

# Drone Surveys Revealed Bottom-Up, And Not Top-Down, Effects On The Marsh Deer Local Abundance

Ismael Verrastro Brack (✉ [ismaelbrack@hotmail.com](mailto:ismaelbrack@hotmail.com))

Federal University of Rio Grande do Sul <https://orcid.org/0000-0003-2988-9811>

Andreas Kindel

Federal University of Rio Grande do Sul

Douglas Oliveira Berto

Federal University of Rio Grande do Sul

José Luis Passos Cordeiro

Fundação Oswaldo Cruz (Fiocruz/Ceará), Eusébio

Igor Pfeifer Coelho

Federal University of Rio Grande do Sul

José Joaquín Lahoz-Monfort

University of Melbourne

Luiz Flamarion Barbosa Oliveira

Federal University of Rio de Janeiro

---

## Research Article

**Keywords:** aerial surveys, imperfect detection, large herbivores, N-mixture models, Pantanal wetland, vegetation greenness

**Posted Date:** September 23rd, 2021

**DOI:** <https://doi.org/10.21203/rs.3.rs-884511/v1>

**License:**  This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

---

# Abstract

**Context:** Spatial variation in large herbivore populations can be highly affected by the availability of resources (bottom-up) but modulated by the presence of predators (top-down). Studying the relative influence of these forces has been a major topic of interest in ecological and conservation research, while it has also been challenging to sample large herbivores.

**Objective:** i) Explore the use of spatiotemporally replicated drone-based counts analysed with  $N$ -mixture models to estimate abundance of large herbivores. ii) Evaluate the relative influence of bottom-up (forage and water) and top-down (jaguars) processes on the local abundance of the threatened marsh deer.

**Methods:** We conducted spatiotemporally replicated drone flights in the dry season of Pantanal wetland (Brazil) and imagery was reviewed by either one or two observers. We fitted counts using  $N$ -mixture models (for single and double observer protocols) and modelled local abundance in relation to vegetation greenness, distance to water bodies, and jaguar density.

**Results:** We found a positive relationship of marsh deer local abundance with vegetation greenness, a negative relationship with distance to water, but no relation with jaguar density. Individuals were concentrated in the lower and wetter region, even though it is the area expected to be more lethal from jaguar predation.

**Conclusions:** Bottom-up processes are shaping the distribution of marsh deer in the dry season; the benefits of accessing high-quality areas outweigh predation risk from jaguars. Spatiotemporally replicated drone-based counts may serve as an accessible and cost-effective protocol for large herbivores abundance estimation and monitoring while accounting for imperfect detection.

## Introduction

Large herbivore populations can be highly affected by resource availability (i.e. bottom-up) and the predator presence (i.e. top-down). Assessing the relative effect of these forces has been a major topic of interest in ecological studies of this group (e.g. Anderson et al., 2010; Hopcraft et al., 2010; Owen-Smith, 2010; Riginos, 2015). As both resource availability and predator presence may commonly vary in space, the local abundance of large herbivores is expected to be heterogeneous in landscapes. Furthermore, individuals can avail of this heterogeneity to access high-quality resources while avoiding predation (Armstrong et al., 2016; Hebblewhite & Merrill, 2009). Understanding these effects is important for wildlife conservation and management since herbivores are considered the trophic group at the highest extinction risk, with consequences for entire ecosystems (Atwood et al., 2020). The knowledge about bottom-up and top-down effects in large herbivores can be used to predict consequences of global climate changes in forage availability, to foresee possible effects of large herbivore or predator extinctions or reintroductions on ecosystem functions, and to manage exotic invasive herbivores or game species.

Beyond primary productivity itself, a major factor influencing large herbivore populations is the distribution of high-quality forage. Large herbivores usually seek vegetation with high nutritional quality, that is, young and fresh plants, easily digestible and rich in protein. As the plant biomass increases, forage quality reduces, thus herbivores tend to optimally choose intermediate forage biomass to maximize energy intake (Fryxell, 1991; Hebblewhite et al., 2008; Hobbs & Gordon, 2010). In heterogeneous landscapes, the variation in vegetation phenology can sustain high herbivore densities. Especially in seasonal environments, high-quality forage is considered the major factor influencing large herbivores migrations, for example, in African savannas (Boone et al., 2006; Purdon et al., 2018) and mountainous regions of North America (Aikens et al., 2017; Hebblewhite et al., 2008; Jakes et al., 2018; Merkle et al., 2016; Sawyer & Kauffman, 2011) and Eurasia (Bischof et al., 2012; Rivrud et al., 2016). The spatial distribution of herbivores in a specific time would be then strongly determined by plants' phenological stage, with higher densities in areas showing higher vegetation greenness values.

Predation is also an important process shaping large herbivore populations, usually modulating the effects of optimal foraging preferences (Hebblewhite et al., 2008; Hopcraft et al., 2010; Rivrud et al., 2018). Predation can be a potential cause of local extinction for large herbivores, even when kill rates are low (Festa-Bianchet et al., 2006). Beyond the direct effect of predation in removing individuals from the population (i.e. consumptive effects), prey species can show behavioural responses as they perceive the risk of predation (Lima & Dill, 1990; Say-Sallaz et al., 2019). When exposed to predation risk, large herbivores can increase vigilance behaviour or herd size, and even change used areas or time of activity (Creel et al., 2014). These non-consumptive effects may have different – and sometimes larger – effects in prey dynamics than direct predation (Creel & Christianson, 2008). Thus, the resulting spatial distribution pattern of large herbivore individuals would be a trade-off between foraging gains and predation effects.

Studying large herbivore populations is challenging, especially at large spatial scales and in remote areas. The influence of forage distribution and predators on herbivore individuals has usually been studied using biotelemetry, by evaluating how landscape variables associated with forage availability and predation affect individuals' movements and space use (Hopcraft et al., 2014; Merkle et al., 2016; Owen-Smith, 2010). Population-level studies of large herbivores are commonly carried out using aerial surveys with manned aircraft (e.g. Caughley, 1974; Vucetich & Peterson, 2004), which is often financially prohibitive and can prevent the necessary amount of spatial or temporal replications for accurate and frequent estimates needed for decisions in conservation (Ferreira & Aarde, 2009; Fritsch & Downs, 2020). Recently, drones (Unmanned Aerial Systems or Remotely Piloted Aircraft) have emerged as an accessible, safe, and cost-effective alternative for aerial surveys and have been tested to sample large herbivore populations (e.g. Barasona et al., 2014; Chrétien et al., 2016; Gentle et al., 2018; Linchant et al., 2018; Rey et al., 2017; Vermeulen et al., 2013).

As for other wildlife survey methods, aerial count data obtained from drone-based surveys are susceptible to imperfect detection. Some individuals present in the sampling area may be unavailable for detection (e.g. under a tree) or, even when available, an observer can fail to detect them when reviewing imagery

(Brack et al., 2018). Addressing these sources of error in count data with a robust framework is imperative to obtain unbiased abundance estimates. Given the potential of hierarchical  $N$ -mixture models to estimate abundance accounting for imperfect detection and without the need of marking individuals (Royle, 2004), they have been proposed as a feasible approach for aerial surveys (Brack et al., 2018; Williams et al., 2017), especially for modelling abundance at large spatial scales (e.g. Martin et al., 2015). Moreover, the typical sampling design for  $N$ -mixture models matches the characteristics of drone surveys, that is, multiple and short flights in spatiotemporally replicated surveys.

Our objective here was two-fold: i) explore the potential of drone surveys and hierarchical  $N$ -mixture models to estimate large herbivore abundance and ii) use this innovative approach to evaluate the relative influence of bottom-up (forage and water) and top-down (predators) factors on the local abundance of marsh deer (*Blastocerus dichotomus*). The marsh deer is the largest cervid in the Neotropics (up to 150 kg), highly adapted to use marshes and swamps, living in low densities in South America's wetlands and savannas. Because of its association with wetlands, marsh deer's current distribution is highly fragmented and the species is listed as Vulnerable with extinction (IUCN; Duarte et al., 2016). Its main predator is the jaguar (*Panthera onca*) and, although marsh deer are considered a valuable prey for jaguars (Hayward et al., 2016), they only compose  $\leq 10\%$  of the jaguar's diet (Cavalcanti & Gese, 2010; Azevedo & Murray, 2007; Perilli et al., 2016). Here, we specifically tested a positive influence of (1) vegetation greenness (as a proxy for high-quality forage availability) and (2) water bodies on the local abundance of marsh deer, and a negative effect of (3) jaguar density. We also tested a modulatory effect of jaguar density on the relation of deer local abundance with vegetation greenness, expecting higher jaguar densities to be associated with weaker positive effects of forage. We assessed these predictions during the dry season of the Pantanal wetland of Brazil. Additionally, we discuss the feasibility of spatiotemporally replicated drone surveys applied here, and compare two hierarchical  $N$ -mixture modelling approaches (single and double observer protocol) for estimating the abundance of large herbivore populations, which can also be employed for other wildlife species in different contexts.

## Materials And Methods

### Study area

The Pantanal wetland, the world's largest tropical floodplain, is an inner lowland region of Quaternary sedimentary deposits in central South America. With a seasonal rainy climate, it receives periodic flooding pulses from the rivers in the surrounding highlands (Junk et al., 2006). This study was conducted in the Sesc Pantanal Private Natural Reserve, a 108,000-ha private reserve created in 1997, located in the Northern Pantanal (16° 45' S and 56° 15' W), and designated as a Ramsar Site (number 1270). The area is characterized by a tropical savanna climate with a pronounced dry season, showing a mean annual temperature of 26°C and an annual average rainfall of 1200 mm concentrated from November to March (Hofmann et al., 2016). The reserve is located between two of the major Pantanal rivers, Cuiabá and São Lourenço, receiving their overflows in the flooding season. The area is composed

of a highly heterogeneous vegetation (grasslands, shrublands, and riparian, flooded, and seasonally dry forests) mainly structured by microrelief differences that receive different flooding regimes (Oliveira et al., 2013). We focused this study on two regions of the Sesc Pantanal Reserve dominated by open vegetation types: (1) the western portion, covered by shrublands, sometimes mixed with flooded forest patches of *Vochysia divergens*, located at lower altitudes and retaining more water in the dry season; and (2) the central region, covered by savannas (woody “cerrado” vegetation and grasslands) and seasonally dry forests, and containing some small artificial water ponds, built before the reserve creation (1997) for cattle watering in the dry season, that are used by marsh deer. Since the reserve creation in 1997, cattle were excluded from the area and wildfires have been fought.

## **N-mixture models for count data from drone surveys**

*N*-mixture models are a family of hierarchical models used to estimate abundance from repeated counts of unmarked individuals while accounting for imperfect detection (Dénes et al., 2015; Royle, 2004). The typical sampling design for *N*-mixture models consists of multiple sites observed multiple times (i.e. spatiotemporally replicated surveys). These count data are modelled in a hierarchical way, as a result of (at least) two processes: i) the biological state process that governs the local abundance at sites, and ii) the observation process, affected by imperfect detection of individuals. In the application of *N*-mixture models for drone surveys we present here, each transect (a flight path) is split into segments, which represent the sites. Each site is flown multiple times and the aerial images captured from the drone are reviewed under a double independent observer protocol (Fig. 1). Thus, the resulting dataset can be represented as a three-dimensional array containing, for each visit in each site, the counts summarized as different possibilities of encounter histories by the observers (i.e. number of individuals detected by both; only by the first observer; and only by the second observer). With this data structure, it is possible to estimate abundance while accounting for the two common sources of false-negative errors in aerial surveys: availability and perception errors (Brack et al., 2018). The availability error refers to individuals that are present in the sampling area but unavailable for detection at the time the image is taken due to, for example, being hidden below vegetation. Perception error occurs when an observer (or an algorithm) fails to detect an individual that is available for detection. Both errors, if not properly addressed, generate underestimation of population size.

For modelling such count data, we used the three-level multinomial *N*-mixture model with a temporary emigration component proposed by Chandler, Royle, & King (2011). Under the assumption site abundance remains constant throughout independent visits, we model the local abundance  $M_i$  at sites  $i \in \{1, \dots, S\}$  as a Poisson distribution (given counts are non-negative integer numbers):

$$M_i \sim \text{Poisson}(\lambda)$$

Then, in each visit  $j \in \{1, \dots, J\}$ , each individual from the population  $M_i$  at site  $i$  has a probability  $\varphi$  of being available for detection, resulting in the number of available individuals  $N_{ij}$ :

$$N_{ij} \sim \text{binomial}(M_i, \varphi).$$

If the sites are truly closed to changes in population (i.e. no departures nor entries), the availability parameter  $\varphi$  corresponds to the probability of an individual present at a site not being hidden, for example, below vegetation, inside a burrow, or, in the case of marine surveys, submerged. However, if there is some movement of individuals in and out of the surveyed area between visits, the availability parameter would correspond to both processes: the probability of the individual being present on the site at the time of survey and not being hidden.

In the last observation level, each individual available for detection  $N_{ij}$  has a probability  $p$  of being detected by each observer independently (i.e. perception probability). With a double independent observer protocol, there are four possible encounter histories for each available individual: detected by both observers (“11”), detected only by the 1st observer (“10”), detected only by the 2nd (“01”), and not detected (“00”). Then, the counts  $Y$  under each observable encounter history  $k \in \{1, 2, 3\}$  are modelled as a function of multinomial conditional cell probabilities  $\pi_k$ , in which  $k_{11} = p^2$ ;  $k_{10} = p(1 - p)$ ;  $k_{01} = (1 - p)p$ :

$$Y_{ijk} \sim \text{multinomial}(N_{ij}, \pi(p)_k).$$

Alternatively, it is possible to estimate abundance with a single observer protocol for image review using the classic binomial  $N$ -mixture model (Kéry et al., 2005; Royle, 2004, and proposed for drone-based surveys in Williams et al., 2017), but forgoing the possibility of segregating both observation processes. In this case, the single observer counts  $Y$  for each site  $i$  in each visit  $j$  are modelled under a binomial distribution in which each individual of the population  $M_i$  has an overall detection probability  $p^*$  that is the product of availability ( $\varphi$ ) and perception ( $p$ ):

$$Y_{ij} \sim \text{binomial}(M_i, p^*), \text{ where } p^* = \varphi \cdot p$$

The use of a double observer protocol for image review is not necessary for the entire image set: a mixed single and double observer protocol (i.e. double observer only in a subset of the imagery) is enough to separately estimate perception and availability probabilities (Brack et al., 2018; Kéry & Royle, 2016).

Further to this constant model, parameters can be estimated as a function of covariates using linear regressions with appropriate link functions (e.g. log for  $\lambda$  and logit for  $\varphi$ ,  $p$ , and  $p^*$ ).

## Drone flights and marsh deer counts

Aerial marsh deer surveys were carried out in preprogrammed flight paths using the drone Echar 20B (XMobots®, <http://xmobots.com/>). Echar 20B is a battery-propelled fixed-wing drone (2 m wingspan, 7 kg) with a flight time of about 1h15min and a cruise speed of 70 km/h. It is launched by a catapult and lands with a parachute. The drone was equipped with either a Sony Alpha500 (24Mpix) or a Sony A7R (36Mpix) RGB sensors. Flight height and lens focal distance were adjusted for each camera in order to

keep a ground sample distance (GSD) of approximately 2 cm/pix (e.g. Sony Alpha A7R, 110 m above ground and 22 mm focal distance). Resulting strip width (photo) was approximately 180–200 m.

We planned six flight paths, ranging from 32 to 42 km in length (Fig. 2 and Table 1). We first defined a 1x1 km grid with a random origin in the study area to guide the flight lines and planned flight paths preferably in separated strips (to avoid deer movements between lines), perpendicular to the flooding pulse (to minimize intra-site and maximize inter-site vegetation and water heterogeneity). Flight paths avoided highly forested areas seldom used by marsh deer and where the availability of individuals for detection would be close to zero. As flight time is a limiting factor for drone surveys (especially battery-propelled), we planned the flight paths to start and finish nearby to minimize wasted flight time outside planned lines. The drone was programmed to take photos with a frontal overlap of 50–60 %, meaning that each point in the ground would appear in 2–3 pictures. We conducted a total of 25 drone flights (2–6 visits in each flight path) in September and October of 2017, resulting in 763 km flown. To define the sites for the *N*-mixture models, we split the six flight paths into segments of 1 km length, expecting to reduce effects of movement of individuals between sites during our sampling window (daily movements of marsh deer intra-season are expected to be short; Piovezan et al., 2010). This resulted in 203 sites with 1–6 visits per site. Flights were operated preferably in the mildest hours of the day (i.e. 6–9 h and 16–18 h) when marsh deer are more active. We first repeated flights in the same path to then go to the next flight path, in order to minimize the effect of individuals entering and leaving the sites between visits (i.e. avoid temporary emigration by movement). Intervals between visits for each flight path are presented in Table 1.

For the approximately 25,000 images collected, the first observer reviewed the entire imagery and the second only 20 % of the flights. Observers were instructed to conduct a careful review of each image with free zooming and to mark each marsh deer found (Fig. 2c) using the software ClickPoints (Gerum et al., 2017). For each site, we got the total marsh deer counts under each observable encounter history for each visit (Fig. 1). The first observer took more than 100 hours to review the entire imagery, with a mean time of 18 seconds per image. Given that the pictures were frontally overlapped, we used only the first appearance of each record and excluded the double counts. The overlapped areas between pictures increased the chance of detection by the observers and were helpful to solve identification uncertainties. We only included a marsh deer as a certain record after all detections were reviewed by experts. Thus, we are confident our dataset does not include false-positive records (which are not accounted for in our modelling approach). We had only two uncertain detections excluded by experts, since the size, shape, and colour of the marsh deer records are usually very conspicuous and differ from any other species or background feature.

## Covariates

We tested the effects of bottom-up (vegetation greenness and distance to water) and top-down (jaguar density) covariates on the local abundance of marsh deer at the sites. Vegetation greenness was calculated using the Normalized Difference Vegetation Index (NDVI) as a proxy for the availability of high-quality forage (Fig.S1.1). The NDVI has been widely used as a proxy for primary productivity and

forage quality for large herbivores (Garrouette et al., 2016; Pettorelli et al., 2005, 2011), presenting a well-documented relation with protein content in vegetation and in herbivores faeces (Hamel et al., 2009; Ryan et al., 2012). We calculated the NDVI from Sentinel-2 satellite images (10 m spatial resolution), obtained in the same period of the drone flights (September/2017). As we avoided flying over forested areas, we assume that NDVI calculated is, at a reasonable extent, related to green and fresh vegetation available for marsh deer at the sites. On the same satellite image, we identified water pixels using low NDVI values, and we calculated, for each 10x10 m cell, the Euclidean distance to the nearest water pixel, resulting in a raster map of distance to water (Fig. S1.2). The jaguar density map (500 m spatial resolution; Fig. S1.3) was derived from a spatial capture-recapture (Royle et al., 2014) study conducted in the same reserve (unpublished data, more info in Fig. S1.3). We do not expect an effect of marsh deer abundance on the distribution of jaguars, which could preclude interpretations of causal relations in this study, because marsh deer are generally not a major prey item of jaguars. Although the cougar (*Puma concolor*), the other large predator in Pantanal, could potentially influence marsh deer, we did not investigate these effects since we did not find any evidence of cougar predation on marsh deer in the literature.

To account for heterogeneity at the observation level, we considered air temperature during flights and forest cover as sources of variation on the availability of individuals. Since temperatures during the day in Pantanal can be high (sometimes close to 40° C), marsh deer probably avoid exposure to sunlight during the hottest times of the day by being hidden below vegetation. Thus, we expect the higher the temperature, the lower the availability of marsh deer for detection. In the same way, in areas where tree cover is higher, there is more chance of marsh deer being hidden below vegetation, and thus we expect the higher the forest cover, the lower the availability of marsh deer for detection. Air temperature was recorded during flights approximately every 10 minutes with a thermometer Incoterm® 7665.02.0.00 (precision = 1° C) about one meter above ground. The forest cover in sites was obtained from a land cover map derived from Landsat satellite scenes of 2016 (30 m resolution), using a supervised classification of images from 3 periods of the year: flooded, discharging and dry seasons.

For each 1km-site, we summarized NDVI, distance to water bodies, and jaguar density by calculating the mean pixel value, and extracted forest cover as the percentage of forest pixels within the site. We obtained a single value of air temperature for each site in each visit.

## Model fitting

We modelled marsh deer drone-based counts in relation to the covariates using the two model structures presented in the modelling description section: i) the single observer binomial  $N$ -mixture model, and ii) double observer multinomial  $N$ -mixture model. We built the models with a maximum of two covariates in the biological process (local abundance  $\lambda$ ), considering the interaction (i.e. modulatory effect) between jaguar density and vegetation greenness and avoiding the inclusion of jaguar density and distance to water bodies in the same model (because jaguar density was modelled in relation to water). In the observation level (availability  $\varphi$  for the multinomial and overall detection  $p^*$  for the binomial  $N$ -mixture), we compared all combinations of forest cover and temperature. For the multinomial  $N$ -mixture model, we

only considered the perception probability  $p$  as constant. This resulted in 28 candidate models for each  $N$ -mixture model structure (Tables S2.1-S.2.2).

We fitted the models under a maximum likelihood approach (data and R script in Supplementary Material S5) using functions *pcount* (single observer) and *gmultmix*, (double observer) from package *unmarked* (Fiske & Chandler, 2011) in the programming language R (R Core Team, 2020). We performed model selection with the Akaike Information Criteria adjusted for small sample sizes (AICc). We chose only a Poisson distribution for the local abundance parameter since the use of the Negative Binomial distribution has been unrecommended because it can provide unreliable very high abundance estimates in  $N$ -mixture models (Joseph et al., 2009; Kéry et al., 2005). All covariates were standardized by subtracting their mean and dividing by their standard deviation. No pairwise correlation between covariates was higher than  $|\rho| = 0.7$ . We applied a visual check of residuals and goodness of fit test for the binomial  $N$ -mixture model using *nmixgof* package (there is no GOF test readily available for the multinomial  $N$ -mixture model), which indicated an adequate fit and presented an estimated overdispersion parameter  $\hat{c} < 1.1$ . Using the best-ranked model for the double observer approach, we produced an abundance map of the marsh deer in the Sesc Pantanal Reserve from the predicted covariate relations and excluding pixels we considered to be non-habitat for the species (i.e. forest cover  $> 80\%$ ).

We also checked whether the choice to segment the flight paths in 1km-sites affected our abundance estimates and if we could detect any effect of spatial temporary emigration. For this, we segmented the flight paths using different site length definitions, ranging from 400 to 2000 m in steps of 50 m, and fitted a null multinomial  $N$ -mixture model ( $\lambda$ ,  $\varphi$ , and  $p$  constants) for each of these 33 scenarios. To be able to compare the abundance estimates between these scenarios with different segment lengths for sites, we added an offset using the logarithm of the segment length in the abundance parameter ( $\lambda$ ).

## Results

From the approximately 25,000 images collected in the 25 flights, we obtained a total of 66 unique marsh deer records by both observers (Fig. 2, Table 1) that appeared in 137 images (the same record usually appeared in more than one image because the pictures were overlapped). For the five flights that have a double observer protocol, 20 deer were detected by both observers, two detected only by the first observer, and two only by the second (Table 1). Marsh deer were detected in 26 of the 203 1km-sites and the maximum count for a visit was four and occurred in two sites. For those 26 sites that presented any marsh deer detection, the mean count per visit was less than one (0.72).

Table 1

Length, number of flights (visits), and marsh deer counts by the 1st and the 2nd observers for the six flight paths planned at Sesc Pantanal Reserve (Brazil). Visits intervals present the median time between visits and maximum time between the first and the last visit. The first observer reviewed the entire imagery and the second only 20% of the flights.

Path ID	Length (km)	N visits	Visits intervals median (max) in hours	Counts obs1	Counts obs2
1	32	2	1 (1)	4 / 7	3 / -
2	38	3	8 (15)	1 / 0 / 0	- / - / -
3	35	5	10 (49)	6 / 5 / 10* / 15 / 7	- / - / 10* / - / 8
4	36	5	16 (200)	0 / 0 / 0 / 0 / 0	- / - / - / - / -
5	34	6	5 (23)	1 / 0 / 0 / 1 / 0 / 0	1 / - / - / - / - / -
6	42	4	24 (72)	3 / 1 / 1 / 2	3 / - / - / -
* total number of detected individuals in this flight was 11 (9 detected by both and 1 by each one).					

Model selection picked up the same covariates for both model structures (single observer binomial and double observer multinomial  $N$ -mixture; Tables S2.1-S2.2) and both approaches presented very similar coefficient estimates in the top-ranked models (Table S2.3). We found a negative effect of the distance to water bodies and a positive effect of vegetation greenness (NDVI) on marsh deer local abundance (Fig. 3). We did not find evidence of an effect of jaguar density on the local abundance of marsh deer. Sites with a higher proportion of forest cover and flights conducted at higher air temperatures had lower detection probabilities (Fig. 3c and 3d). The estimated perception probability of detecting a deer available on the imagery by an observer ( $p$ ) was very high: 0.93 (95 % CI = 0.82–0.97).

Estimated mean marsh deer abundance ( $\lambda$ ) ranged from close to zero (sites with low values of NDVI or with a mean distance of water bodies greater than 2 km) to about one (sites near to water bodies or with high values of vegetation greenness); keeping the mean value of one covariate when varying the other (Fig. 3a and 3b). Predicted abundance for sites near water bodies and with high NDVI values was 3.2 (95 % CI = 1.5–6.7). The total abundance estimated for all 203 sampled sites was 150 individuals (95 % CI = 43–445). The spatial distribution of marsh deer local abundance obtained from the predicted relations indicates consistently higher densities of the population in the western part of the reserve (Fig. 4; lower and upper 95 % CI local abundance maps are provided in Fig. S3.1). The resulting total abundance predicted for the Sesc Pantanal Reserve was 1856 (95 % CI = 951–3710) marsh deer.

For the analysis comparing different choices of site length, we obtained a considerable variation in the precision among scenarios, but the estimates overlapped consistently (Fig. S4.1). Highly uncertain estimates correspond to scenarios where some deer records were excluded by the way flight paths were segmented.

## Discussion

We were able to reveal the effects of bottom-up (forage and water) and top-down (predators) landscape variables on the spatial variation of marsh deer local abundance using spatiotemporally replicated drone flights while accounting for detection errors. We first discuss the methodological implications of our results and then explore the biological interpretations of the tested hypotheses.

## Modelling abundance with spatiotemporally replicated drone surveys

Count data obtained from spatiotemporally replicated drone surveys and analysed with  $N$ -mixture models has proven to be a straightforward method to estimate abundance and its relationship with landscape variables for a low-density large herbivore at a relatively large spatial scale (especially for studies using drone surveys). We were able to reach a coefficient of variation for the mean local abundance estimate

$CV(\hat{\lambda}) = 35\%$  with 66 records collected in 25 flights that surveyed an area of 1080 km<sup>2</sup> in less than 20 days of fieldwork. With this approach, we assessed marsh deer abundance accounting for the two main detection errors in aerial surveys: availability and perception. This is particularly interesting for the availability error, which is rarely addressed in aerial surveys or estimated by using costly auxiliary data, such as from biotelemetry (e.g. Martin et al., 2015). The nature of this method (multiple short flights) can overcome a common limitation of population assessments by drone surveys: the short flight time and range. Finally, local abundance estimates were robust (i.e. no evidence of bias) to the choice of segment length we made to split the flight paths.

The use of single observer counts in image review, instead of a double observer protocol, did not compromise abundance estimates or the relationship of detection parameters with covariates (assumed to affect only the availability process). Both modelling structures (single and double observer) provided very similar estimates for all parameters. This result is due to the very high perception probability we had for the observers ( $p = 93\%$ ; 95% CI = 82–97%). In our case, a double observer protocol in image review could be considered unnecessary. However, this is possibly not the case for many other species, which are, for example, less conspicuous in drone images, or in the case of thermal imagery with lower sensor resolution and often low contrast between background and individuals (Burke et al., 2019). In this case, a double observer protocol could improve abundance estimates by providing more precise estimates in the observation process. The double observer protocol can be applied to a subset of the imagery; we were able to estimate both observation processes (perception and availability) with confidence using a second observer review in only 20% of the flights. With the increase of automated algorithms for drone image reviews (e.g. Gray et al., 2018; Kellenberger et al., 2018), this double observer protocol could be applied manually to an image subset to address the algorithm error. Other situations to apply a double observer protocol to segregate the detection processes include having different hypotheses for availability and perception covariates or when the same covariate is expected to affect both processes in different ways. For example, in drone surveys with thermal cameras under cold weather, temperature may positively

affect availability (individuals seeking sunlight) and negatively affect perception (lower contrast in thermal signature).

One limitation of the approach presented here is that spatial temporary emigration (i.e. individuals entering and leaving the site between visits), if it exists, would bias the estimation of abundance. In such cases, the local abundance parameter should not be used to obtain absolute density numbers (Kéry & Royle, 2016) and could be more adequately interpreted as the intensity of use by the population, that is, the number of individuals of the population that use that site. It is possible to reduce the effects of spatial temporary emigration on abundance estimates by shortening the time between visits, but avoiding a temporal autocorrelation between visits (Brack et al., 2018; Williams et al., 2017). Another factor that can affect the influence of the spatial temporary emigration is the relative magnitude of the individuals' movements in relation to the site size, depending on the site size itself and the home range size of the species (Chandler et al., 2011). In this study, we did not find any trend of the abundance estimates in relation to the choice of segment length (i.e. site size). Although this analysis could not directly detect spatial temporary emigration effects, it apparently indicates no positive bias in abundance estimates. Even though absolute abundance numbers derived from this method should be treated carefully in the presence of spatial temporary emigration, this approach is widely useful for studying the relationship of abundance with spatial variables and as relative abundance estimates for long-term monitoring of population trends.

## **Spatial variation in marsh deer abundance**

We found evidence of bottom-up related processes (water bodies and vegetation greenness as a proxy for available forage) affecting the distribution of marsh deer local abundance in the dry season. Even it is not possible to affirm that there are no predation effects on marsh deer abundance, its relative influence is certainly weaker than the bottom-up processes we studied. Interestingly, the high-quality areas that sustain higher densities of marsh deer in the dry season (i.e. near water bodies and higher levels of vegetation greenness) are the areas that would be expected to be more lethal (i.e. higher jaguar density). Moreover, areas close to water bodies are considered riskier in the dry season because large predators tend to hunt in such regions (Owen-Smith, 2014; Valeix et al., 2011). Although top-down factors (i.e. predation) are expected to significantly affect the distribution of ungulates (McArthur et al., 2014), our result may not be very surprising. In seasonal rainy savannas, remaining areas with available forage in the dry season are considered a major factor limiting large herbivore populations (Owen-Smith, 2014), sometimes overshadowing high risks of predation (Riginos, 2015). Thus, the benefits of accessing high-quality areas (with more food and water) for marsh deer in the dry season may outweigh predation risk from jaguars, resulting in higher marsh deer local abundance. Also, to reduce risks in these areas, marsh deer may present some behavioural mechanisms to prevent predation by, for example, avoiding being active at night, when predation success is higher, or increasing vigilance while foraging (Creel et al., 2014). Furthermore, the presence of predators could influence the local abundance of marsh deer at finer scales than we evaluated here, or the influence of predation on marsh deer may be related to other variables than jaguar density such as the amount and distribution of safe and risky patches in the

landscape (Laundré et al., 2014; Moll et al., 2017). Finally, as marsh deer is not a common prey for jaguars (Cavalcanti & Gese, 2010; Azevedo & Murray, 2007), jaguars may not impose strong predation risks for marsh deer.

The positive relation we found between marsh deer abundance and vegetation greenness corroborates the known pattern that primary productivity is a major factor shaping the distribution of large herbivore populations in landscapes. This relationship is well studied for ungulates in temperate regions of Eurasia, where, with the beginning of the spring season, herbivores track gradients of green and fresh vegetation produced after snow melting in heterogeneous topographic landscapes (Bischof et al., 2012; Hebblewhite et al., 2008; Merkle et al., 2016; Rivrud et al., 2016). In tropical areas, large herbivores in African savannas follow a green-up gradient produced by differences in precipitation among regions (Boone et al., 2006; Cornélis et al., 2011; Purdon et al., 2018). In South America, a similar pattern was found for guanacos in the temperate environments of Patagonia (Schroeder et al., 2014). Similarly, the results presented here suggest that the seasonal dynamics of tropical floodplains may also produce forage quality heterogeneity for large herbivores (in this case, marsh deer). Although we did not evaluate the relation of local abundance and vegetation greenness for the wet season, in the dry season, the marsh deer population was concentrated on the remaining patches of green vegetation in wetter areas of the reserve. Then, we could expect an expansion of the marsh deer population following a vegetation green-up with the rain and the floods of the wet season. While this mechanism was proposed to influence variation in marsh deer abundance in the Pantanal wetland (Tomas et al., 2001), it remains unevaluated.

As expected, we found a strong relationship of marsh deer abundance to water bodies, with the local abundance of marsh deer drastically reduced along the first two kilometres from water bodies. Access to water, especially in the dry season, can be an important factor in shaping ungulate spatial patterns (Owen-Smith, 2014) and severe droughts are a potential cause of local extinctions (Spinage & Matlhare, 1992). Marsh deer is known to be a habitat specialist associated with wetlands: they present long limbs with interdigital webbing to move in flooded areas (Nowak, 1991). Since aquatic macrophytes and other flood-tolerant plants compose a significant part of marsh deer's diet (Costa et al., 2006; Tomas & Salis, 2000), this relationship with water bodies is probably also a consequence of foraging opportunities, beyond water supply. However, marsh deer may occur in low densities in drier areas, since some individuals were found away from wet areas, where small water bodies may be sufficient to sustain low densities. Interestingly, some areas of intermediate local abundance predicted to the central region of the reserve are close to the artificial water ponds (cattle watering holes remnant of the former ranches). These artificial water bodies can play an important role in the maintenance of marsh deer populations in dry areas, especially in severe drought years.

The predicted spatial pattern shows that the population is concentrated in the western portion of the Sesc Pantanal Reserve, the lower and wetter region, presenting incredibly high densities for the species in this area (more than 8 individuals per km<sup>2</sup> in contrast with < 2 ind./km<sup>2</sup> in the drier central region). Most other studies that estimated marsh deer density in different regions obtained a maximum of one individual per km<sup>2</sup> (Andriolo et al., 2005; Mourão et al., 2000; Peres et al., 2017; Ríos-Uzeda & Mourão, 2012; Tiepolo et

al., 2010), with Tomas et al. (2001) reporting a maximum of 1.85 ind./km<sup>2</sup> in some areas of Pantanal in the dry season. Although we should treat our density estimates carefully because of potential spatial temporary emigration, these apparent high densities for marsh deer could be justified by the fact that these previous studies did not account for the availability bias in estimates. As it is clear from our low estimates of the availability parameter ( $\varphi < 0.3$ ), the availability error might have an important influence on aerial counts of marsh deer (and potentially other ungulate species). It is not uncommon to find studies that ignore or poorly address the availability error in aerial surveys (e.g. Barasona et al., 2014; Mourão et al., 2000), providing a biased estimation of abundance. This result highlights the importance of accounting for imperfect detection (here, particularly the availability error) – and modelling its heterogeneity – in large herbivores population assessments.

## Conclusions

Large herbivores are highly threatened because of habitat conversion, overhunting, and livestock diseases and competition, combined with usually large home ranges, migratory behaviour in many species (Gnanadesikan et al., 2017), and low reproductive rates (Ripple et al., 2015). Methods to efficiently estimate population size are important to monitor and evaluate the status of threatened large herbivore populations. Counts from spatiotemporally replicated drone-based surveys analysed with hierarchical  $N$ -mixture models may serve as an accessible and cost-effective protocol for modelling the abundance of large herbivores (and certainly other wildlife species observable from aerial images) accounting for imperfect detection, especially in open vegetation and remote areas.

Marsh deer local abundance in the dry season presented a strong relation with what is expected to be the high-quality areas for the species: high levels of vegetation greenness (that are expected to provide high-quality forage) and close to water bodies (as a habitat specialist associated with wetlands). The distribution of marsh deer abundance was not influenced by its main predator, the jaguar, and the higher densities of the population overlapped with the higher densities of jaguars. Small water bodies (even the artificial ones) may sustain some individuals in drier areas and may be an important resource for the species in severe years. As primary productivity and availability of water bodies present a very contrasting seasonal dynamics associated with flood pulses in Pantanal (and in other marsh deer occurrence areas), it would be interesting to evaluate how the trade-off between these bottom-up and top-down forces behaves in the wet season. Effective conservation actions (e.g. delimitation of protected areas) can be improved by the understanding and prediction of these dynamics to encompass the entire range of high-quality areas for marsh deer.

## Declarations

### ACKNOWLEDGEMENTS

We are especially grateful to Sesc Pantanal managers, Cristina Cuiabália and Christiane C. Rodrigues, and all their team for the fieldwork support. We thank Gabriela Schuck and Thaís Conceição for help in

fieldwork. We also thank Adriano G. Chiarello, Fabiano R. Melo, and Miriam Marmontel for valuable reviews on this manuscript.

## **Funding**

IB was supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (Capes; Finance Code 001). Fieldwork was supported by Sesc Pantanal.

## **Conflicts of interest/Competing interests**

The authors have no conflicts of interest to declare that are relevant to the content of this article. All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

## **Ethics approval**

Not applicable

## **Consent to participate and for publication**

Not applicable

## **Availability of data, material, and code**

Data and codes are available at Figshare repository: <https://figshare.com/s/3b392fce55d83b43cdc1>

## **Authors' contributions**

IB, AK, and LFBO conceived the ideas; IB, AK, JLPC, IPC, and LFBO designed methodology; IB, JLPC, LFBO, IPC, and DBO collected and processed data; IB, IPC and JJLM analysed the data; IB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## **References**

1. Aikens EO, Kauffman MJ, Merkle JA, Dwinnell SPH, Fralick GL, Monteith KL (2017) The greenscape shapes surfing of resource waves in a large migratory herbivore. *Ecol Lett* 20(6):741–750. <https://doi.org/10.1111/ele.12772>
2. Anderson TM, Hopcraft JGC, Eby S, Ritchie M, Grace JB, Olf H (2010) Landscape-scale analyses suggest both nutrient and antipredator advantages to Serengeti herbivore hotspots. *Ecology* 91(5):1519–1529. <https://doi.org/10.1890/09-0739.1>
3. Andriolo A, Piovezan U, Costa MJRP, da, Laake J, Duarte JMB (2005) Aerial line transect survey to estimate abundance of marsh deer (*Blastocerus dichotomus*) (Illiger, 1815). *Brazilian Archives of Biology Technology* 48(5):807–814. <https://doi.org/10.1590/S1516-89132005000600017>

4. Armstrong JB, Takimoto G, Schindler DE, Hayes MM, Kauffman MJ (2016) Resource waves: Phenological diversity enhances foraging opportunities for mobile consumers. *Ecology* 97(5):1099–1112. <https://doi.org/10.1890/15-0554.1/supinfo>
5. Atwood TB, Valentine SA, Hammill E, McCauley DJ, Madin EMP, Beard KH, Pearse WD (2020) Herbivores at the highest risk of extinction among mammals, birds, and reptiles. *Science Advances*, 6(32). <https://doi.org/10.1126/sciadv.abb8458>
6. Azevedo FCC, Murray DL (2007) Spatial organization and food habits of jaguars (*Panthera onca*) in a floodplain forest. *Biol Cons* 137(3):391–402. <https://doi.org/10.1016/j.biocon.2007.02.022>
7. Barasona J, Mulero-Pázmány M, Acevedo P, Negro JJ, Torres MJ, Gortázar C, Vicente J (2014) Unmanned Aircraft Systems for Studying Spatial Abundance of Ungulates: Relevance to Spatial Epidemiology. *PLoS ONE* 9(12):e115608. <https://doi.org/10.1371/journal.pone.0115608>
8. Bischof R, Loe LE, Meisingset EL, Zimmermann B, Van Moorter B, Mysterud A (2012) A Migratory Northern Ungulate in the Pursuit of Spring: Jumping or Surfing the Green Wave? *Am Nat* 180(4):407–424. <https://doi.org/10.1086/667590>
9. Boone RB, Thirgood SJ, Hopcraft JGC (2006) Serengeti wildebeest migratory patterns modeled from rainfall and new vegetation growth. *Ecology* 87(8):1987–1994. [https://doi.org/10.1890/0012-9658\(2006\)87\[1987:SWMPMF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1987:SWMPMF]2.0.CO;2)
10. Brack IV, Kindel A, Oliveira LFB (2018) Detection errors in wildlife abundance estimates from Unmanned Aerial Systems (UAS) surveys: Synthesis, solutions, and challenges. *Methods Ecol Evol* 9(8):1864–1873. <https://doi.org/10.1111/2041-210X.13026>
11. Burke C, Rashman M, Wich S, Symons A, Theron C, Longmore S (2019) Optimizing observing strategies for monitoring animals using drone-mounted thermal infrared cameras. *Int J Remote Sens* 40(2):439–467. <https://doi.org/10.1080/01431161.2018.1558372>
12. Caughley G (1974) Bias in Aerial Survey. *J Wildl Manag* 38(4):921. <https://doi.org/10.2307/3800067>
13. Cavalcanti SMC, Gese EM (2010) Kill rates and predation patterns of jaguars (*Panthera onca*) in the southern Pantanal, Brazil. *J Mammal* 91(3):722–736. <https://doi.org/10.1644/09-MAMM-A-171.1>
14. Chandler RB, Royle JA, King DI (2011) Inference about density and temporary emigration in unmarked populations. *Ecology* 92(7):1429–1435. <https://doi.org/10.1890/10-2433.1>
15. Chrétien L-P, Théau J, Ménard P (2016) Visible and thermal infrared remote sensing for the detection of white-tailed deer using an unmanned aerial system. *Wildl Soc Bull* 40(1):181–191. <https://doi.org/10.1002/wsb.629>
16. Cornélis D, Benhamou S, Janeau G, Morellet N, Ouedraogo M, de Visscher M-N (2011) Spatiotemporal dynamics of forage and water resources shape space use of West African savanna buffaloes. *J Mammal* 92(6):1287–1297. <https://doi.org/10.1644/10-MAMM-A-397.1>
17. Costa SS, Oliveira DB, Manco AM, Melo GO, De, Cordeiro JLP, Zaniolo S, Negrelle R, Oliveira LFB (2006) Plants Composing the Diet of Marsh and Pampas Deer in the Brazilian Pantanal Wetland and Their Ethnomedicinal Properties. *Journal of Biological Sciences* 6(5):840–846. <https://doi.org/10.3923/jbs.2006.840.846>

18. Creel S, Christianson D (2008) Relationships between direct predation and risk effects. *Trends in Ecology Evolution* 23(4):194–201. <https://doi.org/10.1016/j.tree.2007.12.004>
19. Creel S, Schuette P, Christianson D (2014) Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behav Ecol* 25(4):773–784. <https://doi.org/10.1093/beheco/aru050>
20. Dénes FV, Silveira LF, Beissinger SR (2015) Estimating abundance of unmarked animal populations: Accounting for imperfect detection and other sources of zero inflation. *Methods Ecol Evol* 6(5):543–556. <https://doi.org/10.1111/2041-210X.12333>
21. Duarte JMB, Varela D, Piovezan U, Beccaceci MD, Garcia JE (2016) *Blastocerus dichotomus*. The IUCN Red List of Threatened Species 2016: e.T2828A22160916. <https://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T2828A22160916.en>
22. Ferreira SM, Aarde RJ, Van (2009) Aerial Survey Intensity as a Determinant of Estimates of African Elephant Population Sizes and Trends. *South African Journal of Wildlife Research* 39(2):181–191. <https://doi.org/10.3957/056.039.0205>
23. Festa-Bianchet M, Coulson T, Gaillard JM, Hogg JT, Pelletier F (2006) Stochastic predation events and population persistence in bighorn sheep. *Proceedings of the Royal Society B: Biological Sciences*, 273(1593):1537–1543. <https://doi.org/10.1098/rspb.2006.3467>
24. Fiske IJ, Chandler RB (2011) unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. *J Stat Softw* 43(10):1–23. <https://doi.org/10.1002/wics.10>
25. Fritsch CJ, Downs CT (2020) Evaluation of low-cost consumer-grade UAVs for conducting comprehensive high-frequency population censuses of hippopotamus populations. *Conservation Science Practice* 2(12):1–11. <https://doi.org/10.1111/csp2.281>
26. Fryxell JM (1991) Forage Quality and Aggregation by Large Herbivores. *Am Nat* 138(2):478–498. <https://doi.org/10.1086/285227>
27. Garrouste E, Hansen A, Lawrence R (2016) Using NDVI and EVI to Map Spatiotemporal Variation in the Biomass and Quality of Forage for Migratory Elk in the Greater Yellowstone Ecosystem. *Remote Sensing* 8(5):404. <https://doi.org/10.3390/rs8050404>
28. Gentle M, Finch N, Speed J, Pople A (2018) A comparison of unmanned aerial vehicles (drones) and manned helicopters for monitoring macropod populations. *Wildlife Research* 45(7):586. <https://doi.org/10.1071/WR18034>
29. Gerum RC, Richter S, Fabry B, Zitterbart DP (2017) ClickPoints: an expandable toolbox for scientific image annotation and analysis. *Methods Ecol Evol* 8(6):750–756. <https://doi.org/10.1111/2041-210X.12702>
30. Gnanadesikan GE, Pearse WD, Shaw AK (2017) Evolution of mammalian migrations for refuge, breeding, and food. *Ecology Evolution* 7(15):5891–5900. <https://doi.org/10.1002/ece3.3120>
31. Gray PC, Fleishman AB, Klein DJ, McKown MW, Bézy VS, Lohmann KJ, Johnston DW (2019) A Convolutional Neural Network for Detecting Sea Turtles in Drone Imagery. *Methods Ecol Evol* 10(3):345–355. <https://doi.org/10.1111/2041-210X.13132>

32. Hamel S, Garel M, Festa-Bianchet M, Gaillard JM, Côté SD (2009) Spring Normalized Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. *J Appl Ecol* 46(3):582–589. <https://doi.org/10.1111/j.1365-2664.2009.01643.x>
33. Hayward MW, Kamler JF, Montgomery RA, Newlove A, Rostro-García S, Sales LP, Van Valkenburgh B (2016) Prey Preferences of the Jaguar *Panthera onca* Reflect the Post-Pleistocene Demise of Large Prey. *Frontiers in Ecology Evolution* 3(1):148. <https://doi.org/10.3389/fevo.2015.00148>
34. Hebblewhite M, Merrill EH (2009) Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology* 90(12):3445–3454. <https://doi.org/10.1890/08-2090.1>
35. Hebblewhite M, Merrill E, McDermid G (2008) A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecol Monogr* 78(2):141–166. <https://doi.org/10.1890/06-1708.1>
36. Hobbs NT, Gordon IJ (2010) How does Landscape Heterogeneity Shape Dynamics of Large Herbivore Populations? In *Dynamics of Large Herbivore Populations in Changing Environments*. Wiley-Blackwell. pp 141–164. <https://doi.org/10.1002/9781444318593.ch6>
37. Hofmann GS, Coelho IP, Bastazini VAG, Cordeiro JLP, de Oliveira LFB (2016) Implications of climatic seasonality on activity patterns and resource use by sympatric peccaries in northern Pantanal. *Int J Biometeorol* 60(3):421–433. <https://doi.org/10.1007/s00484-015-1040-8>
38. Hopcraft JGC, Morales JM, Beyer HL, Borner M, Mwangomo E, Sinclair ARE, Olf H, Haydon DT (2014) Competition, predation, and migration: Individual choice patterns of Serengeti migrants captured by hierarchical models. *Ecol Monogr* 84(3):355–372. <https://doi.org/10.1890/13-1446.1>
39. Hopcraft JGC, Olf H, Sinclair ARE (2010) Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends in Ecology Evolution* 25(2):119–128. <https://doi.org/10.1016/j.tree.2009.08.001>
40. Jakes AF, Gates CC, DeCesare NJ, Jones PF, Goldberg JF, Kunkel KE, Hebblewhite M (2018) Classifying the migration behaviors of pronghorn on their northern range. *J Wildl Manag* 82(6):1229–1242. <https://doi.org/10.1002/jwmg.21485>
41. Joseph LN, Elkin C, Martin TG, Possingham HP (2009) Modeling abundance using N-mixture models: The importance of considering ecological mechanisms. *Ecol Appl* 19(3):631–642. <https://doi.org/10.1890/07-2107.1>
42. Junk WJ, Cunha D, Wantzen CN, Petermann KM, Strüssmann P, Marques C, M. I., & Adis J (2006) Biodiversity and its conservation in the Pantanal of Mato Grosso, Brazil. *Aquat Sci* 68(3):278–309. <https://doi.org/10.1007/s00027-006-0851-4>
43. Kellenberger B, Marcos D, Tuia D (2018) Detecting mammals in UAV images: Best practices to address a substantially imbalanced dataset with deep learning. *Remote Sens Environ* 216:139–153. <https://doi.org/10.1016/j.rse.2018.06.028>
44. Kéry M, Royle JA (2016) Applied hierarchical modeling in ecology, volume 1 (Prelude and Static model). Academic Press

45. Kéry M, Royle JA, Schmid H (2005) Modeling avian abundance from replicated counts using binomial mixture models. *Ecol Appl* 15(4):1450–1461. <https://doi.org/10.1890/04-1120>
46. Laundré JW, Hernández L, Medina PL, Campanella A, López-Portillo J, González-Romero A, Grajales-Tam KM, Burke AM, Gronemeyer P, Browning DM (2014) The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? *Ecology* 95(5):1141–1152. <https://doi.org/10.1890/13-1083.1>
47. Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68(4):619–640. <https://doi.org/10.1139/z90-092>
48. Linchant J, Lhoest S, Quevauvillers S, Lejeune P, Vermeulen C, Semeki Ngabinzeke J, Luse Belanganayi B, Delvingt W, Bouché P (2018) UAS imagery reveals new survey opportunities for counting hippos. *PLOS ONE* 13(11):e0206413. <https://doi.org/10.1371/journal.pone.0206413>
49. Martin J, Edwards HH, Fonnesebeck CJ, Koslovsky SM, Harmak CW, Dane TM (2015) Combining information for monitoring at large spatial scales: First statewide abundance estimate of the Florida manatee. *Biol Cons* 186:44–51. <https://doi.org/10.1016/j.biocon.2015.02.029>
50. McArthur C, Banks PB, Boonstra R, Forbey JS (2014) The dilemma of foraging herbivores: dealing with food and fear. *Oecologia* 176(3):677–689. <https://doi.org/10.1007/s00442-014-3076-6>
51. Merkle JA, Monteith KL, Aikens EO, Hayes MM, Hersey KR, Middleton AD, Oates BA, Sawyer H, Scurlock BM, Kauffman MJ (2016) Large herbivores surf waves of green-up during spring. *Proceedings of the Royal Society B: Biological Sciences*, 283(1833):20160456. <https://doi.org/10.1098/rspb.2016.0456>
52. Moll RJ, Redilla KM, Mudumba T, Muneza AB, Gray SM, Abade L, Hayward MW, Millspaugh JJ, Montgomery RA (2017) The many faces of fear: a synthesis of the methodological variation in characterizing predation risk. *J Anim Ecol* 86(4):749–765. <https://doi.org/10.1111/1365-2656.12680>
53. Mourão G, Coutinho M, Mauro R, Campos Z, Tomás W, Magnusson W (2000) Aerial surveys of caiman, marsh deer and pampas deer in the Pantanal Wetland of Brazil. *Biol Cons* 92(2):175–183. [https://doi.org/10.1016/S0006-3207\(99\)00051-8](https://doi.org/10.1016/S0006-3207(99)00051-8)
54. Nowak RM (1991) *Walker's Mammals of the World*, 5.ed. Baltimore:John's Hopkins University Press, 1629p
55. Oliveira LFB, Cordeiro JLP, Hasenack H (2013) Padrões e tendências regionais em uma paisagem antropizada no norte do Pantanal: uma perspectiva espaço-temporal. In: Peres CA, Barlow J, Gardner TA, Vieira ICG (eds) *Conservação da biodiversidade em paisagens florestais antropizadas do Brasil*. Editora da Universidade Federal do Paraná, Curitiba, Brasil, pp 231–262
56. Owen-Smith N (2010) Dynamics of Large Herbivore Populations in Changing Environments. In: Owen-Smith N (ed) *Dynamics of Large Herbivore Populations in Changing Environments*. Wiley, <https://doi.org/10.1002/9781444318593>
57. Owen-Smith N (2014) Spatial ecology of large herbivore populations. *Ecography* 37(5):416–430. <https://doi.org/10.1111/j.1600-0587.2013.00613.x>

58. Peres PHF, Polverini MS, Oliveira ML, Duarte JMB (2017) Accessing camera trap survey feasibility for estimating *Blastocerus dichotomus* (Cetartiodactyla, Cervidae) demographic parameters. *Iheringia Série Zoologia* 107:1–8. <https://doi.org/10.1590/1678-4766e2017041>
59. Perilli MLL, Lima F, Rodrigues FHG, Cavalcanti SMC (2016) Can scat analysis describe the feeding habits of big cats? A case study with jaguars (*Panthera onca*) in Southern Pantanal, Brazil. *PLoS ONE* 11(3):1–12. <https://doi.org/10.1371/journal.pone.0151814>
60. Pettorelli N, Ryan S, Mueller T, Bunnefeld N, Jedrzejewska B, Lima M, Kausrud K (2011) The Normalized Difference Vegetation Index (NDVI): Unforeseen successes in animal ecology. *Climate Res* 46(1):15–27. <https://doi.org/10.3354/cr00936>
61. Pettorelli N, Vik JO, Mysterud A, Gaillard JM, Tucker CJ, Stenseth NC (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology Evolution* 20(9):503–510. <https://doi.org/10.1016/j.tree.2005.05.011>
62. Piovezan U, Tiepolo LM, Tomas WM, Duarte JMB, Varela D, Marinho-Filho JS (2010) Marsh deer *Blastocerus dichotomus* (Illiger 1815). In J. M. B. Duarte & S. Gonzalez (Eds.), *Neotropical Cervidology: Biology and Medicine of Latin American Deer*. Funep/IUCN. pp 66–76
63. Purdon A, Mole MA, Chase MJ, van Aarde RJ (2018) Partial migration in savanna elephant populations distributed across southern Africa. *Sci Rep* 8(1):1–11. <https://doi.org/10.1038/s41598-018-29724-9>
64. R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
65. Rey N, Volpi M, Joost S, Tuia D (2017) Detecting animals in African Savanna with UAVs and the crowds. *Remote Sens Environ* 200:341–351. <https://doi.org/10.1016/j.rse.2017.08.026>
66. Riginos C (2015) Climate and the landscape of fear in an African savanna. *J Anim Ecol* 84(1):124–133. <https://doi.org/10.1111/1365-2656.12262>
67. Ríos-Uzeda B, Mourão G (2012) Densities of the Vulnerable marsh deer *Blastocerus dichotomus* in Bolivia's northern savannahs. *Oryx* 46(2):260–265. <https://doi.org/10.1017/S0030605311000238>
68. Ripple WJ, Newsome TM, Wolf C, Dirzo R, Everatt KT, Galetti M, Hayward MW, Kerley GIH, Levi T, Lindsey PA, Macdonald DW, Malhi Y, Painter LE, Sandom CJ, Terborgh J, Van Valkenburgh B (2015) Collapse of the world's largest herbivores. *Science Advances* 1(4):e1400103–e1400103. <https://doi.org/10.1126/sciadv.1400103>
69. Rivrud IM, Heurich M, Krupczynski P, Müller J, Mysterud A, Muller J, Mysterud A (2016) Green wave tracking by large herbivores: An experimental approach. *Ecology* 97(12):3547–3553. <https://doi.org/10.1002/ecy.1596>
70. Rivrud IM, Sivertsen TR, Mysterud A, Åhman B, Støen O-G, Skarin A (2018) Reindeer green-wave surfing constrained by predators. *Ecosphere* 9(5):e02210. <https://doi.org/10.1002/ecs2.2210>
71. Royle JA (2004) N-Mixture Models for Estimating Population Size from Spatially Replicated Counts. *Biometrics* 60(1):108–115. <https://doi.org/10.1111/j.0006-341X.2004.00142.x>

72. Royle JA, Chandler RB, Sollmann R, Gardner B (2014) Spatial Capture-recapture. Elsevier, <https://doi.org/10.1016/C2012-0-01222-7>
73. Ryan SJ, Cross PC, Winnie J, Hay C, Bowers J, Getz WM (2012) The utility of normalized difference vegetation index for predicting African buffalo forage quality. *Journal of Wildlife Management* 76(7):1499–1508. <https://doi.org/10.1002/jwmg.407>
74. Sawyer H, Kauffman MJ (2011) Stopover ecology of a migratory ungulate. *J Anim Ecol* 80(5):1078–1087. <https://doi.org/10.1111/j.1365-2656.2011.01845.x>
75. Say-Sallaz E, Chamaillé-Jammes S, Fritz H, Valeix M (2019) Non-consumptive effects of predation in large terrestrial mammals: Mapping our knowledge and revealing the tip of the iceberg. *Biol Cons* 235:36–52. <https://doi.org/10.1016/j.biocon.2019.03.044>
76. Schroeder NM, Matteucci SD, Moreno PG, Gregorio P, Ovejero R, Taraborelli P, Carmanchahi PD (2014) Spatial and seasonal dynamic of abundance and distribution of guanaco and livestock: Insights from using density surface and null models. *PLoS ONE* 9(1):e85960. <https://doi.org/10.1371/journal.pone.0085960>
77. Spinage CA, Matlhare JM (1992) Is the Kalahari Cornucopia Fact or Fiction? A Predictive Model. *The Journal of Applied Ecology* 29(3):605. <https://doi.org/10.2307/2404468>
78. Tiepolo LM, Tomas WM, Lima-Borges PA (2010) Levantamento populacional do cervo-do-pantanal *Blastocerus dichotomus* (Mammalia, Cervidae) no Parque Nacional de Ilha Grande e entorno: implicações para a conservação. *Iheringia Série Zoologia* 100(2):111–115. <https://doi.org/10.1590/S0073-47212010000200004>
79. Tomas WM, Salis SM (2000) Diet of the marsh deer (*Blastocerus dichotomus*) in the Pantanal wetland, Brazil. *Studies on Neotropical Fauna Environment* 35(3):165–172. <https://doi.org/10.1076/snfe.35.3.165.8861>
80. Tomas WM, Salis SM, Silva MP, Mourão G (2001) Marsh Deer (*Blastocerus dichotomus*) Distribution as a Function of Floods in the Pantanal Wetland, Brazil. *Studies on Neotropical Fauna and Environment*, 36(1):9–13. <https://doi.org/10.1076/snfe.36.1.9.8877>
81. Valeix M, Chamaillé-Jammes S, Loveridge AJ, Davidson Z, Hunt JE, Madzikanda H, Macdonald DW (2011) Understanding patch departure rules for large carnivores: Lion movements support a patch-disturbance hypothesis. *Am Nat* 178(2):269–275. <https://doi.org/10.1086/660824>
82. Vermeulen C, Lejeune P, Lisein J, Sawadogo P, Bouché P (2013) Unmanned Aerial Survey of Elephants. *PLoS ONE*, 8(2):e54700. <https://doi.org/10.1371/journal.pone.0054700>
83. Vucetich JA, Peterson RO (2004) The influence of top-down, bottom-up and abiotic factors on the moose (*Alces alces*) population of Isle Royale. *Proceedings of the Royal Society B: Biological Sciences*, 271(1535):183–189. <https://doi.org/10.1098/rspb.2003.2589>
84. Williams PJ, Hooten MB, Womble JN, Bower MR (2017) Estimating occupancy and abundance using aerial images with imperfect detection. *Methods Ecol Evol* 8(12):1–11. <https://doi.org/10.1111/2041-210X.12815>

# Figures

## SPATIO-TEMPORALLY REPLICATED SURVEYS

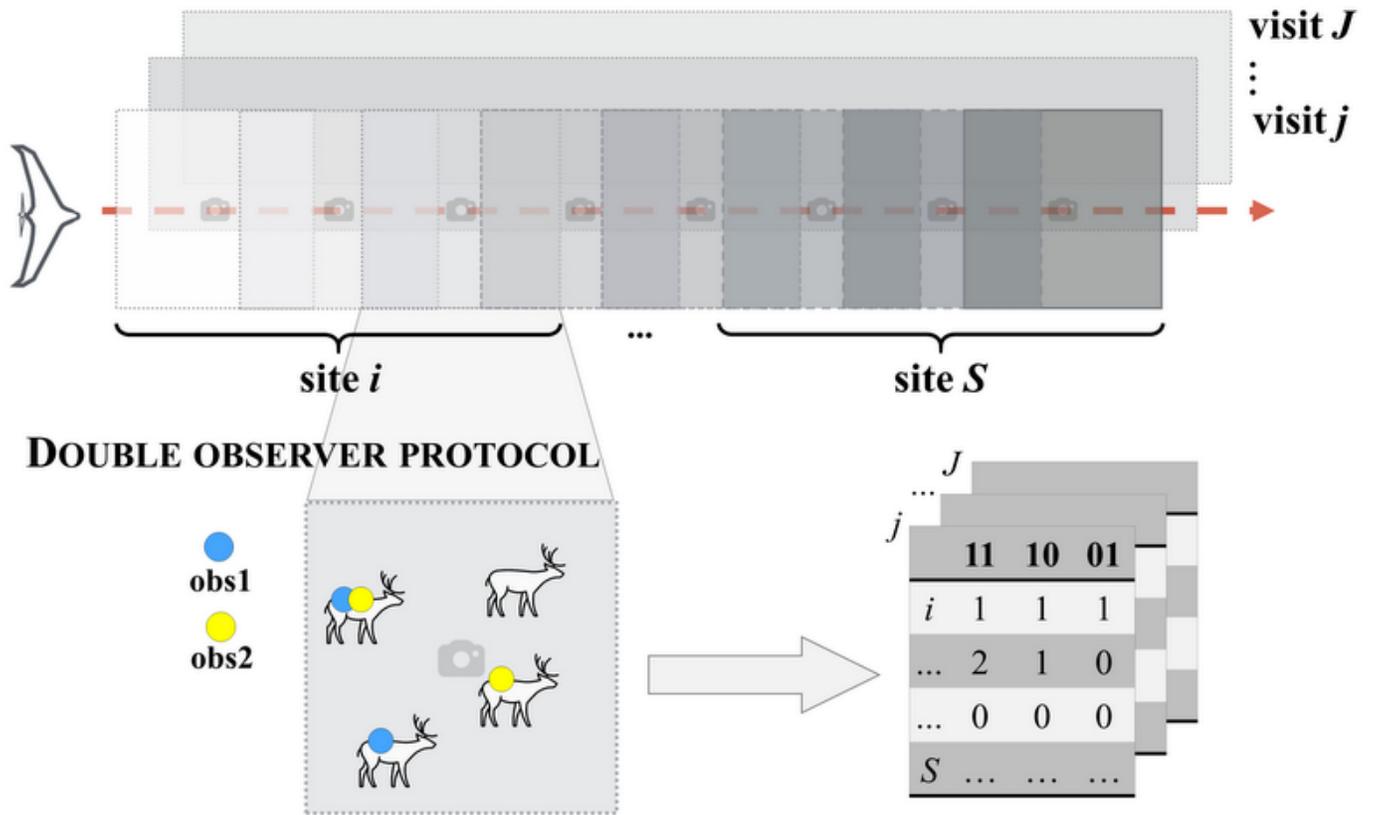
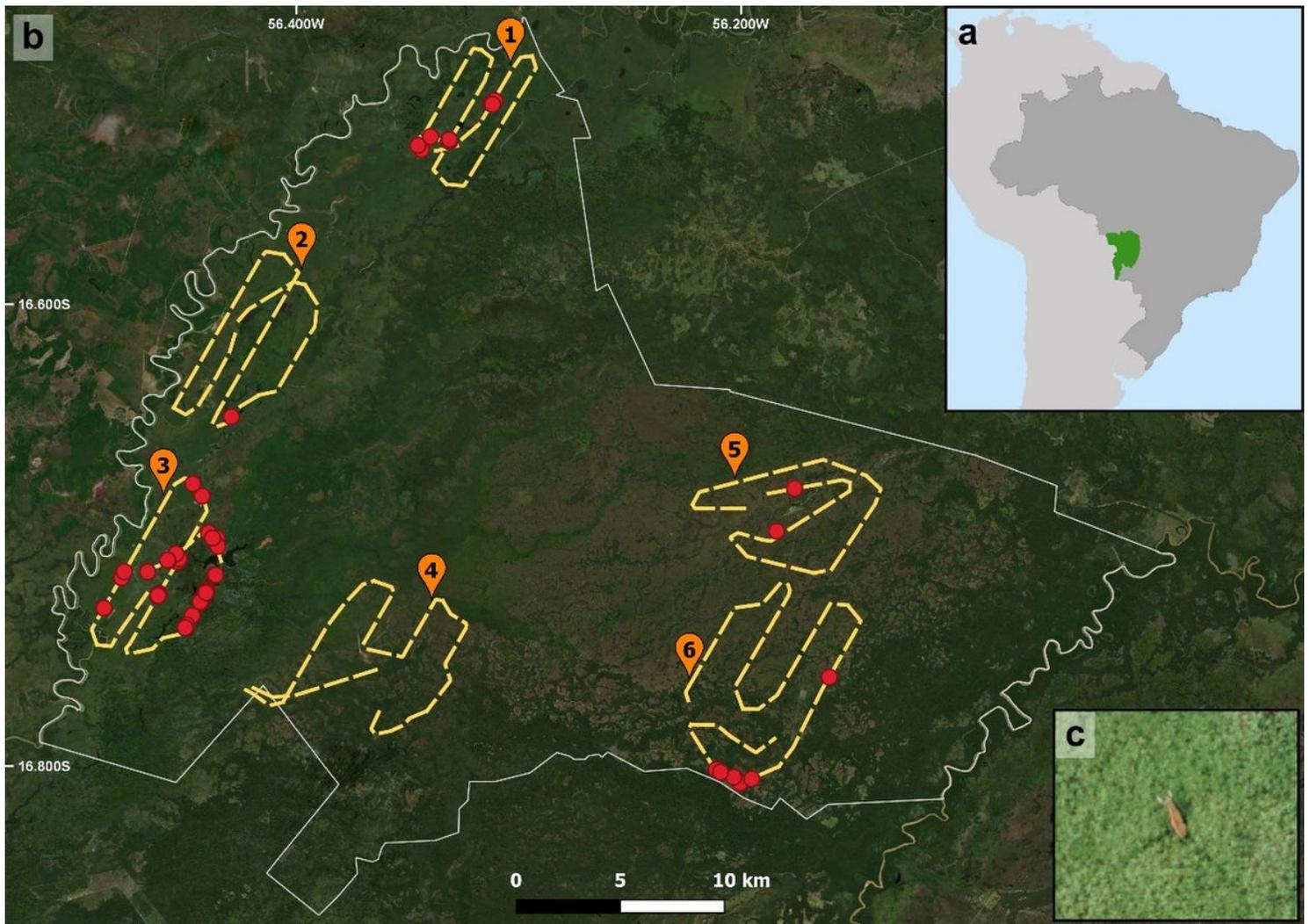


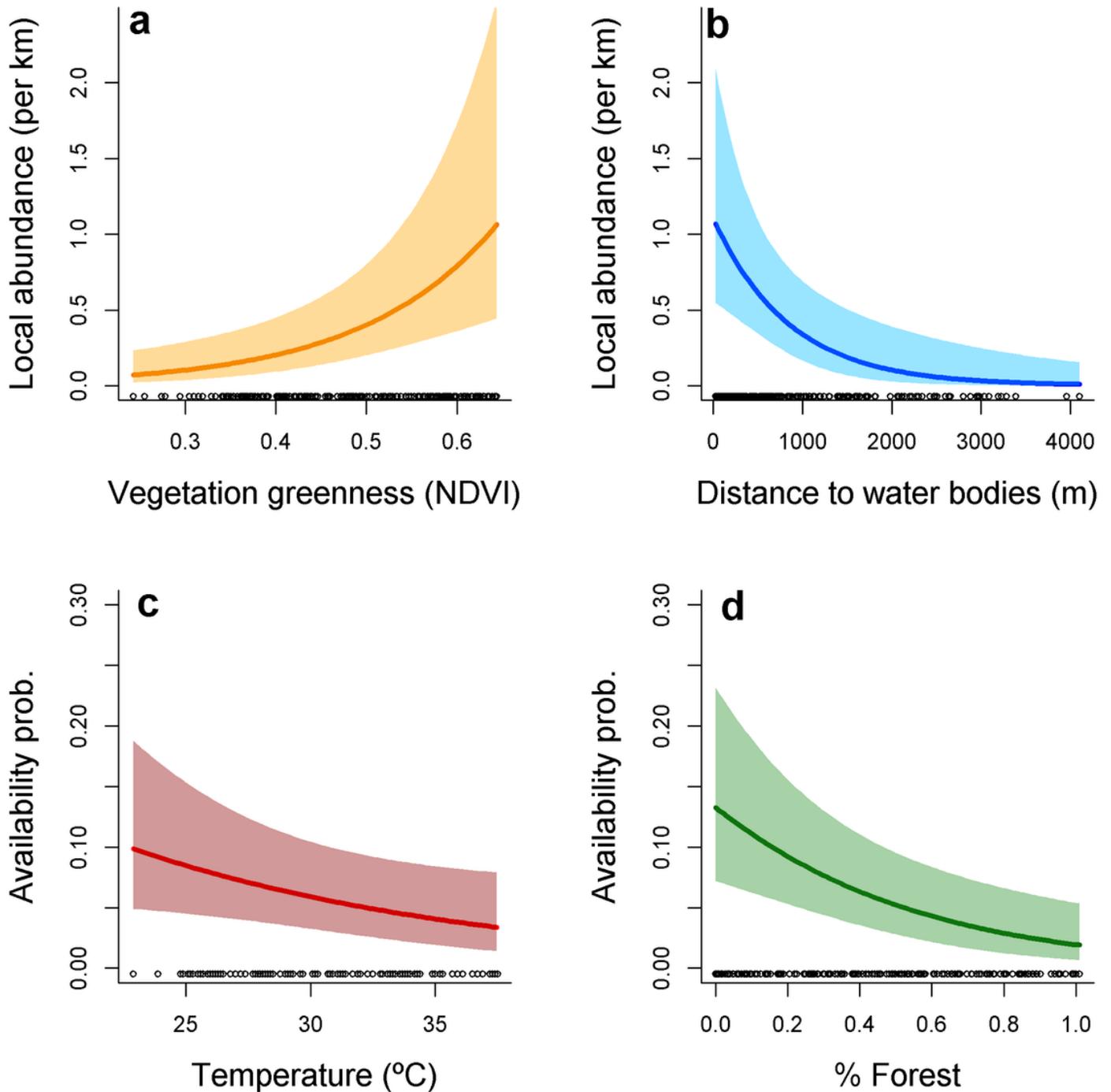
Figure 1

Sampling design and resulting count data to account for availability and perception errors in abundance modelling (for a multinomial N-mixture model with temporary emigration) from drone surveys. The sampling scheme presumes drone flights conducted at multiple sites ( $site\ i=1$  to  $S$ , possibly from segmented flight paths) and with multiple visits ( $visit\ j=1$  to  $J$ ); and a double independent observer protocol for image review. The resulting data is a 3-d array count data ( $S, K, J$ ; in which  $K$  is the number of possible encounter histories, i.e. "11"=detected by both observers, "10"=detected only by the 1st observer, and "01"=detected only by the 2nd).



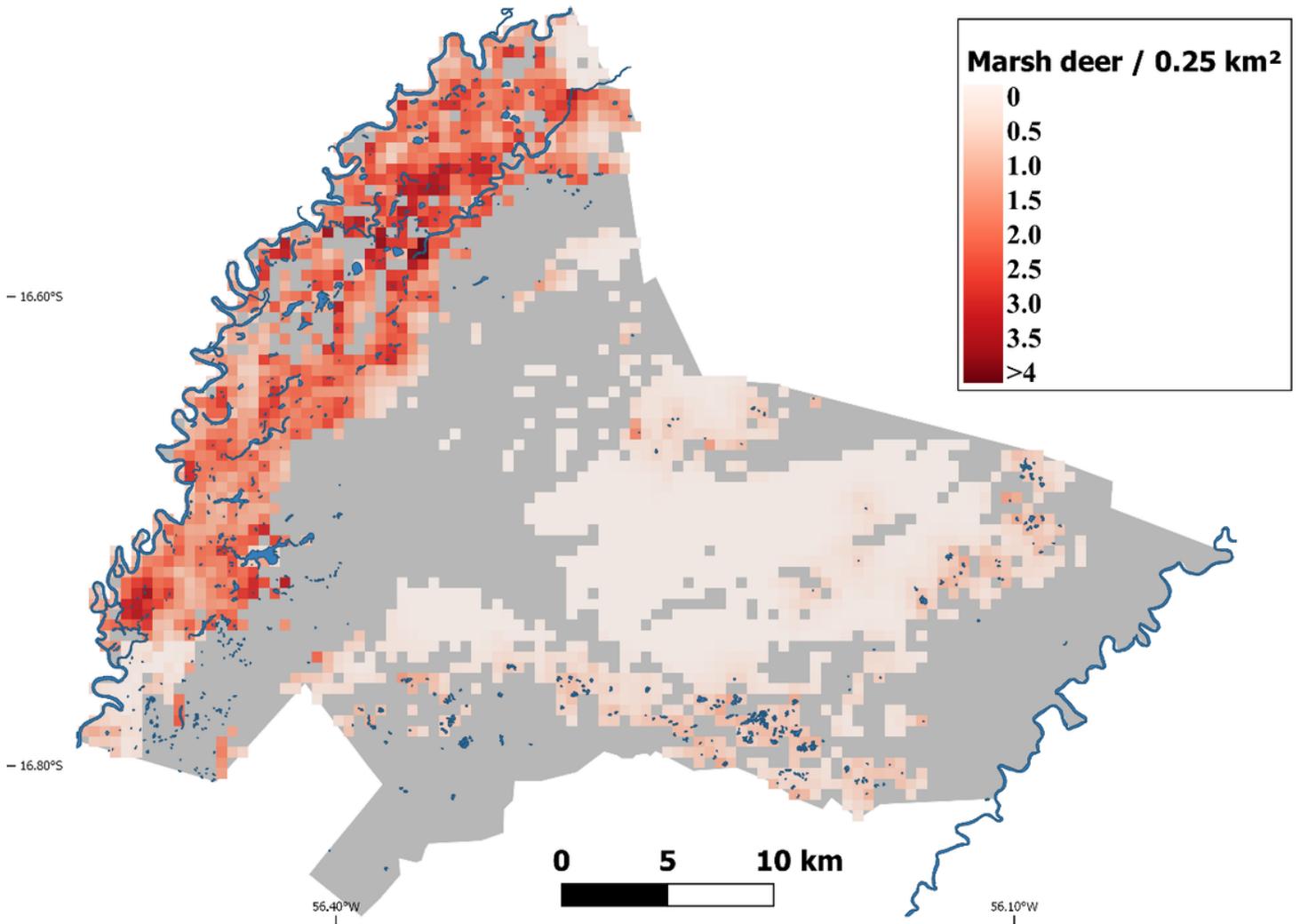
**Figure 2**

(a) Pantanal wetland, Western Brazil; (b) Sesc Pantanal Reserve (white contour) and marsh deer records (red dots) obtained from drone surveys at six flight paths (yellow dashed lines). Detailed information of the flight paths (orange numbered icons) is presented in Table 1. (c) Example of marsh deer record from drone imagery.



**Figure 3**

Predicted relations of marsh deer local abundance with (a) vegetation greenness, and (b) distance to water bodies; and individuals' availability with (c) temperature during flight, and (d) proportion of forest in sampled sites. Relations were predicted by modelling counts from spatiotemporally replicated drone surveys with a double observer protocol, using a Multinomial N-mixture model. Shaded areas represent the 95% confidence interval and the dots in the x-axis indicate the covariate values.



**Figure 4**

Spatial prediction of marsh deer local abundance for the dry season of 2017 in Sesc Pantanal Reserve, derived from spatially replicated drone-based counts. Blue polygons represent water bodies and grey areas correspond to highly forested areas (>80%) for which local abundance was not predicted.

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupMat1covariatesmaps.docx](#)
- [SupMat2modelselectionandcoefficients.docx](#)
- [SupMat3abundancemap95CI.docx](#)
- [SupMat4segmentlengthabundance.docx](#)
- [SupMat5Rscript.docx](#)