 - 0.46)			54.75	52.33	2.43	57.18	3.2
p~M	0.003 (0.001)	0.868(0.11)	0.808(0.141)	-6.01 (-7.1 - -5.05)			0.36 (-0.85 - 1.62)	54.42	51.96	2.46	56.88	2.9
p~D	0.003 (0.001)	0.878(0.103)	0.833(0.129)	-6.04 (-6.81 - -5.33)		0.45 (-0.1 - 0.99)		51.61	49.24	2.37	53.97	0
p~V+M	0.003 (0.002)	0.868(0.11)	0.805(0.142)	-6.06 (-7.18 - -5.07)	-0.15 (-0.89 - 0.46)		0.34 (-0.89 - 1.59)	55.46	52.05	3.42	58.88	4.9
p~V+D	0.003 (0.002)	0.877(0.105)	0.827(0.132)	-6.08 (-6.88 - -5.34)	-0.01 (-0.81 - 0.64)	0.47 (-0.11 - 1.04)		52.74	49.39	3.35	56.09	2.12
p~M+D	0.003 (0.002)	0.873(0.105)	0.825(0.133)	-6.04 (-7.16 - -5.03)		0.47 (-0.12 - 1.09)	-0.05 (-1.47 - 1.32)	52.78	49.42	3.37	56.15	2.17
p~V+M+D	0.003 (0.002)	0.875(0.104)	0.824(0.134)	-6.08 (-7.23 - -5.04)	-0.02 (-0.82 - 0.65)	0.5 (-0.12 - 1.15)	-0.1 (-1.5 - 1.33)	53.9	49.55	4.35	58.25	4.27

Table A5. Model summary tables comparing models with all combinations of covariates on the detection parameter. Bold indicates significant covariate values (i.e. credible interval does not include 0). Asterisk (*) indicates the model selected for further analysis (i.e. most parsimonious model within five DIC units of the best model).

¹Covariates for detection parameter included for the given model. Notations indicate: V = distance to the nearest village, M = side of the river, D = distance to the river.

²Model estimates of detection probability (p), transect use (ψ) and site use (θ). Standard errors are shown in parentheses.

³Estimates of linear model intercept (α) and coefficients (β) of the covariates. Credibility interval are shown in parentheses.

⁴Point estimated deviance (\bar{D}) and posterior estimated deviance (\hat{D}) given by $-2\log(L)$ where L is the likelihood function.

⁵Penalty parameter given by $\bar{D} - \hat{D}$

⁶DIC model selection criterion given by

$$\bar{D} + 2pD$$

Table A5 cont.

Giant armadillo											
Model	p	ψ	θ	α	β [Village]	β [River]	β [Side]	\bar{D}	\hat{D}	pD	Δ DIC
* p~1	0.005 (0.001)	0.848(0.114)	0.826(0.125)					70.18	68.59	1.59	71.77
p~V	0.005 (0.002)	0.858(0.111)	0.837(0.119)	-5.55 (-6.22 - -4.94)	-0.54 (-1.5 - 0.29)			69.43	66.8	2.63	72.06
p~M	0.005 (0.002)	0.832(0.119)	0.836(0.121)	-5.55 (-6.31 - -4.86)			0.37 (-0.64 - 1.39)	70.77	68.14	2.63	73.4
p~D	0.004 (0.001)	0.862(0.109)	0.867(0.107)	-5.58 (-6.19 - -5.01)		0.35 (-0.11 - 0.8)		68.18	65.75	2.43	70.61
p~V+M	0.005 (0.003)	0.846(0.112)	0.838(0.12)	-5.71 (-6.57 - -4.96)	-0.53 (-1.51 - 0.37)		0.33 (-0.67 - 1.37)	70.24	66.53	3.71	73.94
p~V+D	0.004 (0.002)	0.868(0.104)	0.863(0.107)	-5.74 (-6.47 - -5.09)	-0.51 (-1.48 - 0.34)	0.33 (-0.13 - 0.78)		68.02	64.58	3.45	71.47
p~M+D	0.004 (0.002)	0.861(0.109)	0.865(0.108)	-5.59 (-6.34 - -4.91)		0.36 (-0.18 - 0.89)	-0.03 (-1.16 - 1.1)	69.2	65.81	3.39	72.6
p~V+M+D	0.004 (0.002)	0.867(0.106)	0.86(0.11)	-5.74 (-6.56 - -5.01)	-0.52 (-1.53 - 0.36)	0.33 (-0.21 - 0.87)	-0.04 (-1.19 - 1.14)	69.14	64.68	4.46	73.59
Giant anteater											
Model	p	ψ	θ	α	β [Village]	β [River]	β [Side]	\bar{D}	\hat{D}	pD	Δ DIC
* p~1	0.01 (0.003)	0.804(0.133)	0.576(0.14)					84.56	82.27	2.29	86.85
p~V	0.01 (0.003)	0.797(0.133)	0.6(0.142)	-4.69 (-5.27 - -4.18)	-0.24 (-0.79 - 0.26)			84.88	81.56	3.32	88.2
p~M	0.009 (0.003)	0.816(0.127)	0.619(0.148)	-5.09 (-6.05 - -4.21)			0.58 (-0.44 - 1.61)	84.39	81.19	3.2	87.6
p~D	0.011 (0.004)	0.814(0.131)	0.569(0.135)	-4.63 (-5.22 - -4.13)		-0.28 (-0.76 - 0.18)		84.09	80.9	3.19	87.28
p~V+M	0.009 (0.004)	0.802(0.132)	0.625(0.146)	-5.07 (-6.04 - -4.17)	-0.21 (-0.75 - 0.27)		0.52 (-0.51 - 1.57)	84.89	80.74	4.15	89.03
p~V+D	0.011 (0.004)	0.808(0.131)	0.578(0.135)	-4.66 (-5.23 - -4.15)	-0.24 (-0.81 - 0.27)	-0.28 (-0.74 - 0.16)		84.33	80.13	4.2	88.53
p~M+D	0.011 (0.004)	0.826(0.125)	0.595(0.136)	-5.25 (-6.24 - -4.37)		-0.45 (-0.98 - 0.04)	0.93 (-0.15 - 2.04)	82.2	78.07	4.13	86.33
p~V+M+D	0.011 (0.005)	0.82(0.127)	0.608(0.137)	-5.3 (-6.3 - -4.38)	-0.25 (-0.79 - 0.22)	-0.46 (-0.98 - 0.03)	0.94 (-0.16 - 2.07)	82.44	77.36	5.08	87.52
Spotted paca											
Model	p	ψ	θ	α	β [Village]	β [River]	β [Side]	\bar{D}	\hat{D}	pD	Δ DIC
* p~1	0.027 (0.003)	0.87(0.096)	0.572(0.095)					160.49	158.17	2.31	162.8
p~V	0.028 (0.004)	0.869(0.097)	0.576(0.095)	-3.6 (-3.85 - -3.36)	-0.22 (-0.48 - 0.02)			158.33	155.03	3.3	161.64
p~M	0.025 (0.005)	0.873(0.096)	0.579(0.096)	-3.83 (-4.4 - -3.35)			0.29 (-0.28 - 0.92)	160.7	157.39	3.31	164.01
p~D	0.024 (0.004)	0.871(0.096)	0.591(0.096)	-3.74 (-4.04 - -3.46)		0.25 (0.03 - 0.47)		156.75	153.47	3.28	160.03
p~V+M	0.027 (0.006)	0.869(0.097)	0.581(0.096)	-3.77 (-4.33 - -3.28)	-0.21 (-0.47 - 0.03)		0.21 (-0.36 - 0.84)	159.04	154.7	4.33	163.37
p~V+D	0.025 (0.005)	0.871(0.096)	0.589(0.097)	-3.71 (-4.03 - -3.43)	-0.12 (-0.41 - 0.16)	0.2 (-0.05 - 0.46)		157.06	152.79	4.27	161.32
p~M+D	0.024 (0.005)	0.874(0.095)	0.596(0.098)	-3.81 (-4.37 - -3.34)		0.24 (0.01 - 0.49)	0.09 (-0.51 - 0.74)	157.72	153.43	4.29	162.02
p~V+M+D	0.025 (0.006)	0.871(0.096)	0.592(0.097)	-3.77 (-4.32 - -3.29)	-0.12 (-0.42 - 0.16)	0.2 (-0.07 - 0.47)	0.07 (-0.53 - 0.7)	158.05	152.8	5.25	163.29
Black agouti											
Model	p	ψ	θ	α	β [Village]	β [River]	β [Side]	\bar{D}	\hat{D}	pD	Δ DIC
p~1	0.072 (0.004)	0.94(0.057)	0.868(0.055)					483.62	481.65	1.97	485.58
p~V	0.071 (0.005)	0.94(0.056)	0.869(0.054)	-2.57 (-2.69 - -2.46)	0.19 (0.09 - 0.29)			471.56	468.63	2.93	474.49
p~M	0.073 (0.005)	0.941(0.056)	0.868(0.055)	-2.7 (-2.86 - -2.54)			0.28 (0.06 - 0.5)	478.37	475.47	2.9	481.26
p~D	0.069 (0.005)	0.94(0.056)	0.869(0.054)	-2.63 (-2.76 - -2.51)		0.26 (0.15 - 0.37)		462.26	459.24	3.02	465.29
p~V+M	0.072 (0.006)	0.941(0.056)	0.869(0.055)	-2.69 (-2.86 - -2.52)	0.17 (0.07 - 0.27)		0.23 (0 - 0.46)	468.77	464.82	3.96	472.73
* p~V+D	0.067 (0.006)	0.941(0.055)	0.87(0.055)	-2.69 (-2.82 - -2.56)	0.3 (0.19 - 0.41)	0.35 (0.23 - 0.46)		436.81	432.78	4.03	440.84
p~M+D	0.069 (0.006)	0.941(0.055)	0.868(0.054)	-2.67 (-2.84 - -2.51)		0.24 (0.12 - 0.36)	0.09 (-0.15 - 0.33)	462.71	458.75	3.96	466.67
p~V+M+D	0.067 (0.007)	0.941(0.056)	0.872(0.054)	-2.65 (-2.82 - -2.49)	0.31 (0.19 - 0.43)	0.37 (0.24 - 0.5)	-0.09 (-0.35 - 0.16)	437.24	432.27	4.96	442.2
Green acouchi											
Model	p	ψ	θ	α	β [Village]	β [River]	β [Side]	\bar{D}	\hat{D}	pD	Δ DIC
p~1	0.065 (0.005)	0.823(0.114)	0.55(0.098)					243.86	241.41	2.45	246.32
p~V	0.065 (0.007)	0.822(0.114)	0.552(0.097)	-2.67 (-2.84 - -2.51)	0.04 (-0.16 - 0.24)			244.62	241.18	3.44	248.06
p~M	0.07 (0.007)	0.819(0.115)	0.552(0.099)	-3.03 (-3.28 - -2.79)			0.71 (0.38 - 1.03)	226.18	222.7	3.47	229.65
p~D	0.053 (0.005)	0.828(0.114)	0.554(0.098)	-3.01 (-3.23 - -2.8)		0.53 (0.39 - 0.68)		189.14	185.68	3.46	192.59
p~V+M	0.081 (0.012)	0.82(0.115)	0.552(0.099)	-3.11 (-3.38 - -2.86)	0.34 (0.11 - 0.57)		1 (0.62 - 1.4)	218.92	214.45	4.47	223.39
* p~V+D	0.057 (0.008)	0.824(0.112)	0.566(0.1)	-3 (-3.22 - -2.79)	0.45 (0.2 - 0.7)	0.65 (0.49 - 0.82)		178.09	173.67	4.42	182.51
p~M+D	0.052 (0.007)	0.828(0.113)	0.556(0.098)	-2.99 (-3.24 - -2.75)		0.56 (0.38 - 0.76)	-0.09 (-0.53 - 0.33)	189.95	185.52	4.43	194.37
p~V+M+D	0.061 (0.012)	0.823(0.113)	0.564(0.101)	-3.07 (-3.35 - -2.81)	0.5 (0.23 - 0.76)	0.6 (0.41 - 0.8)	0.22 (-0.26 - 0.7)	178.26	172.81	5.45	183.72

Table A5 cont.

Collared peccary												
Model	p	ψ	θ	α	β[Village]	β[River]	β[Side]	\bar{D}	\hat{D}	pD	DIC	ΔDIC
* p~1	0.024 (0.003)	0.942(0.056)	0.724(0.078)					172	170.01	1.99	174	2.19
p~V	0.023 (0.003)	0.941(0.054)	0.724(0.078)	-3.75 (-3.99 - -3.53)	0.18 (-0.02 - 0.37)			169.7	166.68	3.01	172.71	0.91
p~M	0.024 (0.004)	0.942(0.055)	0.714(0.077)	-3.94 (-4.28 - -3.63)			0.42 (-0.03 - 0.87)	169.66	166.69	2.96	172.62	0.82
p~D	0.023 (0.003)	0.942(0.054)	0.725(0.08)	-3.74 (-3.98 - -3.52)		-0.04 (-0.26 - 0.17)		172.95	169.94	3.01	175.96	4.16
p~V+M	0.024 (0.004)	0.942(0.056)	0.715(0.077)	-3.94 (-4.29 - -3.62)	0.16 (-0.03 - 0.35)		0.38 (-0.06 - 0.84)	167.81	163.81	3.99	171.8	0
p~V+D	0.023 (0.004)	0.941(0.056)	0.724(0.079)	-3.76 (-3.99 - -3.54)	0.19 (-0.02 - 0.38)	0.01 (-0.21 - 0.23)		170.66	166.67	3.99	174.64	2.84
p~M+D	0.024 (0.004)	0.942(0.055)	0.718(0.078)	-3.98 (-4.34 - -3.64)		-0.09 (-0.31 - 0.12)	0.46 (-0.01 - 0.93)	170.15	166.12	4.03	174.19	2.39
p~V+M+D	0.024 (0.005)	0.94(0.056)	0.718(0.078)	-3.96 (-4.32 - -3.63)	0.15 (-0.05 - 0.35)	-0.03 (-0.27 - 0.19)	0.4 (-0.06 - 0.86)	168.76	163.81	4.95	173.72	1.91
Lowland tapir												
Model	p	ψ	θ	α	β[Village]	β[River]	β[Side]	\bar{D}	\hat{D}	pD	DIC	ΔDIC
* p~1	0.013 (0.004)	0.815(0.137)	0.38(0.116)					68.36	66.21	2.15	70.52	0
p~V	0.012 (0.004)	0.815(0.136)	0.4(0.129)	-4.46 (-5.12 - -3.91)	0.01 (-0.42 - 0.4)			69.52	66.35	3.17	72.68	2.16
p~M	0.012 (0.005)	0.815(0.138)	0.397(0.121)	-4.27 (-5.08 - -3.6)			-0.38 (-1.43 - 0.67)	68.94	65.81	3.13	72.07	1.55
p~D	0.015 (0.007)	0.816(0.136)	0.39(0.118)	-4.38 (-5 - -3.88)		0.31 (-0.49 - 1.06)		68.57	65.51	3.06	71.63	1.11
p~V+M	0.012 (0.006)	0.813(0.137)	0.421(0.131)	-4.17 (-5.01 - -3.45)	0.23 (-0.33 - 0.81)		-0.8 (-2.31 - 0.57)	69.49	65.43	4.06	73.55	3.03
p~V+D	0.014 (0.007)	0.816(0.137)	0.397(0.122)	-4.42 (-5.07 - -3.89)	0.02 (-0.42 - 0.44)	0.33 (-0.47 - 1.1)		69.64	65.6	4.04	73.68	3.16
p~M+D	0.015 (0.009)	0.816(0.135)	0.398(0.12)	-4.31 (-5.1 - -3.64)		0.21 (-0.67 - 1.06)	-0.24 (-1.45 - 0.9)	69.56	65.58	3.98	73.54	3.02
p~V+M+D	0.014 (0.011)	0.815(0.136)	0.417(0.125)	-4.23 (-5.05 - -3.5)	0.19 (-0.38 - 0.79)	0.17 (-0.68 - 1.04)	-0.62 (-2.24 - 0.91)	70.2	65.42	4.78	74.98	4.46
Razor-billed curassow												
Model	p	ψ	θ	α	β[Village]	β[River]	β[Side]	\bar{D}	\hat{D}	pD	DIC	ΔDIC
p~1	0.026 (0.003)	0.905(0.08)	0.817(0.072)					252.86	250.8	2.07	254.93	60.46
p~V	0.026 (0.003)	0.907(0.08)	0.818(0.072)	-3.65 (-3.85 - -3.45)	-0.05 (-0.27 - 0.16)			253.69	250.61	3.08	256.77	62.29
p~M	0.026 (0.003)	0.914(0.076)	0.82(0.071)	-4.03 (-4.4 - -3.7)			0.63 (0.22 - 1.07)	244.61	241.57	3.04	247.65	53.18
* p~D	0.022 (0.003)	0.927(0.068)	0.87(0.063)	-4.09 (-4.35 - -3.84)		0.78 (0.59 - 0.97)		191.66	188.86	2.81	194.47	0
p~V+M	0.026 (0.004)	0.915(0.076)	0.823(0.071)	-4.05 (-4.41 - -3.71)	-0.08 (-0.28 - 0.12)		0.64 (0.23 - 1.07)	245.06	241.05	4.01	249.07	54.6
p~V+D	0.022 (0.003)	0.927(0.068)	0.873(0.063)	-4.11 (-4.38 - -3.85)	0.16 (-0.07 - 0.38)	0.82 (0.62 - 1.03)		190.74	186.86	3.88	194.62	0.14
p~M+D	0.022 (0.004)	0.928(0.066)	0.87(0.063)	-4.22 (-4.57 - -3.88)		0.74 (0.54 - 0.94)	0.25 (-0.18 - 0.69)	191.47	187.6	3.87	195.34	0.86
p~V+M+D	0.022 (0.004)	0.927(0.068)	0.873(0.063)	-4.22 (-4.58 - -3.88)	0.15 (-0.09 - 0.36)	0.78 (0.57 - 1)	0.22 (-0.21 - 0.66)	190.78	185.92	4.86	195.64	1.17
Spix's guan												
Model	p	ψ	θ	α	β[Village]	β[River]	β[Side]	\bar{D}	\hat{D}	pD	DIC	ΔDIC
* p~1	0.015 (0.002)	0.847(0.093)	0.815(0.096)					124.1	121.62	2.48	126.57	0.02
p~V	0.015 (0.003)	0.848(0.093)	0.818(0.097)	-4.22 (-4.53 - -3.94)	0 (-0.31 - 0.28)			125.11	121.66	3.45	128.55	2
p~M	0.015 (0.003)	0.85(0.091)	0.824(0.095)	-4.09 (-4.5 - -3.7)			-0.29 (-0.86 - 0.27)	124.03	120.62	3.41	127.43	0.88
p~D	0.014 (0.003)	0.847(0.093)	0.837(0.097)	-4.28 (-4.62 - -3.96)		0.11 (-0.17 - 0.39)		124.37	121.12	3.26	127.63	1.08
p~V+M	0.015 (0.003)	0.851(0.091)	0.824(0.094)	-4.09 (-4.52 - -3.72)	0 (-0.3 - 0.28)		-0.29 (-0.87 - 0.27)	124.97	120.64	4.33	129.3	2.75
p~V+D	0.014 (0.003)	0.852(0.092)	0.838(0.097)	-4.3 (-4.65 - -3.97)	0.03 (-0.28 - 0.33)	0.12 (-0.17 - 0.41)		125.26	121.07	4.19	129.45	2.9
p~M+D	0.013 (0.003)	0.857(0.09)	0.862(0.09)	-4.09 (-4.51 - -3.72)		0.24 (-0.08 - 0.56)	-0.55 (-1.19 - 0.12)	122.37	118.19	4.18	126.55	0
p~V+M+D	0.013 (0.004)	0.859(0.09)	0.868(0.089)	-4.1 (-4.51 - -3.72)	0.08 (-0.25 - 0.39)	0.28 (-0.07 - 0.62)	-0.58 (-1.23 - 0.09)	123.06	117.91	5.15	128.21	1.66
Pale-winged trumpeter												
Model	p	ψ	θ	α	β[Village]	β[River]	β[Side]	\bar{D}	\hat{D}	pD	DIC	ΔDIC
p~1	0.03 (0.003)	0.942(0.055)	0.772(0.072)					225.7	223.74	1.96	227.66	40.06
p~V	0.027 (0.004)	0.941(0.055)	0.808(0.075)	-3.63 (-3.88 - -3.4)	-0.3 (-0.62 - -0.01)			222.98	220.08	2.9	225.88	38.27
p~M	0.03 (0.004)	0.941(0.055)	0.766(0.072)	-3.78 (-4.1 - -3.49)			0.49 (0.11 - 0.88)	220.43	217.44	2.99	223.42	35.81
* p~D	0.027 (0.003)	0.941(0.057)	0.792(0.073)	-3.75 (-3.98 - -3.53)		0.55 (0.38 - 0.72)		184.64	181.67	2.97	187.61	0
p~V+M	0.028 (0.005)	0.941(0.056)	0.798(0.077)	-3.88 (-4.23 - -3.56)	-0.27 (-0.61 - 0.02)		0.46 (0.08 - 0.85)	218.57	214.67	3.9	222.47	34.87
p~V+D	0.026 (0.004)	0.941(0.056)	0.804(0.076)	-3.79 (-4.08 - -3.53)	-0.08 (-0.5 - 0.28)	0.55 (0.38 - 0.73)		185.55	181.69	3.85	189.4	1.79
p~M+D	0.026 (0.004)	0.941(0.056)	0.799(0.072)	-3.69 (-4 - -3.4)		0.59 (0.4 - 0.79)	-0.15 (-0.58 - 0.3)	185.18	181.27	3.91	189.09	1.48
p~V+M+D	0.026 (0.005)	0.941(0.056)	0.809(0.075)	-3.73 (-4.1 - -3.4)	-0.08 (-0.49 - 0.29)	0.59 (0.39 - 0.79)	-0.15 (-0.6 - 0.32)	186.12	181.26	4.86	190.98	3.37



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